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LIFETIME REPRODUCTIVE SUCCESS IN ANDROMORPH FEMALES OF THE DAMSELFLY *COENAGRION PUELLA* (L.) (ZYGOPTERA: COENAGRIONIDAE)

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The weight, wing length, lifespan and lifetime reproductive success of heteromorph and andromorph females were compared. No differences between the morphs were discovered in any of these parameters. The results are discussed in the light of recent suggestions concerning the selective advantages of andromorphs.

INTRODUCTION

BANKS & THOMPSON (1985a, 1985b; 1987) have described lifetime mating success in males and females of *Coenagrion puella* (L.). By marking and measuring most of the individuals that emerged from, and/or bred at a small pond and noting which individuals mated together, it was possible to relate lifetime mating success to such parameters as emergence date, date of reaching maturity, mature adult lifespan and measures of body size, such as wing length and body weight.

Females of *C. puella,* like some other odonates, are polymorphic. There were two forms present at the study site; the normal (heteromorph) form and a less frequent andromorph form. It has been proposed that in some ischnurans, at least, by mimicking males, andromorph females avoid male harassment but mate less frequently than do heteromorphs (ROBERTSON 1985). ROBERTSON (1985) and HINNEKINT (1987) both proposed mechanisms for the maintenance of the polymorphism.

The aim of the present paper is to examine the data collected by BANKS & THOMPSON (1985a, 1985b, 1987) and analyse those concerned with female reproductive success with respect to female colour morph.

STUDY SITE

The study was made at Bungalow Pond, Wirral, northern England, Nat. grid ref. SJ 234857 between 15 May and 31 July 1983. A full description of the site is given by BANKS & THOMPSON (1985a).

METHODS

Full descriptions of the methods can be found in BANKS & THOMPSON (1985a, 1985b; 1987). In brief, newly emerged adults of *C. puella* were collected at the study site, taken to the laboratory, weighed, measured, uniquely marked with a number on the left forewing and dot of paint on the dorsum of the thorax, retained overnight and returned to the site in the morning. The frequency of the two morphs was noted. As mature adults appeared at the site, most effort was made to catch them and repeat the procedure described above; the colour morph of the female was again noted. The aim was to mark and measure every mature male and tandem pair present at the pond throughout the entire breeding season. By so doing it was possible to compare the success of andromorph versus heteromorph females for a number of variables.

RESULTS

The results are divided into three sections, illustrated in Tables I-III. Table I compares the females that emerged at Bungalow Pond and returned to breed there. Tables II and III compare females that were captured and marked as mature adults, in June and July respectively. This sub-division has been made because the months of June and July provided quite different climatic conditions in 1983. June was a typical British summer month, with only about half the days suitable for odonate reproductive activity, whereas there were only two overcast days in July. The results are quite clear; there are no significant differences between heteromorph and andromorph females for any of the variables in any of the Tables. The most important result from an evolutionary point of view is that there was no detectable difference in the number of clutches of eggs laid.

One interesting feature to emerge from the data is the frequency of andromorphs observed in the three different categories (13.33%, 17.42% and 6.75% respectively). The first two categories are sampling early emerging adults; the third category is sampling late emergers. The frequency of andromorphs at emergence was 5.37% (n = 1842).

DISCUSSION

Most discussion on female polymorphism in odonates has revolved around coenagrionids, especially ischnurans (e.g. JOHNSON, 1966, 1975; ROBERTSON, 1985; HINNEKINT, 1987). The reason for this is probably that andromorphs are more frequent in ischnurans than other coenagrionids. For example in *Ischnura pumilio* (Charp.), andromorphs are more common than

Table I
Comparisons between the two colour morphs for females that were marked at emergence.

