

FREQUENCY OF FEMALE COLOUR MORPHS IN POPULATIONS OF FOUR COENAGRIONID DAMSELFLIES (ZYGOPTERA: COENAGRIONIDAE)

D. McKEE¹, I.F. HARVEY², D.J. THOMPSON² and T.N. SHERRATT³

¹School of Biological and Biomedical Sciences, University of Durham, Durham, DH1 3LE, United Kingdom

²School of Biological Sciences, Biosciences Building, University of Liverpool, Crown Street,
Liverpool, L69 7ZB, United Kingdom

³Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa ON, K1S 5B6, Canada

Received March 9, 2004 / Reviewed and Accepted May 5, 2004

Knowledge of naturally occurring andromorph and gynomorph frequencies in populations of coenagrionid damselflies is important for understanding the evolution of ♀-limited polymorphism. Here are reported the frequencies of andromorphs and gynomorphs in populations of *Coenagrion puella*, *C. mercuriale*, *Xanthocnemis zealandica* and *Ischnura uviatilis* and a review is presented of the literature for other coenagrionid spp. It is shown that ratios of andromorphs to gynomorphs are often unequal with andromorphs generally being the uncommon morph. Significant inter- and intra-population variation in morph frequency sometimes occurs but is of low magnitude. No evidence was found for spatial segregation of andromorphs and gynomorphs. Andromorph frequency could not be significantly related with sex ratio or ♂ density.

INTRODUCTION

Female-limited colour polymorphism is widespread in coenagrionid damselflies. One female morph, the andromorph, is usually quite brightly coloured and resembles the male of the species. One or more other female morphs, the gynomorphs, are usually drab and little resemble males. How this phenomenon is maintained within populations is currently the focus of two contrasting hypotheses: 'learned mate recognition' theory (MILLER & FINCKE, 1999) and the 'signal detection' model (SHERRATT, 2001). According to learned mate recognition theory, males should attempt to mate most often with the most common female morph in the population. If mate-searching males impose a fitness cost to lone females (through excessive harassment) then males that cue preferentially to the most abundant morph should impose frequency-dependent selection on that morph. In contrast, the signal detection model is based on the premise that andromorphs gain a selective advantage by looking like males (i.e. andromorphs) are

male mimics, (ROBERTSON, 1985). In this case, the level of male sexual attention directed towards andromorphs should increase as the perceived rate of encounter between males and andromorphs increases (sexual attention directed towards gynomorphs should not change with male perceived rate of encounter).

Recent research provides varying degrees of support for both hypotheses (e.g. CORDERO et al., 1998; MILLER & FINCKE, 1999; VAN GOSSUM et al., 1999; SIROT & BROCKMANN, 2001; VAN GOSSUM et al., 2001; ANDRES et al., 2002). One consistent result however is that selective mechanisms, dependent on female morph frequency, appear to be operational in most populations, at least during some of the time. Detailed knowledge of andromorph frequencies in different populations of different damselfly species is therefore important. Here, we report results of surveys of female morph frequencies in populations of four contrasting coenagrionid damselfly species. We also provide a review of andromorph frequencies reported in the literature.

MATERIAL AND METHODS

Coenagrion puella (L.)

This species occurs in suitable habitat throughout Europe. Males are predominantly blue; andromorph females have some blue colouration but are relatively poor male colour mimics; gynomorph females are predominantly brown/olive. Andromorph and gynomorph females do not differ significantly in size (e.g. forewing length) and females, overall, are larger than males (THOMPSON, 1989a, 1989b).

Andromorph frequency was estimated in detail in an adult population at Ness Botanic Gardens (near Liverpool, U.K.; SJ303754; 53° 16.2' N, 3° 02.7' W), on eight days in June 2001, eight days in July 2001 and five days in June 2002. A transect was walked through the gardens on each of these days and all animals encountered were recorded. Areas of ornamental pond and associated waterside vegetation (within 5 m of water), as well as extensive lengths of hedgerow (distant from water by 20-200 m) were included. Equal effort was attached to searching waterside areas and those areas away from water.

Coenagrion mercuriale (Charpentier)

This species is restricted in distribution at both a global and national level. It is concentrated in the south and west of Europe and has populations of unknown status in northern Africa. In Britain it occurs mainly to the south and west of the country. The gynomorph is olive green laterally with small pale marks anteriorly on segments 7-10. In the andromorph the pale colour is more extensive and the rest of the body is blue like the male. Females are larger than males (THOMPSON et al., 2004).

