

Conspicuous body coloration and predation risk in damselflies : are andromorphs easier to detect than gynomorphs ?

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ABSTRACT. The coexistence of multiple female colour morphs in damselflies remains poorly understood. Typically, one of the female morphs is coloured like the male (andromorph), while the other morphs are not (gynomorphs). Andromorphs, by resembling males, are thought to benefit from avoiding male harassment. Some authors have proposed that this benefit is offset by a higher probability of detection for andromorphs compared to gynomorphs owing to differences in body colouration. We experimentally tested detectabilities of the different female colour morphs using human observers as model predators. In contrast to expectation, detection probabilities for andromorphs and gynomorphs were equal. We discuss the use of survival probabilities to test for differences in predation rate between female morphs and consider whether human predators are representative models for the natural predator guild of the studied damselfly.

KEY WORDS : colour polymorphism, predation, detection, Odonata.

INTRODUCTION

Despite many studies, the evolution and maintenance of female-limited colour polymorphism in damselflies remains puzzling (e.g. FINCKE, 1994; CORDERO et al., 1998; ANDRÉS et al., 2000; SHERRATT, 2001; ANDRÉS & CORDERO, 2001). Typically, one of the female morphs (andromorph) is coloured, and in some species also patterned like the male, while the additional morphs (gynomorphs) are not (e.g. CORBET, 1999). Andromorphs, by resembling males, are thought to have a selective advantage through avoiding male harassment (e.g. JOHNSON, 1975; ROBERTSON, 1985; CORDERO et al., 1998; SHERRATT, 2001). Some researchers proposed that this benefit might be offset by a higher probability of detection and predation by visual predators of the conspicuously coloured andromorphs compared to the cryptic gynomorphs (JOHNSON, 1975; ROBERTSON, 1985).

To the best of our knowledge, no study has examined directly whether female morphs differ in probability of detection as a result of differences in body colouration. FORBES (1994) did not find any differential predation by dragonflies on copulating females of the damselfly, *Enallagma boreale* (Selys, 1875). However, in his experiment either the copulating male or the female was alive, wherefore it cannot be excluded that the probability of detection was influenced by the behaviour of the animals under study. Further, because only predation on mating pairs was recorded, it remains inconclusive whether female morphs on their own differ in susceptibility.

Several researchers have studied the potential cost of predation by comparing survival between morphs in the

field (e.g. FORSMAN & APPELQVIST, 1999 for an example on colour polymorphic grasshoppers). Results from field studies using traditional capture-mark-recapture models (SEBER, 1982) showed equal life spans for andro- and gynomorphs (e.g. THOMPSON, 1989; FINCKE, 1994; CORDERO et al., 1998). Recent studies using advanced capture-mark-recapture models (LEBRETON et al., 1992), allowing separate estimation of survival and recapture rates, also did not reveal morph-specific differences in survival (VAN GOSSUM, unpubl.; ANDRÉS & CORDERO, 2001). However, survival probabilities are not predictive if it comes to examining morph differences in probability of detection or predation and, therefore, should not be used to test the hypothesis by JOHNSON (1975) and ROBERTSON (1985) (see Discussion and Fig. 1).

In the present study, we experimentally test the hypothesis that body colouration makes andromorphs easier to detect than gynomorphs in the damselfly, *Ischnura elegans* (Vander Linden, 1820). We further discuss the use of survival rates to assess differences in predation and detection probabilities between female colour morphs.

MATERIAL AND METHODS

The common damselfly *I. elegans* exhibits three mature female morphs, one andromorph and two gynomorphs (PARR, 1965). Andromorphs resemble the males completely in body coloration and pattern. Differences between gynomorphs are restricted to the absence of black humeral stripes on the thorax in one morph, and slight differences in the coloration of the pale parts of the

