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Mating frequency, population density and female polychromatism in the damselfly *Ischnura graellsii*: an analysis of four natural populations

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Abstract. The maintenance of female polychromatism in the damselfly *Ischnura graellsii* is addressed by reanalysing data from two natural populations studied by Cordero (1992, *J. Anim. Ecol.,* 61:769-780) and two additional populations. We used mark-resighting methods to estimate mating frequency by female morphs. Results indicate that female mating probability is positively related to male density in three populations, but androchrome (male-like females) only mated less often than gynochromes in one sample. Female morphs did not differ in size and oviposition frequency. Nevertheless, among populations, androchrome frequency was positively related to an index of male density. We suggest that population density might have an effect on the maintenance of female morphs in *I. graellsii*, but this does not seem to be because androchrome females avoid matings. A more accurate analysis of the benefits and costs of mating in polychromatic damselflies is needed.
Key words: Odonata, damselfly, female-limited polychromatism, density-dependence.

Resumen. Estudiamos el mantenimiento del policromatismo femenino en la libélula *Ischnura graellsii* mediante el reanálisis de los datos de dos poblaciones naturales estudiadas por Cordero (1992, J. *Anim. Ecol.,* 61:769-780) y dos poblaciones adicionales. Usamos métodos de marcaje-reobservación para estimar la frecuencia de apareamientos de las formas femeninas. Los resultados indican que la probabilidad de cópula de las hembras está positivamente relacionada con la densidad de machos en tres poblaciones, pero las hembras androcromas (coloreadas como los machos) sólo se aparearon menos frecuentemente que las ginocromas en una muestra. Las formas femeninas no se diferenciaron en tamaño ni frecuencia de oviposición. Sin embargo, al comparar entre poblaciones, la frecuencia de androcromas resultó positivamente correlacionada con un índice de densidad de machos. Sugerimos que la densidad de población podría ser importante en el mantenimiento de las formas femeninas de *I. graellsii*, pero esto no parece ser debido a que las hembras androcromas eviten apareamientos. Se requiere un análisis más detallado de los beneficios y costes del apareamiento en las libélulas policromáticas.

Introduction

Female colour polymorphism is a widespread characteristic among odonates, specially in Zygoptera, where 54% of European genera have at least one polychromatic species (Cordero & Andrés, 1996). In all cases one of the female morphs has a similar coloration to the con-specific male, which is conspicuous, and the remaining one to three morphs are more cryptic-ally coloured. We will use androchomes for male-like females and gynochromes for "typical" females (Hilton, 1987; Cordero et al., 1998).

The inheritance of female polychromatism has been studied in *Ischnura damula, I. demorsa, I. graellsii* and *Ceriagrion tenellum.* In all cases there is an autosomal locus with sex-limited expression, and two or three alleles, one per phenotype (Johnson, 1964, 1966; Cordero, 1990b; Andrés & Cordero, in press). In *I. graellsii* there are three female morphs: androchromes patterned and coloured like males, *infuscans* patterned but not coloured like males and *aurantiaca* neither patterned nor coloured like males (see the cover of this volume). Female morphs also show age-related colour changes. In *I. graellsii* morphs are controlled by three alleles with a hierarchical dominance, androchrome> *infuscans*> *aurantiaca*. Males of this species are non-territorial, remaining near ponds where mating takes place (Cordero, 1989).

There are three main adaptive hypotheses to explain the maintenance of female poly-morphism in odonates. Johnson (1975) suggested that in *I. damula* and *I. demorsa* androchrome females have greater reproductive isolation when similar species coexist, while gynochromes frequently mate with hetero-specific males, resulting in reduced reproductive success. The androchrome advantage would be balanced by greater predation on this conspicuous morph that would reduce its longevity. The second hypothesis suggests that androchromes are male-mimics, and for this reason they are not recognized by mate-searching males and therefore, after first mating, they can avoid additional unnecessary matings, dedicating this time to feeding and egg maturation. Greater predation on androchormes is also suggested as the balancing mechanism (Robertson, 1985). The third hypothesis suggests that female polymorphism is an adaptation to population density. Androchromes would be favoured at high population density, because its male-like appearence would result in reduced male disturbance, but at low population density they have the risk of never mating (Hinnekint, 1987a). The existence of multiannual cycles in population density is suggested as the maintenance mechanism (Hinnekint & Dumont, 1989). For a review of this topic in odonates see Cordero & Andrés (1996).