Andromorph frequency was estimated from mark-release-recapture studies carried out in two areas of Hampshire, England: the Itchen Valley (populations 1-3, Table II) and Beaulieu Heath (populations 4-11, Table II). Sampling was conducted from 12 June to 14 July 2001 (Itchen Valley) and 11 June to 13 July 2002 (Beaulieu Heath). During these sampling periods field assistants were present at each site for seven hours daily. Searching was restricted to the watercourses. For data analysis, the two summer sampling periods were each divided into three consecutive sub-periods of 10 days.

Xanthocnemis zealandica McLachlan

This species is endemic to New Zealand where it is widespread (ROWE, 1987). Males are predominantly red; andromorph females are substantially red and are reasonable male colour mimics; gynomorph females are predominantly brown/olive. Andromorph females and gynomorph females do not differ significantly in size (mean forewing length of mature andromorphs = 19.4 mm, SD = 1.1, $n = 50$; mean forewing length of mature gynomorphs = 19.8 mm, SD = 1.0, $n = 50$; $t = 1.6$, $df = 98$, $p = 0.111$). Females are larger than males (mean overall mature female forewing length = 19.6 mm, SD = 1.1, $n = 100$; mean mature male forewing length =

18.1 mm, SD = 0.8, $n = 100$; $t = 11.4$, $df = 198$, $p < 0.001$) and there is no significant correlation between the forewing lengths of tandem pairs ($r = 0.09$, $n = 100$, $p = 0.355$; data recalculated from McKee et al., 2003). Andromorph frequency in adult populations of *X. zealandica* was estimated at nine ponds located in the Christchurch area of New Zealand (location references in Table III). Each site was visited three times (between 15-12-01 and 17-01-02; 10:00 to 16:00) and all females in tandem and in copulation were recorded whilst walking around the water's edge (single females were very rarely encountered).

Ischnura fluviatilis Selys

This species seems to occur throughout the pampasic ecotone of southern South America (e.g. BULLA, 1973; VON ELLENRIEDER, 2000). Males have blue post-ocular spots, a blue thorax with yellow/green humeral stripes and a blue tip to their abdomen. Mature andromorph females are excellent male colour mimics. Mature gynomorph females are brown/olive, but younger females are orange.

Andromorph frequency was estimated in four populations in Uruguay (location references in Table IV). Two of these populations (Punta Carretas and Parque Miramar) were each sampled for eight hours over two or three consecutive days of optimum weather during November 2002, December 2002, January 2003 and February 2003. One population (Mendoza) was sampled for five hours over two days during January 2003 and during February 2003 and the final population (Puente Sarandi) was sampled once for five hours during January 2003. We attempted to capture and mark (wing-spot of indelible ink) all individuals encountered whilst randomly walking around the ponds. A minimum period of two weeks elapsed between all monthly estimates.

Forewing lengths of ten copulating pairs including an andromorph female and ten copulating pairs including a gynomorph female were measured (Punta Carretas population, December 2002). Andromorphs and gynomorphs did not differ significantly in size (mean forewing length of andromorphs = 16.3 mm, SD = 0.9, $n = 10$; mean forewing length of gynomorphs = 16.7 mm, SD = 1.1, $n = 10$; $t = 0.9$, $df = 18$, $p = 0.384$). Females were larger than males (mean overall female forewing length = 16.5 mm, SD = 1.0, $n = 20$; mean male forewing length = 14.7 mm, SD = 0.6, $n = 20$; $t = 7.1$, $df = 38$, $p < 0.001$) and there was no significant correlation between the forewing lengths of tandem pairs ($r = 0.07$, $n = 20$, $p = 0.774$).

RESULTS

COENAGRION PUELLA

At Ness Botanic Gardens during 2001, *C. puella* andromorph frequency was 40% in June and 19% in July. During June 2002 it was 26%. The ratio of andromorphs to gynomorphs differed significantly from equality according to the later two estimates (Chi-square tests: $\chi^2 = 2.9$, $p = 0.087$; $\chi^2 = 10.7$, $p = 0.001$; $\chi^2 = 37.4$, $p < 0.001$; respectively). There was a significant decrease in andromorph frequency between June 2001 and July 2001 ($\chi^2 = 5.5$, $p = 0.019$); and a significant increase between July 2001 and June 2002 ($\chi^2 = 5.6$, $p = 0.018$). The significant inter-annual difference also holds when the overall mean andromorph frequency during 2001 (35%) is used in the comparison ($\chi^2 = 5.2$, $p = 0.023$).