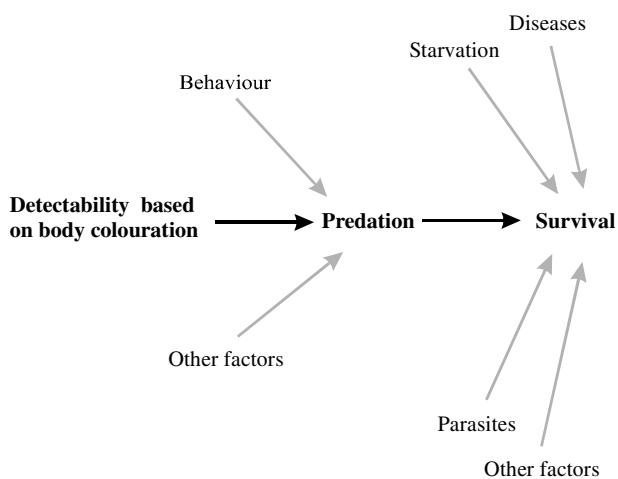


Fig. 1. – Factors that may induce survival differences between female colour morphs. The black arrows represent the hypothesised pathway following JOHNSON (1975) and ROBERTSON (1985) to explain a lower survival for the conspicuously coloured andromorphs compared to the more cryptic gynomorphs. The first step of the hypothesis was tested in the present article. The grey arrows indicate other, potentially confounding, factors that may contribute to selective predation and/or survival but that were not considered by JOHNSON (1975) and ROBERTSON (1985).

thorax. Gynomorphs were treated as one group in this study.

We performed experiments with twenty-two naïve human observers (model predators) and dead damselflies in “De Biotuin” (Belgium, Antwerp) on 2 July 1999 between 0900 and 1600h. Experimental damselflies were collected from a population in Niel (Belgium) (where both colour morphs are abundant) the day before the experiment. To exclude behavioural differences between morphs, damselflies were killed in a bowl with chloroform one hour before the experiment. This allowed the explicit testing of differences in probability of detection based on colour differences between female morphs. The experiment was conducted at a pond with a small resident natural population of the study species. Hence, we consider it reasonable to assume that the background applied in the experiment was relevant to examine differential detectability between female morphs. Human observers were asked to walk along thirteen stops each marked with a wooden stick while accompanied by one of the authors (HVG). The author always preceded the human observer to arrive before the observer at the next stick. A few times the author needed to chase away a foraging damselfly of the resident population, an action always done without notice by the human observer. The sticks guided the observers along the “predation” sites. At each stick, within a radius of 0.5m, one dead andro- and one dead gynomorph were glued onto stems or leaves (using a drop of instant glue on the legs and at the abdomen of the animals). Care was taken to position animals in a natural and random way. Therefore, we selected two comparable locations at a stick before randomly attaching the two morphs. Damselflies were glued on positions between 20–90cm height in the vegetation in an upright position.

A single human observer was asked to squat down at each stick and to screen the area for small insects without

touching the vegetation. Screening was confined within a 0.5m radius of the stick. Preliminary tests showed that when the radius was larger, search time increased considerably, and/or the human observers failed to find the animals. After detection of one damselfly or after a maximum search time of thirty seconds, the observer was asked to move on to the next stick and to repeat the search until all sticks were visited. Human observers only knew they had to search for dead insects and were not provided with any further information concerning species, colour patterns, number of animals hidden or aim of the study. Consequently, during the first encounter the human observer could be regarded as inexperienced with the presented prey species. In field conditions, however, predators are often experienced and search actively for a particular prey species (e.g. KREBS & DAVIES, 1997). Thus, repeating the search sessions using the same human observer over several sticks mimics to some extent the increasing experience of natural predators hunting for prey.

To test for differences in detectability between morphs we performed a repeated measure logistic regression with the detected morph (gynomorphs=0; andromorph=1) as dependent variable. Since subsequent observations of the same test person are not statistically independent, observer was added as repeated measure. Several covariance structures were modelled, but they all gave identical results. To account for differences in morph detectability among sticks, stick was added to the model as a random variable (GLIMMIX macro SAS 8.02; LITTELL et al., 1996). We tested 1) whether, in general, andromorphs are more conspicuous than gynomorphs, 2) whether this conspicuousness increases during the course of the experiment (stick number as fixed effect), and 3) whether morph-specific encounter experience influences detectability (cumulative morph-specific previous encounters as fixed effect). Correct degrees of freedom were obtained by the satterthwaite formula.

