

COMMENT

On the difficulty of detecting density-dependent selection on polymorphic females of the damselfly *Ischnura graellsii*: failure to reject the null

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Female colour polymorphism is a prevalent, but perplexing characteristic of many species of coenagrionid damselflies. The colour of the thorax and abdomen of an 'andromorphic' female is similar to that of the male, whereas the colour of a 'heteromorphic' female differs from that of the male. Robertson (1985) proposed that andromorphs were 'male mimics' and, thus, more likely than heteromorphs to be ignored by males as potential mates. He suggested that the benefit of avoiding time-consuming supernumerary matings balanced the cost of relatively greater predation on the purportedly more conspicuous andromorphs.

Hinnekin (1987) later used 'male mimicry' as the mechanism underlying his density-dependent selection model. Hinnekin's hypothesis stated that at high male density, andromorphs were better able to avoid unnecessary matings, but at low male density, they incurred a greater risk of not mating at all. Both Robertson (1985) and Hinnekin (1987) predict that at any male density, andromorphs mate less frequently than heteromorphs. To test that prediction, Cordero (1992) quantified lifetime mating frequency and survivorship of three colour morphs of the damselfly *Ischnura graellsii* in two populations in Spain. Within both populations, neither the mean number of matings per female nor their mean life-span differed among the andromorphic (A) females and the two types of heteromorphic (I and O) females.

Nevertheless, Cordero (1992) concluded that his data supported Hinnekin's (1987) density-dependent hypothesis. Although Cordero did not quantify population density, in the population he designated as 'low density', he found that andromorphs were less likely than heteromorphs to be seen to mate at least once. In the 'high-density' population, Cordero found no difference in mating failure among morphs. But Cordero's data failed to reject the null hypothesis that female coloration makes no difference to a female's fitness. In what follows, I show that the null hypothesis appears to be the best.

All females in Cordero's study mated less frequently at the low-density site than they did at the high-density site. However, that cannot explain the maintenance of the colour polymorphism because, within either site, mating frequency did not differ between morph types.

Cordero's argument hung on his conclusion that fewer andromorphs than 'I' heteromorphs mated in the low-density population. But Cordero miscalculated the critical statistic ($\chi^2 = 6.76$; Cordero, 1992, Table 7). The correct χ^2 value is 4.78, indicating that andromorphs were no more likely to fail to mate than heteromorphs ($p > 0.05$). Moreover, in the low-density population, andromorphs and 'O' heteromorphs mated with virtually equal success ($\chi^2 = 0.38$, $df = 1$, $p > 0.5$). Thus, contrary to Hinnekin's hypothesis, andromorphs did not pay a mating cost for resembling males.

Cordero (personal communication) also analysed his larger data set of all marked females. He used the same type of χ^2 analysis as for females for which he had lifetime data. Again, he found

that fewer andromorphs than heteromorphs were seen to mate in the low-density population, a difference significant at $p = 0.05$. Encouraging though that may be, I should like to have corroborating evidence. For example, among equal-aged females carrying mature eggs, do relatively more heteromorphs carry sperm? If not, then the greater mating failure by andromorphs in this larger sample might be explained by morph differences in life-span, age or the number of days females were observed.

The mating frequency of females was random with respect to colour morph, so any differential mating failure of *I. graellsii* andromorphs in the low-density population is unlikely to have resulted from male discrimination among morphs as mates. I calculated the total number of observed matings accounted for by andromorphs and heteromorphs (I and O females pooled) from Cordero's (1992, Table 7) data. I multiplied the mean number of matings per female for each morph by the sample size. Thus, in the low-density population, andromorphic females represented 11% of the 155 females for which Cordero had lifetime data and 7% (8/111) of the total matings ($\chi^2 = 1.6$, $df = 1$, $p > 0.1$). In the high-density population, andromorphs represented 16.7% of the total 203 females and accounted for 16.2% of the 277 matings observed ($\chi^2 = 0.05$, $df = 1$, $p > 0.5$). Similarly, analysis of the larger data set revealed both morphs mated randomly. At the low-density site, andromorphs represented 10% of the total 1097 females marked and accounted for 8.3% of the 420 matings observed ($\chi^2 = 1.33$, $df = 1$, $p > 0.1$). At the high-density site, 92 of the 668 females (13.8%) were andromorphs, accounting for 16.0% of the 387 matings observed ($\chi^2 = 1.65$, $df = 1$, $p > 0.1$; data from Cordero (personal communication).

Given the lack of any fitness cost to andromorphs, we must not be surprised that Cordero found no selective benefit to andromorphic *I. graellsii* in either population. Cordero suggested that the relatively longer intermating interval of andromorphs in the high-density population was advantageous. However, he did not get this result from the same sample of females in which he measured mating frequency and survivorship. A Mann-Whitney *U*-test performed on the latter sample revealed no morph differences in intermating intervals $U = -1.5$, $p = 0.13$; Cordero (personal communication). In addition, contrary to the density-dependent hypothesis, andromorphs in the low-density population did not mate at longer intervals than heteromorphs.

In its failure to reject the null hypothesis that colour polymorphisms of female damselflies are selectively neutral traits, Cordero's (1992) study on *I. graellsii* corroborates results from the only other studies in which lifetime fitness correlates of female colour morphs have been measured (Thompson 1989; Fincke, in press).

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