

# Survival rates in a natural population of the damselfly *Ceriagrion tenellum*: effects of sex and female phenotype

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**Abstract.** 1. *Ceriagrion tenellum* females show genetic colour polymorphism. Androchrome (*erythrogastrum*) females are brightly (male-like) coloured while gynochrome females (*typica* and *melanogastrum*) show cryptic colouration.

2. Several hypotheses have been proposed to explain the existence of more than one female morph in damselfly populations. The *reproductive isolation* and *intraspecific mimicry* hypotheses predict greater survival of gynochrome females, while the *density dependent* hypothesis predicts no differential survival between morphs.

3. Mature males had greater recapture probability than females while the survival probability was similar for both sexes. Survival and recapture rates were similar for androchrome and gynochrome females.

4. Gynochrome females showed greater mortality or migration rate than androchrome females during the pre-reproductive period. This result is not predicted by the above hypotheses or by the null hypothesis that colour polymorphism is only maintained by random factors: founder effects, genetic drift, and migration.

**Key words.** Damselflies, female colour polymorphism, recapture probability, survival probability.

## Introduction

Female colour polymorphism is a widespread characteristic of many Odonata. One of the female morphs is brightly coloured like the conspecific male (androchrome females) whereas one or more additional morphs are generally cryptic (gynochrome females). Three main hypotheses have been proposed to explain the coexistence of more than one female phenotype in natural populations:

### *Reproductive isolation hypothesis*

Johnson (1975) proposed a post-zygotic reproductive mechanism as the force maintaining different female morphs. According to Johnson, gynochrome females are commonly involved in heterospecific (sterile) matings whereas andro-

chromes have greater reproductive isolation. Differential predation pressures would counterbalance the disadvantage of the gynochromes: brightly-coloured individuals (males and androchrome females) would have greater predation intensity and this would reduce their longevity. Because longevity is one of the main factors in the variance of reproductive success in odonates (Banks & Thompson, 1985, 1987; Fincke, 1986, 1988; McVey, 1988; Michiels & Dhondt, 1991; Cordero, 1995), colouration-dependent predation would reduce the lifetime reproductive success of androchrome females.

### *Frequency-dependent hypothesis*

Robertson (1985) proposed a second explanation, referred to as the *intraspecific mimetism* hypothesis. He suggested that a single mating is enough to fertilise all the eggs that a female would lay throughout its life. Thus by mimicking males, androchrome females avoid unnecessary (and costly) matings. This advantage would be counterbalanced by a frequency-independent mechanism: more intense predation on andro-

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chrome females. Thus, as in Johnson's hypothesis, androchromes are predicted to suffer a higher predation rate. Fincke (1994) and Grether and Grey (1996) proposed two slightly different frequency-dependent models, in which less frequent female morphs enjoy a greater fitness as long as they remain at low frequencies. Fincke's hypothesis assumes that benefits and costs (lower fecundity and/or shorter lifespan) are associated with long copulations and male harassment. Grether and Grey (1996) assumed that androchrome females are always at low frequencies so that they will benefit from reduced rates of male harassment. On the other hand, bright colours may make androchrome females more conspicuous to their prey, reducing their hunting efficiency and therefore reducing their fitness.

#### Density-dependent hypothesis

Hinneking (1987) proposed a third explanation: if males cannot distinguish between androchrome females and other males, at high male densities (when the sex ratio is more male biased) androchrome females would have an advantage avoiding costly extra matings, but at low densities some would not be able to mate at all. The existence of cyclic variations in population density would allow the co-existence of the different female morphs (Hinneking & Dumont, 1989).

#### Null hypothesis

Despite all these adaptive hypotheses, female morphs could also be neutral with regard to natural and sexual selection (Fincke, 1994).

Both the reproductive isolation (Johnson, 1975) and the intraspecific mimetism (Robertson, 1985) hypotheses predict that androchromes have a lower probability of survival than gynochromes. On the other hand, if population density is the main factor explaining the maintenance of female polymorphism (Hinneking, 1987) or if the different female morphs are neutral to selection (Fincke, 1994), the longevity of all morphs will be the same.

