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Behavioural differences across contexts may indicate morph-specific strategies in the lizard *Ctenophorus decresii*

Madeleine St Clair Yewers [a,*], Sarah Pryke [b], Devi Stuart-Fox [a]

[a] *School of BioSciences, The University of Melbourne, Australia*
[b] *Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, Australia*

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Discrete colour polymorphisms are often genetically correlated with other traits under natural and sexual selection, such as behaviour, life history and physiology. Elucidating such correlations is essential to understand the adoption of alternative strategies between morphs and the role they play in the maintenance of colour polymorphisms within a population. Using field experiments, we tested the hypothesis that four visually discrete morphs (orange, yellow, yellow with a central orange patch (orange-yellow) and grey) of the tawny dragon lizard, *Ctenophorus decresii*, display alternative behavioural strategies. Specifically, we compared the response of colour morphs to simulated conspecific territorial intruders and predators in the wild. Although the orange-yellow morph can be objectively classified, it may behaviourally resemble the orange or yellow morph; therefore we compared statistical models in which the orange-yellow morph was considered a separate morph (four-morph model) or grouped with either pure orange or pure yellow individuals (three-morph models). For aggression, a three-morph model with orange-yellow individuals grouped as yellow morphs best fitted the data. The orange morph showed consistently high aggression to all morphs, while the grey morph showed consistently low aggression. Aggression of the yellow morph was conditional on the morph of the intruder. In addition to being the least aggressive, the grey morph was the least bold. Although the orange morph was the most aggressive, it was only the boldest under a three-morph model, which was equally likely compared to a four-morph model. Overall our results support the view that tawny dragon lizard morphs adopt different behavioural strategies, the orange and grey morphs exhibiting more aggressive and cautious strategies, respectively, and the yellow morph changing its aggression depending on its competitor's colour.

Colour-polymorphic species are model biological systems to understand the generation and maintenance of intraspecific phenotypic and genetic diversity (Ford, 1945; Gross, 1991; Hugall & Stuart-Fox, 2012; Huxley, 1955; McKinnon & Pierotti, 2010; Paulson, 1973). Colour polymorphism, defined as the occurrence of two or more discrete, genetically determined colour morphs within age and sex classes within an interbreeding population (Huxley, 1955), is often correlated with differences in other traits such as behaviour, life history and physiology. Such differences between morphs constitute alternative strategies when they combine multiple traits, which affect fitness in combination and are under correlational selection (Miles, Sinervo, Hazard, Svensson, & Costa, 2007; Roulin, 2004; Sinervo & Svensson, 2002). Although many colour-polymorphic species display alternative strategies (Cox & Calsbeek, 2011; Lank, Smith, Hanotte, Burke, & Cooke, 1995; Vercken, Massot, Sinervo, & Clobert, 2007; reviewed in McKinnon & Pierotti, 2010) few studies have specifically examined behaviours in different contexts (e.g. foraging, mating, aggression, antipredator behaviour; but see Da Silva et al., 2013; Mafli, Wakamatsu, & Roulin, 2011; Williams, King, & Mettke-Hofmann, 2012). Such studies are essential to identify alternative strategies of morphs, which is the first step to understanding the evolutionary maintenance of the polymorphism.

Conspecific aggression and antipredator behaviours are frequently assessed in unison and in many species there is a positive correlation between aggression to conspecifics and boldness to predators (Bell & Sih, 2007; Dingemanse et al., 2007; Huntingford, 1976; Kortet & Hedrick, 2007). High individual aggression and

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* Correspondence: M. Yewers, School of BioSciences, University of Melbourne, Victoria 3010, Australia.
E-mail address: myewers@gmail.com (M. S. C. Yewers).

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boldness are commonly associated with dominance (Dahlbom, Lagman, Lundstedt-Enkel, Sundström, & Winberg, 2011; Ficken, Weise, & Popp, 1990; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004) and reproductive success (Ariyomo & Watt, 2012; Colléter & Brown, 2011; Reaney & Backwell, 2007). However, being more aggressive and bold is associated with costs. Bolder individuals may have a higher predation risk (Bremner-Harrison, Prodohl, & Elwood, 2004; Dugatkin, 1992; Smith & Blumstein, 2008). As such, bolder, more aggressive individuals may differ in their allocation of resources to current versus future reproductive success resulting in different life history strategies (Schuett, Tregenza, & Dall, 2010; Stearns, 1992; Wolf, van Doorn, Leimar, & Weissing, 2007). Despite the importance of aggression and boldness in response to predators for defining potential alternative strategies of colour morphs (Healey, Uller, & Olsson, 2007; Pryke, 2007), bold behaviours and differences between morphs in multiple behavioural traits are not often examined in colour-polymorphic systems (but see Calsbeek & Cox, 2012; Da Silva et al., 2013; Iii, 1992; Mafli et al., 2011; Mettke-Hofmann, 2012; Williams et al., 2012).