Table I shows numbers of animals encountered along the transect. The data are divided into those observations recorded at water (< 5m distant) and those recorded away from water (20 – 200m distant). Andromorphs and gynomorphs did not segregate according to area of habitat. The ratio of single andromorphs to single gynomorphs was independent of whether the animals were encountered at or away from water (contingency Chi-square: June 2001 $\chi^2 = 0.09$, $p = 0.770$; July 2001 $\chi^2 = 0.38$, $p = 0.537$; June 2002

Table I
C. puella recorded at Ness Botanic Gardens

		At water	Away from water
Males	Jun-01	545	189
	Jul-01	196	73
	Jun-02	247	206
Single andromorphs	Jun-01	3	14
	Jul-01	0	2
	Jun-02	1	36
Single gynomorphs	Jun-01	4	10
	Jul-01	1	5
	Jun-02	3	78
Paired andromorphs	Jun-01	11	3
	Jul-01	1	2
	Jun-02	7	0
Paired gynomorphs	Jun-01	25	7
	Jul-01	11	5
	Jun-02	41	1

$\chi^2 = 0.07, p = 0.788$). Similarly, the ratio of paired andromorphs to paired gynomorphs was independent of whether the animals were encountered at or away from water (contingency Chi-square: June 2001 $\chi^2 = 0.13, p = 0.723$; July 2001 $\chi^2 = 0.27, p = 0.607$; June 2002 $\chi^2 = 1.06, p = 0.303$).

Sex ratio was calculated as total number of males/total number of females. It was male biased, ranging from 1.1 to 12.2. Andromorph frequency was not significantly correlated with sex ratio: $r = 0.40, n = 14, p = 0.151$ (Fig. 1a, analy-

sis used all the daily transect estimates from Ness Gardens where andromorphs were recorded); nor was it significantly correlated with male density: $r = 0.27, n = 14, p = 0.354$ (Fig. 2a).

COENAGRION MERCURIALE

In the Itchen Valley there were three distinct populations. At the most northerly sites, Mariner's Meadow and Highbridge, andromorphs were not found (Tab. II). In the largest population, Lower Itchen, mean andromorph frequency was low, 6% (Tab. II). The ratio of andromorphs to gynomorphs differed significantly from equality in the Lower Itchen population (Tab. II).

Around Beaulieu Heath mean andromorph frequency ranged from 9 to 33% and the ratio of andromorphs to gynomorphs differed significantly from equality in all eight populations (Tab. II). However, between populations, andromorph frequency did not significantly differ (one-way Anova, data arcsine square-root transformed: $F_{7,16} = 1.1, p = 0.394$) and the intraclass correlation coefficient suggested that temporal variation within populations was relatively high ($r_1 = 0.04$). This temporal variation was significant in two cases but showed no particular pattern: Hatchet Stream (consecutive estimates of 9%, 9%, 0%), maximum likelihood $\chi^2 = 7.0, df = 2, p = 0.030$; Deep Moor (consecutive estimates of 10%, 35%, 9%), maximum likelihood $\chi^2 = 7.9, df = 2, p = 0.020$. There was no significant correlation between andromorph frequency and sex ratio: $r = -0.07, n = 27, p = 0.712$ (Fig. 1b). Neither was there a significant correlation between andromorph frequency and male density: $r = -0.34, n = 27, p = 0.080$ (Fig. 2b).

*XANTHOCNEMIS
ZEALANDICA*

Overall, andromorph frequency was 9% (SD = 4.5, $n = 27$). Frequency in most of the nine separate populations was rather similar (Tab. III) and, although analysis of variance indicated significant difference between populations (one-way Anova, data arcsine square-root transformed: $F_{8,18} = 5.9, p < 0.001$), this was entirely due to population 2. Tukey-tests showed that population 2 had a significantly lower andromorph frequency than all other populations except population 4. However, it is possible that population 2 yielded an anomalous result simply because it

was the least dense of all the populations surveyed and sample size was concomitantly low. The intra-class correlation coefficient indicated high concordance between within-population andromorph frequency estimates ($r_1 = 0.61$). In all nine populations the ratio of andromorphs to gynomorphs differed significantly from equality (Tab. III).