In spite of the importance of estimating survival rates correctly, previous field studies have not separated survival and recapture probabilities. Differences in the rates of recapture of males and females or of female morphs could therefore produce spurious differences or mask real differences in survival rates of the different classes of individuals. The recent theoretical advances in mark-recapture models allow the separation of recapture and survival probabilities (Lebreton *et al.*, 1992). Thus, it is possible to test the predictions of the different hypotheses independently of the effect of colouration on female recapture rates. Among the Odonata, these methods have been applied only to sex differences in survival in the lestid *Lestes disjunctus* (Anholt, 1997) and the coenagrionid *Ischnura pumilio* (Cordero & Andrés, 1999).

In the work reported here, these mark-recapture methods were used to analyse recapture and survival probabilities in a population of *Ceriagrion tenellum*. This species is a non-territorial coenagrionid whose females show polymorphism of

colouration. Three different female morphs co-exist in the studied population: *erythrogastrum*, which is male-like coloured, and two gynochrome morphs, *typica* and *melanogastrum* [see Andrés and Cordero (1999) for colour pictures and a detailed description of female morphs]. Colour polymorphism has a genetic basis in this species (Andrés & Cordero, 1999) and testing for the existence of survival differences among morphs could help understanding of the underlying mechanisms for the maintenance of female polychromatism.

#### Methods

The studied population inhabits a natural wetland at A Castiñeira (Trazo, A Coruña province, NW Spain, 43°00'N, 8°30'W) and was described by Andrés and Cordero (1998). Individuals were captured using a net and marked by writing a number on one wing using an indelible marker (Staedtler® Pancolor 303f, Germany). The observations were concentrated on the edge of the pond because almost no *C. tenellum* were found in the adjacent fields.

A total of 1728 mature adults was captured and marked during 35 days in August–September 1995. Forty-six per cent (800) of these individuals were recaptured at least once. During the following season, 1980 teneral individuals were marked during 59 days in June–July 1996 to study survival rates during the pre-reproductive period. Only 14% (287) of these marked individuals were recaptured as mature. The last observation of a marked animal might not coincide with its death because an individual that has not been recaptured for some time may have survived and escaped recapture by chance or for biological reasons (e.g. temporary emigration). Therefore, to model the recapture histories of marked animals, the probability of survival  $\phi$ , the recapture probability  $p$ , and the product of these two parameters (denominated  $\beta$  by Lebreton *et al.*, 1992) are needed for those dates when survival and recapture probabilities cannot be estimated separately (for instance for the last sample).

The Cormack-Jolly-Seber model was used. This model assumes a multinomial distribution of the observed number of animals sharing a particular recapture history. The goodness-of-fit of field data to this model was tested by means of the bootstrap procedure of the program MARK (White & Burnham, 1999), which allowed the overdispersion quasi-likelihood parameter ( $c$ ) to be estimated for the data sets. This parameter was calculated as the observed deviance of the global model divided by its expected deviance, and provides a measure of the amount of overdispersion in the original data set.

The analysis of survival and recapture probabilities was only carried out with the 1995 data set because of the low recapture rate of teneral individuals in 1996.

#### Model selection and comparison among groups

Because it was expected that the survival and the recapture probabilities were dependent on sex and/or female phenotype

**Table 1.** Males vs. females. Quasi-likelihood Akaike information criterion (QAICc), quasi-likelihood Akaike information criterion differences ( $\Delta$ QAICc), normalised quasi-likelihood Akaike information criterion weights (QAICc W), number of parameters, and deviance values for each of the tested models. The estimated quasi-likelihood parameter ( $c=1.085$ ) was used to adjust the QAICc values for overdispersion in the original data.