RESULTS

In the majority (75%) of the cases a damselfly was detected at a stick ($N=286$). Mean detectability over all encounters was equal for andromorphs and gynomorphs ($t=1.20$; $df=10.6$; $p=0.26$). The detectability of andromorphs did not change with increasing number of sticks visited ($F_{1, 9.55}=0.87$; $p=0.37$), neither did the detectability of andromorphs change with the number of previous encounters with that specific morph ($F_{1, 68}=0.60$; $p=0.44$).

DISCUSSION

This study is the first that experimentally tests and rejects the hypothesis that andromorph damselflies are easier to detect by a predator (human observer) due to their body colouration. Our observations support the hypothesis that survival is equal in the two female colour morphs, and this should be interpreted as evidence against selective detection.

However, detection in living damselflies can also be induced by other factors than colour alone (Fig. 1). Indeed, andro- and gynomorphs also differ in activity pat-

terns (e.g. VAN GOSSUM et al., 2001), mating avoidance tactics (e.g. ROBERTSON, 1985; VAN GOSSUM et al., 2001; SIROT et al., 2003) and habitat use (e.g. FORBES et al., 1995; VAN GOSSUM et al., 2001). Gynomorphs occupy less open habitat and often fly away when a male approaches, while andromorphs use more open habitat, do not fly large distances and directly face approaching males (VAN GOSSUM et al., 2001). Evidently, such differences may lead to differences between morphs in probability of detection and/or predation. REHFELDT (1995), for example, found that territorial damselflies were more likely to get trapped in spider webs than non-territorial ones. Therefore, the absence of differences in probability of detection may not be extrapolated to the field if other differences besides body colouration between female morphs are included.

Further, we have to question whether human predators can serve as a model for the natural predator guild (see also BENNETT et al., 1994; MAJERUS et al., 2000). Earlier studies, nevertheless, showed that the use of human observers to test ecological questions can render very interesting insights into poorly understood mechanisms (e.g. GÖTMARK & HOHFÄLT, 1995; VAN DAMME & VAN DOOREN, 1999; CUADRADO et al., 2001). Predation on adult damselflies is recorded for spiders, waterstriders, wasps, robberflies, dragonflies, frogs and birds (JOHNSON, 1975; PARR & PARR, 1972; REHFELDT, 1995; STOKS & DE BRUYN, 1996; CORBET, 1999). Although web spiders are commonly recorded as predators (LAROCHELLE, 1978; REHFELDT, 1995; CORDERO et al., 1998), they do not actively search for prey. Some spiders do actively search for prey (e.g. Thomisidae, Pisauridae, Salticidae) and are able to distinguish between different prey (e.g. JACKSON & LI, 1998). Frogs are very common but not selective, attacking any moving object (e.g. MICHIELS & DHONDT 1990). Among the remaining groups, at least dragonflies and birds are known to possess excellent vision and the ability to develop a search image (e.g. BOND & KAMIL, 2002; CORBET, 1999). Together, some groups of predators may be very similar to humans if it comes to detection of damselflies. Future experiments will be needed to shed more light on the possible impact of these predators.

Some researchers have used survival probabilities of morphs to study the potential cost of predation (e.g. CORDERO et al., 1998). Capture-mark-recapture models, however, only generate survival probabilities, but do not provide any information on the mechanisms shaping these probabilities. Therefore, we question whether survival probabilities are informative on the probability of detection? As for other insects in general, mortality in natural damselfly populations can be caused by many factors such as predation, interactions with conspecifics, dehydration, starvation, parasites and diseases (Fig. 1; CORBET, 1999). The absence of morph-specific differences in survival implies that andro- and gynomorphs suffer equally from the sum of all these mortality factors, although there may be significant differences in the respective contributions of these factors. In other words, equal (or unequal) survival probabilities among morphs do not necessarily give information on differences in mortality due to predation or on probability on detection (see also ANDRÉS & CORDERO, 2001). That other mechanisms besides predation are at work in shaping survival in

female damselflies is supported by an experiment with *I. elegans* where survival differences between female colour morphs were recorded, while cannibalism and predation were excluded (VAN GOSSUM, 2001). Therefore, we do not favour the use of survival probabilities for examining selective pressures such as predation.

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