The density-dependent hypothesis has been supported by previous field work with *I. graellsii* (Cordero, 1992), *I. denticollis* (Córdoba Aguilar, 1992), *Nehalennia irene* (Forbes et al., 1995) and *I. elegans* (Cordero et al., 1998). Nevertheless, in many other studies no differences between female morphs have been detected (Conrad & Pritchard, 1989; Thompson, 1989; Fincke, 1994a, 1997; Andrés, 1998).

In *I. graellsii* results are controversial because although Cordero found that androchrome females were rarer (Cordero, 1990b) and a greater fraction compared to gynochromes remained unmated at low density (Cordero, 1992), the critical test was miscalculated and differences between morphs were only marginally significant (see also Fincke, 1994b). For this reason we decided to test the maintenance of female morphs in two additional natural populations. Furthermore, we reanalysed the data presented in Cordero (1992) because in that paper only a subset of the marked females were used. This paper therefore compares mating frequency and its relation to population density in four populations of *I. graellsii* (Odonata, Coenagrionidae).

Methods

Populations were studied using marking-resighting methods. Adult damselflies were netted either singly or in small groups, measured, identified to sex and female morph, aged by thoracic colour (Cordero, 1987) and marked by writing a number on their wing. They were released in the place of capture and followed afterwards. We recorded the identity of all mating pairs seen during the field work, trying to cover all the area where the damselflies were concentrated at least once every 30-40 min. Marking was made mainly during the morning, because mating activity is maximum in the afternoon (Cordero, 1992).

Populations studied by Cordero were previously described (Cordero, 1992, 1995). The first population was studied in 1987 at a coastal marsh with tidal influence (Lourizán). The second population inhabited an artificial pond and was studied in 1990 (O Rosal). In 1995 we marked damselflies at a man-made pond at the Campus of the University of Vigo. This pond is about 18 x 90 m, situated in a garden area, with some shrubs. We searched a wider area, but damselflies were only found in the immediate vicinity of the pond, where marking was concentrated. *I. graellsii* was the dominant damselfly at the pond, but its numbers were low probably due to the presence of a high number of fish in the pond. In 1996 we studied damselflies at a coastal lagoon in the beach of Barra (Cangas, Pontevedra). This small water body (300 m^2) is formed during summer at the end of a seasonal stream. We marked damselflies in a grass area about 2600 m^2. In nearby dune vegetation we were unable to find damselflies. At this place *I. graellsii* was also the dominant damselfly, but a small population of *Ischnura pumilio* was also found (Cordero & Andrés, in press). All populations are in NW Spain. Table 1 summarizes the period of study, sampling effort and number of animals marked and resighted at each population.

Table 1. Characteristics of the studied populations.

	Lourizán marsh UTM: 29TNG2797	**O Rosal pond** UTM: 29TNG1743	**Campus pond** UTM: 29TNG2568	**Barra lagoon** UTM: 29TNG1279
Study period	36 days	28 days	29 days	31 days
	15 Aug-20 Sep 1987	11 Aug-8 Sep 1990	11 Jul-12 Aug 1995	14 Aug-17 Sep 1996
Hours of observation	155 (6.3±1.2 h/day)	286 (9.8±0.2 h/day)	234 (8.1±0.5 h/day)	161 (5.2±0.4 h/day)
Marked animals				
males (% on total)	979 (59.5)	1070 (50.4)	464 (51.3)	863 (53.0)
androchromes (% on females)	92 (13.8)	110 (10.0)	22 (5.0)	110 (14.4)
infuscans (% on females)	509 (76.5)	855 (77.9)	345 (78.4)	583 (76.1)
aurantiaca (% on females)	71 (10.7)	132 (12.0)	73 (16.6)	73 (9.5)
Resighted animals (% on marked)				
males	526 (53.7)	665 (62.1)	254 (54.7)	599 (69.4)
androchromes	51 (55.4)	56 (50.9)	15 (68.2)	74 (67.3)
infuscans	245 (48.1)	394 (46.1)	216 (62.6)	397 (68.1)
aurantiaca	32 (45.1)	59 (44.7)	53 (72.6)	55 (75.3)