| Model               | QAICc     | $\Delta$ QAICc | QAICc W | Number of parameters | Deviance |
|---------------------|-----------|----------------|---------|----------------------|----------|
| $\phi_{st}P_{s+t}$  | 9708.471  | 0.00           | 0.58267 | 65                   | 3944.447 |
| $\phi_{t}P_{s+t}$   | 9710.318  | 1.85           | 0.23139 | 51                   | 3977.876 |
| $\phi P_{s+t}$      | 9712.029  | 3.56           | 0.09836 | 29                   | 4028.599 |
| $\phi_{s}P_{s+t}$   | 9712.524  | 4.05           | 0.07679 | 30                   | 4026.928 |
| $\phi_{s+t}P_{s+t}$ | 9716.705  | 8.23           | 0.00949 | 57                   | 3971.360 |
| $\phi_{t}P_{st}$    | 9723.481  | 15.01          | 0.00032 | 75                   | 3935.860 |
| $\phi_{s+t}P_{st}$  | 9721.587  | 13.12          | 0.00083 | 76                   | 3933.805 |
| $\phi P_{st}$       | 9725.784  | 17.31          | 0.00010 | 53                   | 3990.182 |
| $\phi_{s}P_{st}$    | 9727.537  | 19.07          | 0.00004 | 54                   | 3989.845 |
| $\phi_{st}P_{st}$   | 9802.162  | 93.69          | 0.00000 | 122                  | 3915.446 |
| $\phi_{s+t}P_{t}$   | 9822.163  | 113.69         | 0.00000 | 54                   | 4092.503 |
| $\phi_{s}P_{t}$     | 9843.415  | 134.94         | 0.00000 | 29                   | 4171.140 |
| $\phi_{t}P_{t}$     | 9874.068  | 165.60         | 0.00000 | 49                   | 4159.997 |
| $\phi_{st}P_{t}$    | 9881.280  | 172.81         | 0.00000 | 91                   | 4072.879 |
| $\phi P_{t}$        | 9892.428  | 183.96         | 0.00000 | 28                   | 4226.520 |
| $\phi_{t}P_{s}$     | 10531.553 | 823.08         | 0.00000 | 17                   | 4944.093 |
| $\phi_{s+t}P_{s}$   | 10532.373 | 823.90         | 0.00000 | 18                   | 4942.791 |
| $\phi_{s}P_{s}$     | 10619.691 | 911.22         | 0.00000 | 74                   | 4912.692 |
| $\phi_{s+t}P$       | 10663.992 | 955.45         | 0.00000 | 16                   | 5089.891 |
| $\phi_{st}P$        | 10669.004 | 960.53         | 0.00000 | 31                   | 5064.226 |
| $\phi_{t}P$         | 10707.973 | 999.50         | 0.00000 | 15                   | 5139.873 |
| $\phi P_{s}$        | 11152.639 | 1444.1         | 0.00000 | 3                    | 5648.471 |
| $\phi_{s}P_{s}$     | 11154.643 | 1446.1         | 0.00000 | 4                    | 5648.471 |
| $\phi_{s}P$         | 11284.790 | 1576.3         | 0.00000 | 3                    | 5791.842 |
| $\phi P$            | 11324.738 | 1616.2         | 0.00000 | 2                    | 5837.355 |

and because for any given sex or female colouration both probabilities could also vary with time (e.g. seasonal changes), an *a priori* selection of models was carried out including and excluding these variables as well as their interactions (see Tables 1 and 2 for the list of selected models).

The effect of sex and colouration on the recapture and survival probabilities was analysed by means of a quasi-likelihood Akaike information criterion (QAICc), defined as:

$$QAICc = \frac{-2\ln(L)}{c} + 2np + \frac{2np(np+1)}{n_{ess} - np - 1} \quad (1)$$

where  $np$  is the number of parameters in the model,  $c$  is the estimated overdispersion quasi-likelihood parameter, and  $n_{ess}$  is the effective sample size.

