



## Parental phenotype not predator cues influence egg warning coloration and defence levels<sup>☆</sup>

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In species that advertise their toxicity to predators through visual signals, there is considerable variation among individuals in both signal appearance and levels of defence. Parental effects, a type of nongenetic inheritance, may play a key role in creating and maintaining this within-species diversity in aposematic signals; however, a comprehensive test of this notion is lacking. Using the ladybird *Adalia bipunctata*, we assessed how egg coloration and defence level (concentration of the toxic alkaloid (-)-adaline) is influenced both by simulated predation risk in the egg-laying environment and by parental phenotype (coloration and toxin level). We found that egg toxin level and colour were predicted by parental phenotype but were not altered in response to cues of egg predators. Egg luminance (lightness) was positively correlated with paternal elytral luminance, while maternal toxin level positively predicted egg toxin level. In response to egg predator cues, ladybird mothers altered the timing of laying and total egg number, but not egg toxin level or colour. It appears therefore that in *A. bipunctata* variation between individuals of the same morph in the colour and toxin level of the eggs they lay, that is, egg aposematic phenotype, is more strongly influenced by individual variation in parental aposematic traits than by environmental cues of egg predation risk. Furthermore, these results provide the first indication that, in a warningly coloured species, male coloration may play a dual role as predator deterrent and indicator of paternal quality, influencing maternal investment in offspring.

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Prey can gain protection from predators through the association of a colourful warning signal with a toxic or distasteful defence (aposematism; Poulton, 1890). Individuals within a species may therefore benefit from sharing similar levels of defence and conspicuousness (Rowland, Hoogesteger, Ruxton, Speed, & Mappes, 2010). Despite this expectation, considerable variation in signal expression and associated toxin level is found among individuals of the same aposematic species (Merrill et al., 2015) and even within the same morph (e.g. Blount et al., 2012). Within morphs, individuals can vary in their conspicuousness and toxicity (Manuel Vidal-Cordero et al., 2012). A number of hypotheses have recently been proposed that help to explain the existence of such apparently

paradoxical variation, yet they focus almost exclusively on adult phenotypes (e.g. Summers, Speed, Blount, & Stuckert, 2015). Natural selection, however, acts at every stage of an organism's life cycle (Stearns, 1992), with both the strength and nature of selection pressures varying according to life stage (Moran, 1992). This is especially relevant for aposematic species, many of which have complex life cycles (Joron, 2003) where each discrete phase (i.e. egg, larva or adult) is likely to have different predators with very different sensory systems (e.g. Hemptinne, Magro, Saladin, & Dixon, 2012). Furthermore, not only is offspring phenotype key in determining which individuals survive to contribute to the adult population, but also many aspects of offspring phenotype carry over into adulthood (Burton & Metcalfe, 2014), including toxicity and warning coloration (Winters, Stevens, Mitchell, Blomberg, & Blount, 2014). It is clear therefore that a full understanding of warning signal variation requires consideration of how offspring aposematic phenotype is determined (Day & Bonduriansky, 2011; Marshall & Morgan, 2011).

<sup>☆</sup> Data can be accessed from <https://doi.org/10.24378/exe.163>.

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In addition to genetic inheritance, parental effects are a powerful determinant of offspring phenotype (Mousseau & Fox, 1998), influencing key offspring traits in a way that reflects parentally detected environmental variation (Fox, Thakar, & Mousseau, 1997; Rollinson & Hutchings, 2013) and/or parental phenotype (Bonduriansky & Head, 2007). A large number of aposematic species are egg-laying insects with no parental care (Joron, 2003) and egg provisioning is therefore the main conduit via which parental effects may occur (Newcombe, Moore, & Moore, 2015). Maternal egg investment in a number of nonaposematic species has been shown to vary in response to reliable cues of environmental change (so called 'anticipatory maternal effects' or AMEs; Marshall & Uller, 2007). This enables mothers to fine-tune their investment per reproductive event, maximizing the total number of surviving offspring (reproductive success) and thereby maternal fitness (Bernardo, 1996). Maternally controlled alteration of offspring toxin level in aposematic species is known to occur in response to environmental variation (Paul, Pell, & Blount, 2015). However, aposematism is the direct relationship between a conspicuous signal and an associated defence. To date, no evaluation of the effects of offspring predation risk on maternal investment in both offspring colour and defence has been carried out in any aposematic species.