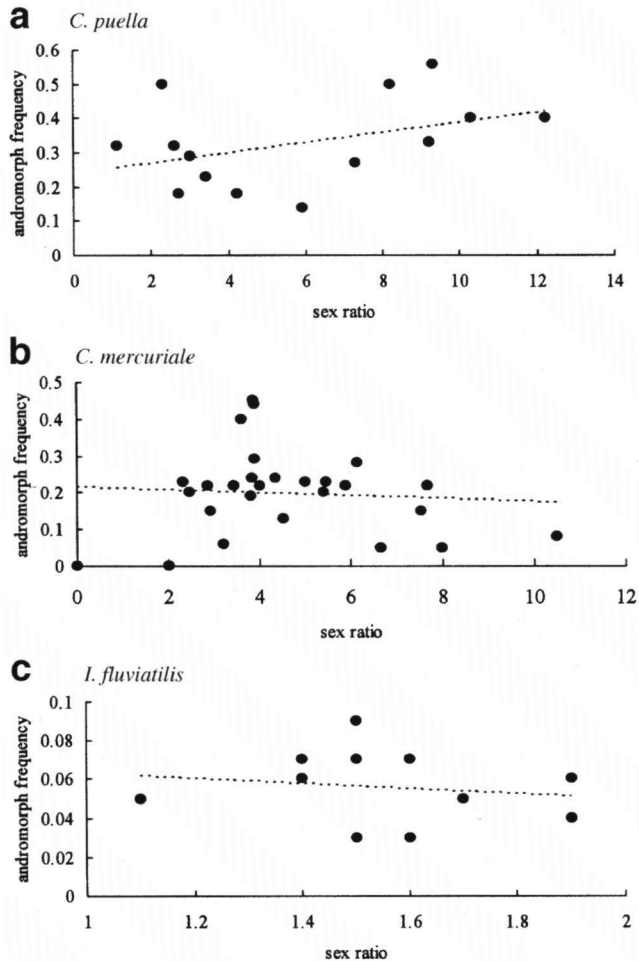


Fig. 1. Relationship between andromorph frequency and sex ratio for: (a) *C. puella*; - (b) *C. mercuriale* and - (c) *I. fluviatilis*.

ISCHNURA FLUVIATILIS

Populations of *I. fluviatilis* were widely distributed but characterised by low density. We searched extensively for populations in the departments of Montevideo, Canalones,

Table II

Mean andromorph frequency (%) in eleven populations of *C. mercuriale*. The significance of Chi-square tests examining whether the ratio of andromorphs to gynomorphs differed from equality is shown using asterisks (***) $p < 0.001$. Standard deviation (SD) and the total number of females and males recorded at each site are shown

Locality	Latitude, Longitude	U.K. National Grid Reference	Mean %	SD	Females	Males
(1) Mariner's Meadow	51° 1'N, 1°19'W	SU476240	0	0	185	959
(2) Highbridge	50°59'N, 1°20'W	SU465209	0	0	36	716
(3) Lower Itchen	50°54'N, 1°22'W	SU446117	6 ***	1.7	717	5492
(4) Roundhill	50°49'N, 1°32'W	SU330019	23 ***	1.2	379	1368
(5) Hatchet Stream	50°49'N, 1°29'W	SU359012	23 ***	22.5	65	179
(6) Greenmoor	51°41'N, 1°31'W	SU338988	33 ***	15.7	34	118
(7) Bagshot Moor	50°48'N, 1°29'W	SU369000	9 ***	10.3	21	80
(8) Deep Moor	51°42'N, 1°30'W	SU348999	19 ***	8.1	256	1552
(9) Two Bridges Bottom	51°42'N, 1°30'W	SU343999	25 ***	3.8	182	961
(10) Lower Crockford	51°41'N, 1°29'W	SU354989	23 ***	1.2	310	1608
(11) Peaked Hill	51°42'N, 1°29'W	SU361991	21 ***	2.1	609	2249