The quasi-likelihood Akaike information criterion was calculated for each tested model and the model with the lowest value was used as the basis for estimating survival and recapture probabilities. This method was used because when the original data are overdispersed, it performs better than the alternative likelihood ratio tests (Anderson *et al.*, 1994) and

**Table 2.** Androchrome vs. gynochrome females. Quasi-likelihood Akaike information criterion (QAICc), quasi-likelihood Akaike information criterion differences ( $\Delta$ QAICc), normalised quasi-likelihood Akaike information criterion weights (QAICc W), number of parameters, and deviance values for each of the tested models. The estimated quasi-likelihood parameter ( $c=1.107$ ) was used to adjust the QAICc values for overdispersion in the original data.

| Model               | QAICc    | $\Delta$ QAICc | QAICc W | Number of parameters | Deviance |
|---------------------|----------|----------------|---------|----------------------|----------|
| $\phi P_{t}$        | 2549.304 | 0.00           | 0.31453 | 26                   | 1086.489 |
| $\phi_{t}P_{t}$     | 2550.291 | 0.99           | 0.19201 | 38                   | 1059.239 |
| $\phi_{t}P_{c+t}$   | 2550.299 | 0.99           | 0.19125 | 38                   | 1059.248 |
| $\phi_{c}P_{t}$     | 2551.050 | 1.75           | 0.13138 | 27                   | 1086.087 |
| $\phi P_{c+t}$      | 2551.409 | 2.11           | 0.10979 | 27                   | 1086.484 |
| $\phi_{c}P_{c+t}$   | 2552.941 | 3.64           | 0.05104 | 28                   | 1085.839 |
| $\phi_{c+t}P_{t}$   | 2556.284 | 6.98           | 0.00959 | 41                   | 1058.678 |
| $\phi_{c+t}P_{c+t}$ | 2562.719 | 13.41          | 0.00038 | 44                   | 1058.564 |
| $\phi P_{ct}$       | 2569.618 | 20.31          | 0.00001 | 44                   | 1066.200 |
| $\phi_{ct}P_{c+t}$  | 2570.332 | 21.03          | 0.00001 | 51                   | 1049.927 |
| $\phi_{c}P_{st}$    | 2571.040 | 21.74          | 0.00001 | 45                   | 1065.352 |
| $\phi_{ct}P_{t}$    | 2571.555 | 22.25          | 0.00000 | 51                   | 1051.281 |
| $\phi_{c+t}P_{ct}$  | 2575.055 | 25.75          | 0.00000 | 58                   | 1037.843 |
| $\phi_{t}P_{ct}$    | 2577.831 | 28.53          | 0.00000 | 59                   | 1038.423 |
| $\phi_{ct}P_{ct}$   | 2586.403 | 37.10          | 0.00000 | 67                   | 1027.774 |
| $\phi_{t}P_{c}$     | 2658.404 | 109.10         | 0.00000 | 12                   | 1239.477 |
| $\phi_{c+t}P_{c}$   | 2659.576 | 110.27         | 0.00000 | 13                   | 1238.503 |
| $\phi_{t}P$         | 2660.415 | 111.11         | 0.00000 | 13                   | 1239.432 |
| $\phi_{c+t}P$       | 2661.597 | 112.29         | 0.00000 | 14                   | 1238.464 |
| $\phi_{ct}P$        | 2668.839 | 119.53         | 0.00000 | 20                   | 1232.730 |
| $\phi_{ct}P_{c}$    | 2670.739 | 121.43         | 0.00000 | 21                   | 1232.525 |
| $\phi P$            | 2793.129 | 243.82         | 0.00000 | 2                    | 1411.084 |
| $\phi_{c}P$         | 2794.976 | 245.67         | 0.00000 | 3                    | 1410.902 |
| $\phi P_{c}$        | 2795.138 | 245.83         | 0.00000 | 3                    | 1411.082 |
| $\phi_{c}P_{c}$     | 2796.945 | 247.64         | 0.00000 | 4                    | 1410.850 |

because reliability of the result is not affected by the number of tests performed.