Paternal quality can also influence maternal investment in eggs (Burley, 1986, 1988), and this so called 'differential allocation' (DA) can be positive or negative depending on the species (Ratikainen & Kokko, 2010). Females can increase their per egg investment when mating with attractive males to maximize the survival of the resulting 'good-quality' offspring (positive DA; D'Alba et al., 2010; Sheldon, 2000). Alternatively, they may increase per egg investment when mating with less attractive males to compensate for their partner's poor quality (negative DA; Badas et al., 2017; Bolund, Schielzeth, & Forstmeier, 2009). In some aposematic species, the conspicuousness of male warning coloration appears to act as a signal to females of the male's quality (Summers, Symula, Clough, & Cronin, 1999), and influences mate choice (Finkbeiner, Briscoe, & Reed, 2014; Maan & Cummings, 2008); whether it also influences maternal investment in offspring is unknown. Finally, maternal phenotype itself can dictate egg investment (Berkeley, Chapman, & Sogard, 2004; Donelson, McCormick, & Munday, 2008). For example, mothers often provision their eggs and larvae with chemical defences in proportion to their own defence levels, leading to a positive correlation between maternal and offspring defence levels (Hanifin & Brodie, 2003; Hutchinson, Savitzky, Mori, Meinwald, & Schroeder, 2008). Therefore, parental effects have the potential to create variation in aposematic phenotype, via maternal response to environmental and paternal cues, as well as maintaining it, perpetuating parental levels of conspicuousness and toxicity. Here we used the ladybird beetle *Adalia bipunctata* to investigate whether maternal investment, specifically changes in egg toxin level and egg coloration, varies with egg predation risk and both paternal and maternal aposematic phenotype. *Adalia bipunctata* is an ideal study species as it is aposematic at all stages of its complex life cycle (egg, larva, pupa and adult). We envisage three alternative pathways by which maternal investment in eggs may vary (Fig. 1).

(1) Influence of egg predator cues on egg phenotype via maternal investment (AMEs). *Adalia bipunctata* eggs are aposematic and laid in environments with high levels of predation from the larvae of ladybird competitors (intraguild predation; Polis, Myers, & Holt, 1989). Egg toxins deter heterospecific predators, but attract conspecific cannibals (Kajita, Obrycki, Sloggett, & Haynes, 2010) and females can alter egg-laying behaviour in response to chemical cues of offspring predators (Seagraves, 2009). However, whether they also alter egg toxin level and conspicuousness in response to

conspecific or native heterospecific predatory larvae is unknown; to date only changes in egg toxin level in response to invasive predators have been investigated (Paul et al., 2015). We predicted that (a) in the presence of conspecific larval tracks egg toxin level and conspicuousness would decrease in order to decrease the risk of egg cannibalism and (b) in the presence of heterospecific larval tracks egg toxin level and conspicuousness would increase, strengthening the egg aposematic signal.

(2) Influence of paternal phenotype on egg phenotype via maternal investment (DA). In common with many other aposematic species, male conspicuousness is known to influence female mate choice in *A. bipunctata* (Majerus, Odonald, & Weir, 1982); however, whether it also influences maternal investment in offspring is unknown. If positive differential allocation occurs then a positive correlation between paternal and egg conspicuousness and/or toxin level would be expected, whereas if negative differential allocation occurs the reverse of this scenario could reasonably be predicted.

(3) Influence of maternal phenotype on egg phenotype. In aposematic species, including another species of ladybird (*Coccinella septempunctata*), both maternal and offspring conspicuousness and toxin level are known to correlate positively (e.g. Stynowski, Torres-Mendoza, Sasa-Marin, & Saporito, 2014; Winters et al., 2014). We therefore predicted that in *A. bipunctata*, maternal and egg toxin level and conspicuousness would be positively correlated.

## METHODS

### *Culture and Experimental Set up*

Stock culture of *A. bipunctata* (*typica*), obtained from Gardening Naturally (Love Lane Industrial Estate, Cirencester, U.K.), were maintained in culture on an ad libitum diet of pea aphids, *Acyrtosiphon pisum* (reared on dwarf bean, *Vicia faba*, Sutton variety) at 18 °C with a 16:8 h light:dark period. Experimental individuals were first-generation virgin adults of known age (mean = 21 days posteclosion) obtained from stock culture: 104 females and 104 males from 20 families. Females and males were weighed to the nearest 0.01 mg (analytical balance GR-200 A&D Gemini). Females were mated with a nonsibling male, and 24 h after pairing males were removed, photographed and stored at –80 °C prior to toxin analysis (see below for colour and toxin analysis method details). Females were then placed into a clean petri dish with ad libitum aphids (0.01 g, ca. 40 aphids; Hodek, van Emden, & Honek, 2012). After 24 h a cluster of eggs was randomly selected from those laid by the females and a subset of three eggs from the cluster were photographed and stored at –80 °C. Females were then placed into an individual experimental arena, in one of three treatments (control (NN), conspecific risk (CP) or heterospecific risk (HP)), with an ad libitum aphid supply. Females from different sibling clusters were distributed evenly between the treatment levels, so that family ID and mate ID were represented equally in all three treatments (NN:  $N = 41$ ; CP:  $N = 41$ ; HP:  $N = 22$ ). The simulated predation risk treatment levels were created using tracks of either fourth-instar *A. bipunctata* larvae (CP) or *C. septempunctata* larvae (HP). For each replicate, tracks were created using five larvae, which were placed, without food, into individual sterile petri dishes (9 cm diameter), each containing a semicircle of corrugated filter paper (9 cm diameter) and left for 24 h (Doubtina, Hemptinne, & Dixon, 1998; Magro, Tene, Bastin, Dixon, & Hemptinne, 2007). The control environment of no simulated predation risk (NN) consisted of a sterile petri dish (9 cm diameter) and a clean semicircle of corrugated filter paper that had not been in contact with any ladybird larvae. Each female was left in its experimental arena for 2 days (48 h), with additional aphids being added after 24 h. Laying behaviour was monitored at 1, 3, 6, 9 and 24 h intervals over the

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