Table 2. A reanalysis of Cordero's (1992) data. Reproductive success of the three female phenotypes of *I. graellsii* at high (Lourizán) and low (O Rosal) density (mean±SE(n)). P after c^2 or Kruskal-Wallis test.

Variable and population	androchromes	infuscans	aurantiaca	P
% of unmated females				
Lourizán	32.1 (17/53)	41.6 (114/274)	47.4 (18/38)	0.298
O Rosal	77.7 (14/18)	38.0 (49/129)	56.3 (18/32)	0.003
Matings per individual				
Lourizán	1.019±0.136 (53)	0.927±0.067 (274)	0.895±0.188 (38)	0.457
O Rosal	0.278±0.135 (18)	0.698±0.055 (129)	0.500±0.110 (32)	0.006
% failed reproduction[a]				
O Rosal	33.3 (6/18)	14.0 (18/129)	21.9 (7/32)	0.095

[a] Females never seen to mate or to oviposit.

Table 3. Lifespan and mating frequency in male and female *I. graellsii*. Unrecaptured individuals have been included with lifespan=1. P indicates the probability from a Kruskal-Wallis or χ^2 test comparing female morphs.

Variable and population	males	androchromes	infuscans	aurantiaca	P
Lifespan					
Lourizán	3.84±0.13 (979)	4.89±0.53 (92)	3.41±0.16 (506)	3.01±0.38 (70)	0.049
O Rosal	4.73±0.15 (1086)	3.68±0.41 (110)	3.42±0.14 (855)	3.40±0.34 (132)	0.737
Campus	5.58±0.284 (464)	7.73±1.666 (22)	7.07±0.383 (345)	7.82±0.805 (73)	0.401
Barra	6.77±0.22 (863)	8.15±0.72 (110)	7.27±0.28 (583)	7.99±0.83 (73)	0.521
Matings/individual					
Lourizán	0.36±0.02 (979)	0.68±0.10 (92)	0.57±0.04 (506)	0.54±0.12 (70)	0.179
O Rosal	0.38±0.02 (1086)	0.32±0.06 (110)	0.41±0.02 (855)	0.31±0.05 (132)	0.065
Campus	0.57±0.04 (464)	1.18±0.21 (22)	0.99±0.06 (345)	0.99±0.13 (73)	0.518
Barra	0.91±0.05 (863)	1.08± 0.15 (110)	1.04±0.06 (583)	0.99±0.13 (73)	0.743
Individuals never mating (%)					
Lourizán	719/979 (73.4)	49/92 (53.2)	319/506 (63.0)	47/70 (67.1)	0.135
O Rosal	734/1086 (67.6)	81/110 (73.6)	558/855 (63.1)	97/132 (73.5)	0.053
Campus	287/464 (61.9)	6/22 (27.3)	134/345 (38.8)	28/73 (38.4)	0.556
Barra	475/863 (55.0)	59/110 (53.6)	292/583 (50.0)	32/73 (43.8)	0.429
Ovipositions/individual					
O Rosal	-	0.73±0.09 (110)	0.87±0.04 (855)	0.80±0.09 (132)	0.481
Campus	-	0.55±0.25 (22)	0.82±0.07 (345)	0.85±0.13 (73)	0.254
Barra	-	1.90±0.23 (110)	1.77±0.09 (583)	2.10±0.30 (73)	0.779
% Failed reproduction[a]					
O Rosal	-	36/110 (32.7)	213/855 (24.9)	39/132 (29.5)	0.141
Campus	-	6/22 (27.3)	92/345 (26.7)	17/73 (23.3)	0.830
Barra	-	37/110 (33.6)	158/583 (27.1)	15/73 (20.5)	0.142

[a] Females never seen to mate or to oviposit.