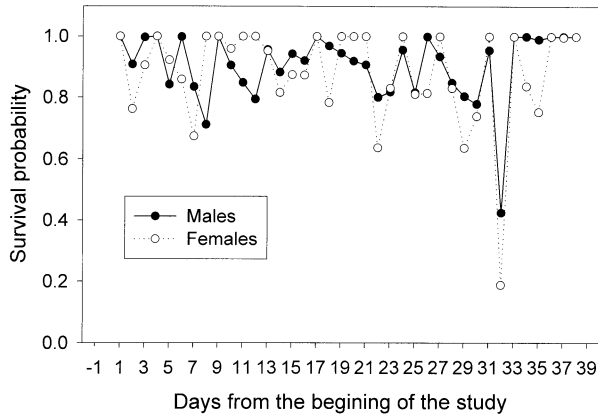
To provide an index of plausibility of competing models, the normalised quasi-likelihood Akaike weights ( $W$ ) were used. These weights estimate the likelihood of a given model given the data and were calculated for each model ( $i$ ) as:

$$W_i = \left[ \exp\left(\frac{-\Delta QAICc}{2}\right) \right] / \sum \left[ \exp\left(\frac{-\Delta QAICc}{2}\right) \right] \quad (2)$$

The differences of quasi-likelihood Akaike weights between competing models were calculated as:

$$\Delta QAICc = QAICc_i - \min QAICc \quad (3)$$

These differences provide an estimate of the relative support for each of the tested models. Thus, the greater the difference of the quasi-likelihood Akaike information criterion, the smaller the quasi Akaike weight, and the less plausible a given model. All the above calculations were made using the program MARK (White & Burnham, 1999).



**Fig. 1.** Maximum likelihood estimates for the recapture probabilities of *Ceriagrion tenellum* males and females during the reproductive period. Estimates were calculated from the model  $\phi_{st}p_{s+t}$ .

## Results

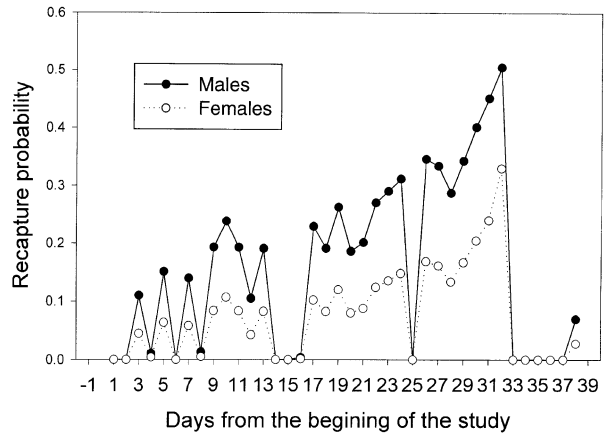
### Survival during the pre-reproductive period

Cormack-Jolly-Seber models could not be applied to study survival during the pre-reproductive period because most animals disappeared from the pond during this phase. The proportion of teneral males marked during 1996 that was recaptured as mature adults (177/1045) was significantly smaller than the proportion of females (110/845;  $\chi^2_2=4.12$ ,  $P<0.05$ ). Significant differences in recapture rates were also observed among female morphs ( $\chi^2_2=8.247$ ,  $P<0.05$ ). Androchromes (20/83) were recaptured as mature adults in a greater proportion than gynochromes (90/762;  $\chi^2_2=7.730$ ,  $P<0.05$ ) but no differences were found between the two gynochromes (*typica*: 34/243, *melanogastrum*: 56/519;  $\chi^2_2=1.853$ ,  $P=NS$ ).