Lavallega, Maldonado and Rocha but typically encountered only a few individuals on most ponds (including on a small pool at approximately 490 m altitude on Cerro Catedral). Andromorph frequency ranged between 3 and 9% (Tab. IV). It did not vary temporally within the populations (Punta Carretas, maximum likelihood $\chi^2 = 1.0$, $df = 3$, $p = 0.799$; Parque Mirramar, maximum likelihood $\chi^2 = 2.3$, $df = 3$, $p = 0.520$; Mendoza, maximum likelihood $\chi^2 = 0.9$, $df = 1$, $p = 0.337$) or between the populations during any month (November 2002, maximum likelihood $\chi^2 = 1.9$, $df = 1$, $p = 0.173$; December 2002, maximum likelihood $\chi^2 = 1.1$, $df = 1$, $p = 0.287$; January 2002, maximum likelihood $\chi^2 = 1.9$, $df = 3$, $p = 0.593$; February 2003, maximum likelihood $\chi^2 = 0.1$, $df = 2$,

Table III

Mean andromorph frequency (%) in nine populations of *X. zealandica*. The significance of Chi-square tests examining whether the ratio of andromorphs to gynomorphs differed from equality is shown using asterisks (***) $p < 0.001$. Standard deviation (SD) and the total number of females recorded at each site are shown

Locality	Latitude, Longitude	N.Z. National Grid Reference	Mean %	SD	Females
(1) The Groynes	43°27'S, 172°36'E	M35 783490	10 ***	1.6	554
(2) Lincoln Gravel Pit	43°38'S, 172°27'E	M36&M37 657298	2 ***	3.4	29
(3) Styx Mill Reserve	43°28'S, 172°36'E	M35 783490	14 ***	3.5	276
(4) Halswell Quarry	43°36'S, 172°35'E	M36&M37 757344	5 ***	0.6	509
(5) Hart Creek Pond	43°47'S, 172°19'E	M36&M37 545128	8 ***	0.6	276
(6) Shag Pond	43°42'S, 172°26'E	M36&M37 644232	13 ***	1.5	239
(7) Fenland House Pond	43°43'S, 172°27'E	M36&M37 633218	13 ***	5.5	200
(8) Kaipoi Gravel Pit	43°22'S, 172°40'E	M35 826607	8 ***	4.0	94
(9) Regents Park Pond	43°28'S, 172°36'E	M35 785485	9 ***	3.2	58

Table V

Andromorph frequencies (%) reported in the literature. For a particular species, estimates from different populations are indicated as 1, 2, 3 etc. Different estimates from the same population are indicated as a, b, c etc. Total number of females recorded is given (Females). The significance (p) of Chi-square tests examining whether the ratio of andromorphs to gynomorphs differed from equality is shown using asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns $p > 0.05$). † Two types of gynomorph are recognised for these species.

†† Frequencies calculated from a graph

Species	Source of data		Freq. (%)	Females	p
<i>Argia vivida</i>	CONRAD & PRITCHARD (1989)	1a	64	78	*
		1b	66	448	***
		2a	48	33	ns
<i>Ceriatrion tenellum</i> †	ANDRÉS & CORDERO (1999)	1	12	26	***
		2	0	34	
		3	19	16	*
		4	27	152	***
		5a	15	54	***
		5b	19	525	***
		5c	14	221	***
		6a	13	657	***
		6b	10	662	***
		6c	10	263	***
		6d	12	362	***
<i>Coenagrion puella</i>	THOMPSON (1989a)	6e	11	158	***
		7	0	43	
		8	12	82	***
		9	9	53	***
		1a	12	170	***
		1b	15	209	***
		1c	6	174	***
		1	45	554	*
<i>Enallagma boreale</i>	FINCKE (1994)	1	68	485	***
	FORBES (1994)	1	17	312	***
<i>Enallagma civile</i>	MILLER & FINCKE (1999)	1	15	70	***
<i>Enallagma ebrium</i>	MILLER & FINCKE (1999)	1	15	70	***
<i>Enallagma hageni</i>	FINCKE (1994)	1a	26	370	***
		1b	31	166	***
		1c	36	103	***
		2	26	39	**
		1a	14	63	***
<i>Ischnura damula</i>	JOHNSON (1964)	1b	14	52	***
		1c	10	58	***
		1d	11	72	***
		1e	14	50	***
		1f	14	65	***
		1g	13	48	***
		1h	14	51	***
		1i	12	43	***
		2a	11	53	***
		2b	12	42	***