We followed two strategies to reanalyse Cordero's (1992) data. In a first analysis, we selected a group of females whose mature lifespan was included into the sampling period, because some females were already mature when sampling started. Age at marking was estimated from thoracic coloration (Cordero, 1987) and date of emergence as date of marking minus age at marking. All females that emerged more than 6 days before the start of the sampling period were excluded (as in Cordero, 1995). This reduces sample size to 516 females at Lourizán and 217 at O Rosal. To analyse mating frequency we concentrated on the subset of females that reached sexual maturation (i.e. lived at least 6 days from emergence): 365 females at Lourizán and 179 at O Rosal. The present subset of females is slightly greater than that analysed in Cordero (1992), because in that study Cordero excluded females never resighted (now included), and females that emerged more than 5 days before the first sampling date (now we exclude all females that emerged more than 6 days before the first sampling, because the maturation period is about 5-6 days, Cordero, 1987). The reason for this procedure is to increase sample size for statistical comparations between morphs. This first analysis allows a comparison with Cordero (1992).

In a second analysis we included all females marked during the period of study. This analysis was made for all populations and is therefore the way to compare all four populations. All tests are two-tailed and were made with SPSS, BIOMstat and xlStat. Population estimates were obtained from recapture histories of marked animals using Popan (Arnason et al., 1998).

Results

Reanalysis of Cordero's (1992) data

Cordero (1992) presented data on mating frequency for females whose mature lifespan was included into the sampling period, and were recaptured at least once, and concluded that the proportion of unmated females at the low density population (O Rosal) was significantly different between phenotypes. This conclusion has been questioned by Fincke (1994b) because Cordero miscalculated the critical statistical test. The value of the c^2 test for that comparison and sample size is 4.78 and the probability level 0.091, rather than 0.034 as was reported (Table 7 in Cordero, 1992). In our reanalysis, including unrecaptured females and females that emerged on day 6 before the first sampling date, the differences between phenotypes in the number of matings per lifetime and the proportion of unmated females are highly significant at O Rosal population, but again not significant at Lourizán (Table 2). The difference between phenotypes at O Rosal is still significant if lifespan is entered as a covariate (ANCOVA, main effects, F=4.824, p=0.009; covariate, F=1.247, p=0.266), indicating that the mating failure of androchromes was not due to a shorter lifespan.

Nevertheless, given the possibility that some matings were unnoticed (Cordero, 1995), a better test of the density-dependent hypothesis is to compare reproductive success among phenotypes. At O Rosal, about 40% of females that were never seen to mate oviposited, indicating that some matings were not observed. The proportion of females that oviposited without having been observed in copula was similar in all morphs (χ^2=3.420, p=0.181). There were no significant differences between phenotypes in the proportion of females that were never seen to reproduce (copulate or oviposit) at O Rosal population (Table 2).

A comparison of four natural populations

Table 3 presents the average lifespan, mean number of matings and percentage of males and females never seen in copula for the complete sample at all the studied populations. At Lourizán we detected a significant difference between female morphs in lifespan, with androchromes living longer. This difference is still significant if date of marking is entered as a covariate in an ANCOVA (p=0.005). Nevertheless, daily survival rate was not significantly different between morphs (Cordero, 1992).