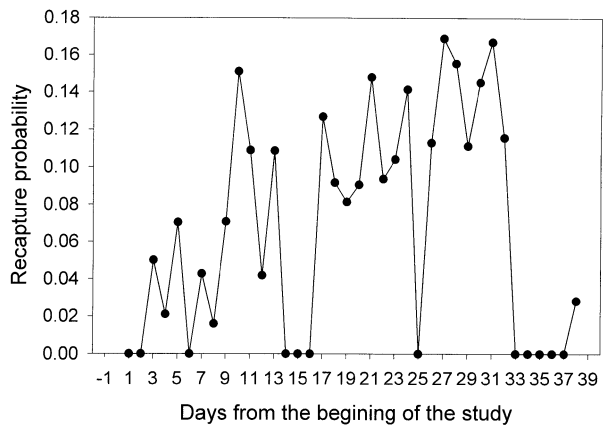
### Survival during the reproductive period

*Are survival and recapture probabilities sex-dependent?* The estimates of the quasi-likelihood information criterion, normalised quasi-likelihood Akaike information criterion weights, their differences, and the number of parameters and deviance values for each of the tested models are shown in Table 1. Using the Akaike information criterion as the tool for model selection, the model  $\phi_{st}p_{s+t}$  was the best explaining the 1995 male–female data set, indicating that the combination of sex and time had an important effect on survival and recapture rates. The Akaike weight values showed that this model had nearly double the support of the next model ( $\phi_{t}p_{s+t}$ ) and much more support than the models  $\phi_{s}p_{s+t}$  and  $\phi_{s+t}p_{s+t}$ . The  $\phi_{st}p_{s+t}$  model was therefore used to obtain the estimates of survival and recapture probabilities for both sexes (see Figs 1 and 2).

Based on the  $\phi_{st}p_{s+t}$  model, recapture probabilities were greater for males (Fig. 1) while survival probabilities were similar for both sexes (Fig. 2).



**Fig. 2.** Maximum likelihood estimates for the survival probabilities of *Ceriagrion tenellum* males and females during the reproductive period. Estimates were calculated from the model  $\phi_{st}p_{s+t}$ .



**Fig. 3.** Maximum likelihood estimates for the recapture probabilities of females (phenotypes combined) during the reproductive period. Estimates were calculated from the model  $\phi_{pt}$ .

*Do androchrome females have a lower probability of survival?* The same strategy was used to analyse the 1995 female (androchrome vs. gynochrome) data set. The estimates of the quasi-likelihood Akaike information criterion, normalised quasi-likelihood Akaike weights, their differences, and the number of parameters and deviance values for each of the tested models are shown in Table 2.

In this case, the best model ( $\phi_{pt}$ ) is approximately as good as the models  $\phi_{t}p_t$  and  $\phi_{t}p_{c+t}$  and had only twice as much support as the model  $\phi_{c}p_t$  (see Table 2). These results suggest that colouration might have an effect on the survival probability of females. Thus, the model  $\phi_{c}p_t$  was used to evaluate the magnitude of the difference in survival rate between androchrome and gynochrome females; however this analysis showed that survival probability was only slightly greater for gynochrome females ( $0.894 \pm 0.009$ ) than for androchrome females ( $0.881 \pm 0.020$ ). Recapture probabilities were estimated from the most parsimonious of the competing models (the one with fewest parameters),  $\phi_{pt}$  (see Fig. 3).