Table V, continued

		2c	14	42	***
		2d	9	54	***
		2e	12	60	***
		2f	12	58	***
		2g	12	50	***
		2h	14	42	***
		2i	13	39	***
		3a	18	40	***
		3b	16	38	***
		3c	16	32	***
		3d	17	30	***
		3e	16	43	***
		3f	15	40	***
		3g	16	32	***
		4a	17	48	***
		4b	16	51	***
		4c	14	42	***
		4d	15	32	**
		4e	15	39	***
		4f	16	44	***
		4g	16	37	***
<i>Ischnura elegans</i> [†]	PARR (1969)	1	36	99	**
		2	34	217	***
		3	23	111	***
	VAN GOSSUM et al. (1999) ^{††}	1	7	13	**
		2	27	17	ns
		3	12	15	**
		4	70	10	ns
		5	18	11	ns
<i>Ischnura graellsii</i> [†]	CORDERO et al. (1998)	1	55	957	**
	CORDERO (1990)	1	18	523	***
		2a	21	29	**
		2b	17	65	***
		2c	14	685	***
		2d	8	85	***
		2e	18	107	***
		3	7	46	***
		4a	18	94	***
		4b	11	97	***
		5	30	37	*
<i>Ischnura ramburi</i>	ROBERTSON (1985)	1	31	90	***
		2	25	44	***
	SIROT et al. (2003)	1a	48	48	ns
		1b	39	83	*
		1c	36	94	**
		1d	39	49	ns
		1e	50	48	
		1f	48	75	ns

Table V, continued

<i>Nehalennia irene</i>	FORBES et al. (1995)	1	3	31	***
		2	7	15	***
		3	2	48	***
		4	12	34	***
		5	3	30	***
		6	28	31	*
		7	26	145	***
		8	24	156	***

dromorph frequency estimates taken from the literature. For 91% (86/94) of these estimates (where andromorphs were recorded) the ratio of andromorphs to gynomorphs differed significantly from equality.

If a species displays female-limited polymorphism then most populations appear to possess andromorphs. They occurred in all but two of the populations we examined and in all but two (*Ceriagrion tenellum*: ANDRES & CORDERO, 1999) of the populations listed in Table V. However, although andromorphs are almost always present within populations, they often occur with relatively low frequency. We encountered no situations where andromorphs were more common than gynomorphs. For the populations in Table V there are only four instances where andromorph frequency can be shown statistically to be significantly greater than 50% (Table V). This suggests that instances where andromorphs are more frequent than gynomorphs may be atypical. If male encounter rate with different female morphs is directly proportional to overall female morph frequency, then implications for the learned mate recognition model are clear: cases where males preferentially choose to mate with andromorphs may be infrequent because andromorphs are infrequently the most common morph.

Variation in andromorph frequency sometimes exists within and between populations. We found marginally significant variation in andromorph frequency within the Ness Gardens population of *C. puella*, within two populations of *C. mercuriale* and between populations of *X. zealandica*. We did not find similar variation for *I. fluviatilis*. FORBES et al. (1995) determined significant differences between andromorph frequencies in populations of *Nehalennia irene* during a single season in Canada and, although ANDRES & CORDERO (1999) did not find intra-population variation for *C. tenellum*, evidence for inter-population variation exists (our calculations from Table V making comparisons within years: populations 1 and 5a, maximum likelihood $\chi^2 = 0.2$, $df = 1$, $p = 0.6886$; populations 5b and 6a, $\chi^2 = 8.6$, $df = 1$, $p = 0.003$; populations 2, 3 and mean of 6b, 6c and 6d, $\chi^2 = 8.6$, $df = 2$, $p = 0.014$; populations 4, 5c and 6e, $\chi^2 = 14.8$, $df = 2$, $p < 0.001$; populations 7, 8 and 9, $\chi^2 = 9.0$, $df = 2$, $p = 0.011$). In contrast, data reported by CORDERO (1990) for Spanish *Ischnura graellsii* populations does not show intra-population variation in andromorph frequency (our calculations from Table V: population 2, maximum likelihood $\chi^2 = 5.4$, $df = 4$, $p = 0.252$; population 4, $\chi^2 = 1.7$, $df = 1$, $p = 0.186$); FINCKE (1994) found no significant inter-annual differences in andromorph frequency for *Enallagma hageni* at a Michigan pond; and SIROT et al. (2003) did not find significant

differences between andromorph frequencies over a 12 month study period of *I. ramburi* in a Florida pond. JOHNSON (1964) reports the results of a particularly comprehensive survey of *Ischnura damula* andromorph frequencies in four New Mexico populations: neither significant intra-population nor significant inter-population variation is evident (our maximum likelihood χ^2 calculations from Table V: four intra-population comparisons, range of $p = 0.944$ to 0.999 ; nine inter-population comparisons, range of $p = 0.449$ to 0.992). JOHNSON's within-population frequency estimates were highly concordant ($r_1 = 0.64$).