Variable		Mean	SD	n	t	p
Date of emergence (days since 15 May)	heteromorph	14.71	5.05	150	0.43	0.670
	andromorph	14.20	5.05	20		
Weight (mg)	heteromorph	39.33	2.57	150	1.69	0.105
	andromorph	37.98	3.46	20		
Forewing length (mm)	heteromorph	22.74	0.57	150	0.09	0.931
	andromorph	22.73	0.53	20		
Mature adult lifespan (days)	heteromorph	3.11	4.44	150	0.23	0.815
	andromorph	3.35	3.69	20		
Number of clutches	heteromorph	1.70	1.67	150	0.26	0.795
	andromorph	1.60	1.05	20		

Table II
Comparisons between the two colour morphs for females marked as mature adults in June

Variable		Mean	SD	n	t	p
Date of reaching maturity (days since 15 May)	heteromorph	32.25	5.21	178	0.50	0.615
	andromorph	31.74	5.28	31		
Weight (mg)	heteromorph	51.99	6.20	178	0.31	0.758
	andromorph	51.63	5.02	31		
Forewing length (mm)	heteromorph	22.73	0.65	178	1.24	0.215
	andromorph	22.58	0.52	31		
Mature adult lifespan (days)	heteromorph	4.18	6.02	178	0.13	0.898
	andromorph	4.03	5.08	31		
Number of clutches	heteromorph	1.92	1.72	178	0.06	0.953
	andromorph	1.94	1.65	31		

Table III
Comparisons between the two colour morphs for females marked as mature adults in July

Variable		Mean	SD	n	t	p
Date of reaching maturity (days since 15 May)	heteromorph	55.15	4.68	163	1.04	0.298
	andromorph	53.64	4.37	11		
Weight (mg)	heteromorph	48.78	4.77	163	0.62	0.536
	andromorph	49.71	5.41	11		
Forewing length (mm)	heteromorph	21.98	0.63	163	1.48	0.142
	andromorph	22.27	0.82	11		
Mature adult lifespan (days)	heteromorph	5.35	4.34	163	1.87	0.064
	andromorph	7.91	5.19	11		
Number of clutches	heteromorph	3.74	2.82	163	1.81	0.072
	andromorph	5.36	3.67	11		

hetermorphs in the British Isles (CORBET, LONGFIELD & MOORE 1960). ROBERTSON (1985) has claimed that andromorphs mimic male behaviour in interactions with males. As a result, they copulate less frequently than heteromorphs. If females only need to copulate once, then by avoiding extra, unnecessary copulations, andromorphs avoid the extra predation risk which one might suppose accompanies copulation. This seems a plausible explanation given the long copulation times observed in ischnurans. There are two problems with this explanation. One is that it requires that the more brightly coloured andromorphs suffer increased predation (or other mortality) over heteromorphs in order to balance the polymorphism. There is no such supporting evidence; indeed if brightly coloured ischnurans suffered increased predation, one might expect to find female biassed sex ratios at the breeding sites. The second problem is that if andromorphs are at no selective disadvantage, they should be increasing. HINNEKINT (1987) accepted that andromorphs would have a selective advantage at high population densities, but argued that this would become a disadvantage at low densities, thus providing an explanation for a balanced polymorphism. Unfortunately the evidence is lacking.

In two very detailed studies of long-term mating and reproductive success in non-ischnuran coenagrionids,no evidence has been found to suggest any advantage of andromorphs over heteromorphs in the parameter on which selection

is most likely to operate, lifetime reproductive success (present work and FINCKE, 1982, 1988). Fincke found no difference in the average number of matings, lifespan or size between andromorph and heteromorph females. She was able to show that when males were experimentally presented with tethered females of each morph they took heteromorph females in tandem more quickly than andromorphs. However, since tandem pairs were harassed regardless of female colour morph, any general advantage accruing to coenagrionid andromorphs during oviposition must be confined to ischnurans, which oviposit alone.

In the present study, the frequency of andromorphs at emergence and the frequency that returned to the study site to breed were quite different (5.37% compared with 13.33%). Since the frequency of andromorphs breeding at the pond early in the season, but which emerged elsewhere, was similar to the frequency of those that emerged from the study pond, there is some evidence that andromorphs suffered less mortality than hetermorphs in the pre-reproductive period. This is based on only one study, but it is interesting to note that it is the exact opposite of the prediction made by ROBERTSON (1985).

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