## Discussion

Different evolutionary mechanisms, including reproductive isolation (Johnson, 1975) and frequency- (Robertson, 1985; Fincke, 1994; Grether & Grey, 1996) or density-dependent (Hinneking, 1987) selection have been proposed to explain the maintenance of several female colour morphs in damselflies. The existence of differences in mortality rates among female morphs is one of the key points in understanding the maintenance of colour polymorphism in odonates. Early explanations such as the reproductive isolation (Johnson, 1975) and the intraspecific mimetism (Robertson, 1985) hypotheses predict differential predation pressures on the different female morphs because brightly coloured androchrome females would suffer the highest predation rates. Other adaptive explanations (Hinneking, 1987; Fincke, 1994; Grether & Grey, 1996) assume that sexual conflict over remating rate is one of the main selective forces maintaining female colour polymorphism in damselflies. While male fitness is related positively to the number of matings, insect females typically maximise their fitness at intermediate (re)mating rates (Arnqvist & Nilsson, 2000). So, less attractive morphs could benefit from avoiding the costs of *extra* copulations and/or male harassment (Fincke, 1994; Grether & Grey, 1996). Fitness costs for females could be mediated not only by a reduced lifespan but also by reduced fecundity and/or fertility. So no differences in survival probability among female morphs could be expected if only male harassment or selective predation and male harassment acting together are the main forces maintaining female colour polymorphism in odonates. The same prediction holds if morph frequencies are only determined by random factors (i.e. founder effects, genetic drift, migration). Given that the male mating attempts vary among female morphs (see Cordero & Andrés, 1996 for a review), survival probability could be the same for all females if male harassment (and/or long copulations) has no effect on female lifespan but has a negative effect on other female fitness components (i.e. fecundity or fertility). Alternatively, no significant differences in survival probability among morphs could arise from mortality factors differing among female morphs. Thus, overall, the survival probability would not differ among females but androchrome (or less common) morphs would suffer the greatest predation rate, while gynochrome (or most common) morphs would suffer the greatest mortality rate due to male harassment (cf. Cordero & Andrés, 1996).

The survival probability of the mature (fully coloured) andro- and gyno-chrome *Ceragrion tenellum* females was similar, suggesting that in the studied population survival probability is, at best, related weakly to female colouration. Unfortunately, neither the weight of different mortality factors (e.g. predation, male harassment) nor the fitness components affected by male harassment are known in this species. Thus, it was not possible to test the different alternative hypotheses predicting this result (see above). Colouration did not have a significant effect on the recapture probability of sexually mature females, suggesting that the number of visits to the breeding area and the rate of migration of mature females are

not colour dependent. In contrast, androchrome females marked as tenerals were recaptured more often as mature adults than were gynochromes. This could be explained by greater mortality or emigration of gynochromes during the pre-reproductive period. This result is not predicted by any of the above hypotheses. Given that there were almost no differences in survival or recapture probabilities during the reproductive period, then, if other selective agents are absent, androchrome frequency should increase until fixation of this morph; however morph frequency remained constant for 3 years in the studied population (Andrés & Cordero, 1999). The probability of recapture of mature males was slightly greater than that of females. This effect has been reported for two other damselflies (Anholt, 1997; Cordero & Andrés, 1999) and could be explained because observations were restricted to the pond and sexes might differ in the use of this space (R. Stoks, pers. comm.). Thus, mature males are usually found at the breeding site almost every day while females (perhaps to avoid male disturbance) only appear at the water when they have matured a clutch of eggs. It is also possible that, even if females are present, males choose more prominent perches and are therefore recaptured more easily (Anholt, 1997). During the pre-reproductive period, males suffered greater mortality or emigration. This difference is more likely to arise from different mortality rates in males and females during this period. *Ceragrion tenellum* males maintained in the laboratory showed greater mortality during the pre-reproductive period (J. A. Andrés, unpublished), and the same result has been found in four other zygopterans (Cordero, 1994). In contrast, mature males survived slightly better than females.

In conclusion, during the reproductive period, males survived only slightly better than females and there were no differences in the survival probability among female morphs, but during sexual maturation males and gynochrome females had the greatest mortality (and/or emigration) rate. These results are not predicted by the null hypothesis (Fincke, 1994) or by previously proposed adaptive hypotheses (Johnson, 1975; Robertson, 1985; Hinneking, 1987; Fincke, 1994; Grether & Grey, 1996). For a better understanding of the adaptive significance, if any, of colour polymorphism in odonates, new studies are needed to test for differences between female morphs in, first, survival and migration rates during the pre-reproductive period, second, the effect of male harassment and predation on the survival probability, and, third, the effect of male harassment on fecundity and fertility.

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