For the complete sample, mating frequency and proportion of females never seen in copula were not significantly different between morphs at the O Rosal population (Table 3). Note that in this sample the proportion of *aurantiaca* females that were never seen in copula was as high as in androchromes (74%). Mating frequency in the new populations was not significantly different between morphs. At the Campus population

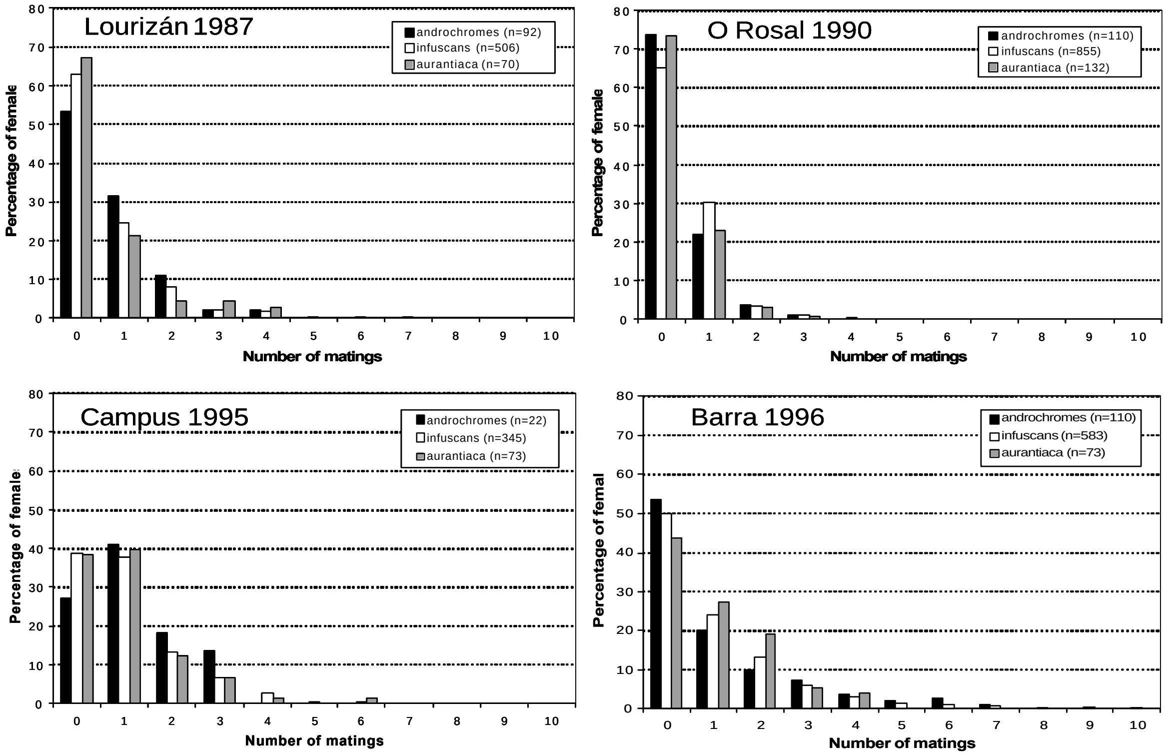

Figure 1. The frequency distribution of matings by female morphs in four natural populations of *I. graellsii*. In all cases mating frequency was similar between morphs.

Table 4. Body size comparisons (body length in mm) between morphs at Campus and Barra populations. P after ANOVA comparing female morphs.

Population	male	androchromes	*infuscans*	*aurantiaca*	P
Campus	25.84±0.06 (386)	26.72±0.34 (16)	26.59±0.08 (258)	26.49±0.22 (61)	0.820
Barra	27.20±0.04 (818)	27.86±0.12 (107)	27.87±0.05 (552)	27.69±0.14 (68)	0.520

we observed a total of 425 matings by 275 females. The observed frequencies for females in copula (16 androchromes, 214 *infuscans* and 45 *aurantiaca*) are not significantly different (p=0.827) from thoose expected from their population frequencies (Table 1). Similar results were obtained at Barra, where we observed 798 matings by 383 females (51:291:41), and again there were no significant differences with the population frequencies (p=0.629).