Even if the overall number of andromorphs within a population is lower than the overall number of gynomorphs, males may encounter andromorphs at higher rates than gynomorphs if andromorphs more often occur in areas of higher male density. Littoral zones of water bodies are typically the areas of highest male density and, for *C. puella* at Ness Gardens, males were recorded in highest numbers at the water's edge. However, we found no evidence to suggest that andromorph *C. puella* were any more likely than gynomorphs to occur at the water's edge. Similar observations have been made by MILLER & FINCKE, (1999) for *Enallagma civile*. In addition, our qualitative impres-

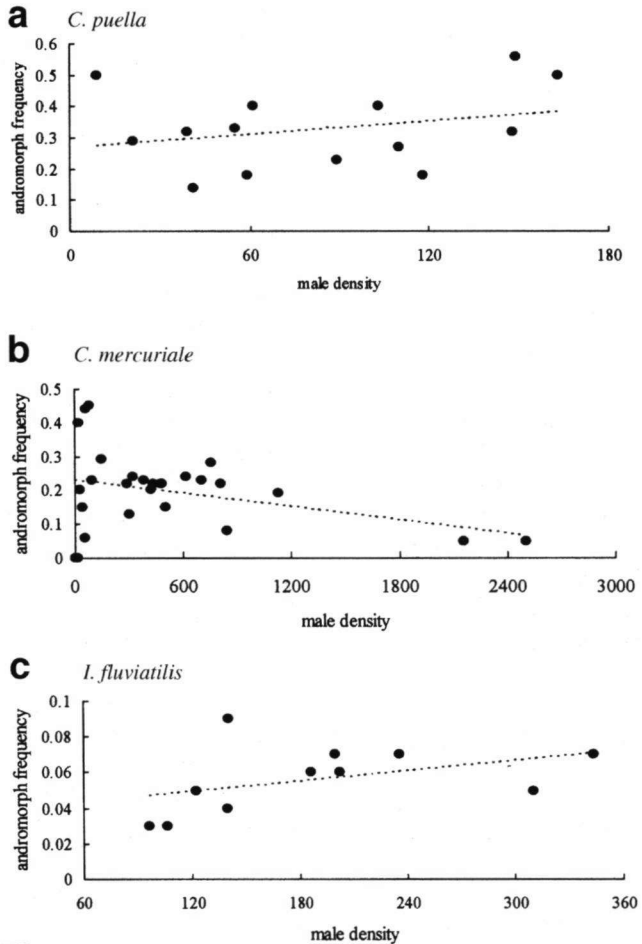


Fig. 2. Relationship between andromorph frequency and male density for (a) *C. puella*; - (b) *C. mercuriale* and - (c) *I. fluviatilis*.

sion from surveying *X. zealandica* and *I. fluviatilis* is that, in these species also, andromorphs and gynomorphs do not concentrate in different areas. Although FORBES et al. (1995) found that andromorph *N. irene* tend to occur at site edges where male densities were higher, it would seem generally that female morphs do not segregate according to habitat, at least at a relatively coarse spatial scale.

A number of studies present evidence for positive correlation between measures of male frequency (i.e. sex ratio and male density) and andromorph frequency (e.g. HINNEKINT, 1987; CORDERO, 1992; FORBES et al., 1995; CORDERO et al., 1998). This might be expected if andromorphs gain a selective advantage by resembling males. We did not find this. Recently, SIROT et al. (2003) also reported no significant correlation between sex ratio and andromorph frequency for *I. ramburi*.

ACKNOWLEDGEMENTS

We thank staff at Ness Botanic Gardens (Liverpool University), Professor STEVE WRATTEN (Lincoln University, New Zealand) and MARIANA MEERHOFF (Universidad de la Republica, Uruguay). This work was supported by the Leverhulme Trust (F/00128/M), the Environment Agency and the Natural Environment Research Council (NER/A/S/2000/01322). Marking of *C. mercuriale* was carried out under licence (to DJT) from English Nature.