Although colour morphs often differ in aggressive behaviours to conspecifics (fish: Barlow, 1976; invertebrates: Brace, Pavey, & Quicke, 1979; birds: Pryke, 2006; reptiles: Thompson & Moore, 1991), the nature of these differences varies between species. In some colour-polymorphic species, morphs can differ in their levels of aggression regardless of the colour of their competitor. For example, the dominant red morph of the Gouldian finch, *Erythrura gouldiae*, is more aggressive than the black morph (Pryke, 2006); however, the red morph experiences increased stress and physiological costs when present in high frequencies within a population, thereby promoting a low and stable frequency of red morphs (Pryke, Astheimer, Buttemer, & Griffith, 2007). Alternatively, a particular colour morph can vary its aggressive response depending on the colour of the competitor. For example, male morphs that mimic female coloration and/or behaviour may be subjected to less aggression from other male morphs (Dominey, 1980; Sinervo & DeNardo, 1996). Under the above scenarios, colour morphs are indicative of alternative behavioural or reproductive strategies that are generally under balancing or frequency-dependent selection, thereby maintaining the polymorphism (Bleay, Comendant, & Sinervo, 2007; Gross, 1991). Additionally, numerous colour-polymorphic systems show like-morph aggression bias (Dijkstra, Seehausen, Pierotti, & Groothuis, 2007; Horton, Hauber, & Maney, 2012; Pauers, Kapfer, Fendos, & Berg, 2008). Morphs show the greatest levels of aggression to individuals of the same colour morph, which could result in a frequency-dependent advantage for the rare morph as it may face lower overall levels of aggression (Seehausen & Schluter, 2004). This promotes negative frequency-dependent selection and polymorphism maintenance if morphs are behaviourally similar in other ways i.e. they are equally likely to encounter aggressive individuals (Dijkstra et al., 2010; Qvarnström, Vallin, & Rudh, 2012). However, like-morph aggression bias can alternatively indicate divergence between morphs if it is associated with assortative mating (Dijkstra & Groothuis, 2011; Seehausen & Schluter, 2004). Individuals may direct more aggression towards like-morphs if they pose a greater threat to their reproductive resources. This is expected to lead to differentiation between morphs, and potentially speciation (van Doorn, Dieckmann, & Weissing, 2004). Therefore, assessing the nature of colour-biased aggression is important to understand evolutionary processes maintaining the polymorphism or alternatively leading to divergence between morphs.

Here, we used field experiments to test the hypothesis that the visually discrete throat colour morphs of the tawny dragon lizard, *Ctenophorus decresii*, exhibit different behavioural strategies. In polymorphic populations of this species, individual male throat colour falls into one of four discrete colour morphs, which can be reliably classified into orange, yellow, grey and orange-yellow (Teasdale, Stevens, & Stuart-Fox, 2013; Fig. 1). Throat colour develops before sexual maturity, is chromatically conspicuous against native backgrounds and is highly heritable and fixed for life based on long-term studies of captive populations (McLean, Moussalli, & Stuart-Fox, 2014; Osborne, 2004; Rankin, 2014) and 3 years of mark-recapture data from our study population (Yewers & Stuart-Fox, 2013b). Throat colour morph does not vary with body size, such that all morphs are observed in the same age(s) (Teasdale et al. 2013). Thus, like other lizards (Olsson et al., 2007; Sinervo & Zamudio, 2001), the colour polymorphism in this species is likely to have a genetic basis and is not conditionally expressed. Tawny dragon lizards are highly territorial and have discrete territories with an average size of 213 m^2 which they maintain over consecutive years (Yewers & Stuart-Fox, 2012). To defend territories and court females, males engage in complex displays in which individuals extend and lower their throats, laterally compress their bodies and perform head bobs and push-ups on all four legs (Gibbons, 1979; Osborne, 2005a; Stuart-Fox & Johnston, 2005; Umbers, Osborne, & Keogh, 2012). In male–male contests individuals recognize rivals based on their throat colour pattern (Osborne, Umbers, Backwell, & Keogh, 2012) suggesting that colour is used as a social signal. Males adjust their aggressive response to competitors based on prior experience, residency and the proximity and body size of the rival; however, aggressive response to throat colour morph has not been studied (Osborne, Umbers, & Keogh, 2013; Stuart-Fox & Johnston, 2005; Umbers et al., 2012). As territory establishment and the outcome of male contests are arguably the two most critical factors determining male mating success in lizards (Gullberg, Olsson, & Tegelström, 1997; Simon, 2011; Stamps & Krishnan, 1997; Tokarz, 1998), and antipredator

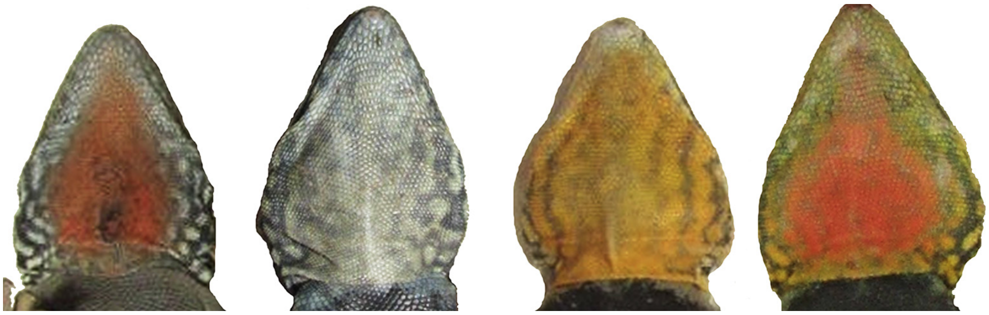

Figure 1. Examples of *Ctenophorus decresii* male throat colour morphs. From left: orange, grey, yellow and orange-yellow.