Figure 1 shows the distribution of matings by female morph for all populations. Note that at Barra one androchrome was observed seven times in copula. It is clear that female mating rate was different between populations, but androchrome females did not mate less frequently than gynochromes. The same results were obtained analysing females by groups of age (teneral, young or mature; as in Cordero et al., 1998). Note that the percentage of unmated females was lowest at the Campus population, where density was also the lowest. This result is at variance with the density-dependent hypothesis.

Table 3 shows the number of days of oviposition by female morph in three populations. In all cases no significant difference was found, suggesting that the reproductive success by morph was similar. This table also shows the percentage of females never seen in copula or oviposition, a value not significantly different between morphs.

Androchrome females were larger at Lourizán population but not at O Rosal (Cordero, 1992). We found no significant differences in the other populations (Table 4).

The relationship between male density and female mating frequency

Hinnekint's (1987) density dependent hypothesis predicts that more androchrome than gynochrome females will remain unmated at low male density, because female mating probability depends on the number of mate-searching males and androchromes are less attractive to males. To test this prediction, we analyzed the data on a daily basis to look for a positive relationship between female mating rate and male density (estimated from the method of Jolly-Seber). Figure 2 shows the relationship between both variables at the studied populations. The slope of the relationship was significantly positive in 3 populations (Lourizán, p=0.003; O Rosal, p=0.018; Barra, p=0.001). At the Campus population, female mating probability was higher and not related to male density (p=0.172).

The *infuscans* morph was always the commonest female morph in all the studied populations of *I. graellsii* (see also Cordero, 1990b). Figure 3 presents the relationship between male density (estimated as the number of males marked per hour) and morph frequency for the four studied populations. We tested the relationship between both variables using isotonic regression, a method that allows to relax the assumptions of linear regression and test simply for the presence of a consistent increase in the dependent variable, as a function of the rank order of the values of the independent variable (Sokal & Rohlf, 1995). This analysis suggests that the frequency of androchromes increases with male density, although the relationship is only marginally significant ($p_{one\text{-}tail}=0.052$). The frequency of *aurantiaca* and *infuscans* females is not related to male density (p=1 in both cases).

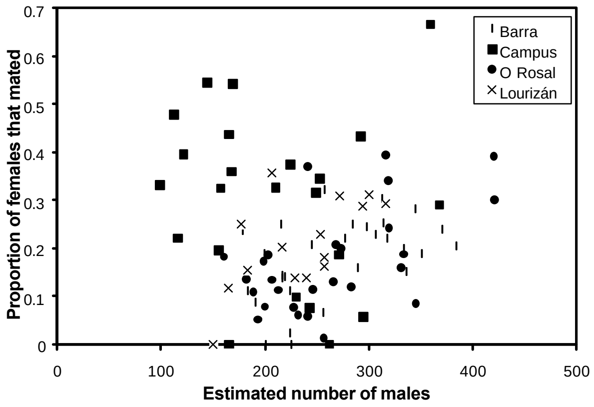

Figure 2. The relationship between female mating probability and male density (estimated from the Jolly-Seber method). The slope is significantly possitive at Barra, O Rosal and Lourizán.

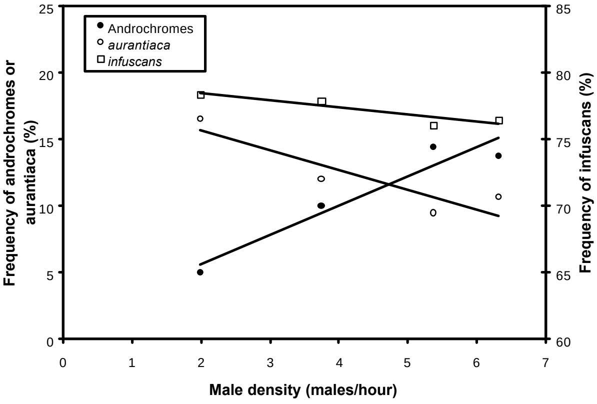

Figure 3. The relationship between male density and morph frequency for the four studied populations.