REFERENCES

- ANDRES, J.A. & A. CORDERO, 1999. The inheritance of female colour morphs in the damselfly *Ceriatrigon tenellum* (Odonata, Coenagrionidae). *Heredity* 82: 328-335.
- ANDRES, J.A., R.A. SANCHEZ-GUILLEN & A. CORDERO-RIVERA, 2002. Evolution of female colour polymorphism in damselflies: testing the hypotheses. *Anim. Behav.* 63: 677-685.
- BULLA, L.A., 1973-1974. Clave para la identificacion de los Odonata Zygoptera de la Republica Argentina al sur del paralelo 30 °S. *Revta Soc. Ent. Argent.* 34: 217-228.
- CONRAD, K.F. & G. PRITCHARD, 1989. Female dimorphism and physiological colour change in the damselfly *Argia vivida* Hagen (Odonata: Coenagrionidae). *Can. J. Zool.* 67: 298-304.
- CORDERO, A., 1990. The inheritance of female polymorphism in the damselfly *Ischnura graellsii* (Rambur) (Odonata: Coenagrionidae). *Heredity* 64: 341-346.
- CORDERO, A., 1992. Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *J. Anim. Ecol.* 61: 769-780.
- CORDERO, A., S. SANTOLAMAZZA CARBONNE & C. UTZERI, 1998. Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). *Anim. Behav.* 55: 185-197.
- FINCKE, O.M., 1994. Female colour polymorphism in damselflies: failure to reject the null hypothesis. *Anim. Behav.* 47: 1249-1266.
- FORBES, M., 1994. Tests of hypotheses for female-limited polymorphism in the damselfly, *Enallagma boreale* Selys. *Anim. Behav.* 47: 724-726.
- FORBES, M.R.L., J.M.L. RICHARDSON & R.L. BAKER, 1995. Frequency of female morphs is related to an index of male density in the damselfly, *Nehalennia irene* (Hagen). *Ecoscience* 2: 28-33.
- HINNEKINT, B.O.N., 1987. Population dynamics of *Ischnura e. elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia* 146: 3-31.
- JOHNSON, C., 1964. The inheritance of female dimorphism in the damselfly, *Ischnura damula*. *Genetics*

49: 513-519.

- McKEE, D., I. HARVEY, M. THOMAS & T.N. SHERRATT, 2003. Mite infestation of *Xanthocnemis zealandica* (McLachlan) in a Christchurch pond. *N. Z. J. Zool.* 30: 17-20.
- MILLER, M.N. & O.M. FINCKE, 1999. Cues for mate recognition and the effect of prior experience on mate recognition in *Enallagma damselflies*. *J. Insect Behav.* 12: 801-814.
- PARR, M.J., 1969. *Population studies of some zygopteran dragonflies (Odonata)*. PhD Thesis, Univ. Salford.
- ROBERTSON, H.M., 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* 33: 805-809.
- ROWE, R.J., 1987. *The dragonflies of New Zealand*. Auckland Univ. Press.
- SHERRATT, T.N., 2001. The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecology Letters* 4: 22-29.
- SIROT, L.K. & H.J. BROCKMANN, 2001. Costs of sexual interactions to females in Rambur's forktail damselfly, *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Anim. Behav.* 61: 415-424.
- SIROT, L.K., H.J. BROCKMANN, C. MARINIS & G. MUSCHETT, 2003. Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Anim. Behav.* 66: 763-775.
- THOMPSON, D.J., 1989a. Lifetime reproductive success in andromorph females of the damselfly *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 209-213.
- THOMPSON, D.J., 1989b. Sexual size dimorphism in *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Adv. Odonatol.* 4: 123-131.
- THOMPSON, D.J., J.R. ROUQUETTE & B.V. PURSE, 2004. *Ecology of the Southern Damselfly, Coenagrion mercuriale*. Conserving Natura 2000 Rivers Ecology Series No. 8. English Nature, Peterborough.
- VAN GOSSUM, H., R. STOKS, E. MATTHYSEN, F. VALCK & L. DE BRUYN, 1999. Male choice for female colour morphs in *Ischnura elegans* (Odonata, Coenagrionidae): testing the hypotheses. *Anim. Behav.* 57: 1229-1232.
- VAN GOSSUM, H., R. STOKS, & L. DE BRUYN, 2001. Frequency-dependent male mate harassment and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*. *Behav. Ecol. Sociobiol.* 51: 69-75.
- VON ELLENRIEDER, N., 2000. Species composition and temporal variation of odonate assemblages in the subtropical-pampasic ecotone, Buenos Aires, Argentina. *Odonatologica* 29: 17-30.