Discussion

The maintenance of several female colour morphs in odonates has been explained by means of three main adaptive hypotheses (Johnson, 1975; Robertson, 1985; Hinnekint, 1987). The hypotheses of Robertson (1985) and Hinnekint (1987) are based on the resemblance of the androchrome female to the conspecific male, resulting in a lower mating success of these females. When the population is of low density, androchrome females could remain unmated, as Cordero (1992) concluded for the O Rosal population (but see Fincke, 1994a, 1994b). The present reanalysis of Cordero's populations and the new data sets indicate that androchrome females mated significantly less often than gynochrome females only for the partial data set at O Rosal population (Table 2). Female mating probability was positively correlated with the density of males, but this relationship is true for all female morphs, and not only for androchromes as the density-dependent hypothesis predicts. Our results also suggest that androchrome frequency is positively related to male density (Fig. 3). This finding should be corroborated with a study of a greater number of populations. On the other hand, at the lowest male density (Campus) only a minority of females were never seen to mate (Fig. 1), exactly the opposite as predicted by the density-dependent hypothesis. The results obtained at this population are very different to the remaining populations. This population was small, but during the period of study, individuals were highly concentrated on the shoreline, due to the absence of tall grasses on which to perch. This was due to the gardening of the area. Therefore, the probability of contact between sexes was very high, and this might explain why most females were observed in copula. A low density population was converted to a high density situation by the absence of perches.

Androchromes did not mate less often than gynochromes in most populations. If matings are costly, as the mimicry hypothesis assumes (Robertson, 1985), then androchromes should avoid matings specially at high density, when copulation duration is longer (Cordero, 1990a). One reasonable cost of mating may be increased predation risk (Daly, 1978), but this seems very rare in damselflies. The fact that one androchrome mated seven times (Fig. 1) suggests that mating is not costly and therefore this is not the benefit that androchromes have at high population density. We think that this is because even if copulation duration may last for 5-6 h, most matings do not last so long. The average copulation duration of this species at Barra was 1-2 h (pers. obs.). The alternative possibility is that male disturbance to females is costly, as Hinnekint (1987) suggested, but this assumption has never been tested. One possibility is that male disturbance diminishes female feeding efficiency, or forces females to move to areas with poor prey availability. If females are food-limited, their fecundity might be reduced (Richardson & Baker, 1997). Females escaping from mate-searching males fly erratically and this could increase the probability of falling in a spider web. Male disturbance has been also suggested as an important factor in the maintenance of female polychromatism in the swallowtail butterfly *Papilio dardanus* (Cook et al., 1994). We conclude that population density may have an effect on the maintenance of androchrome coloration in *I. graellsii* (Fig. 3), but this is probably not due to androchrome avoidance of unneccessary matings. Nevertheless, the density-dependent hypothesis seems able to explain the maintenance of female morphs in *I. elegans* whose androchromes mate less often (Cordero et al., 1998), and are sometimes the dominant morph (Hinnekint, 1987a).

The number of ovipositions by morph was not significantly different in any population of *I. graellsii*, as was also found in *I. elegans* (Cordero et al., 1998). This result agrees with an adaptive hypothesis for the maintenance of the female polymorphism of coloration when the different morphs are in a state of evolutionary equilibrium, but it is also predicted by a non-adaptive hypothesis in the absence of migration, mutation or genetic drift (Fincke, 1994a). Taking into account that the non-adaptive hypothesis does not predict differences between phenotypes in mating success, neither any kind of relationship between female (mating) frequency and the density of males, our results suggest that the maintenance of female polymorphism could be explained by an adaptive hypothesis. Nevertheless none of the available adaptive hypotheses agrees with all results. Future work should concentrate on the measurement of male harassment to female morphs, the study of the benefits and costs of multiple matings to females and the behaviour and spatial distribution of female morphs in nature.

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