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Exciting discoveries in animal signalling and sexual dichromatism

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Territorial animals often use signals, such as scent marks, colourful plumage and vocalizations, to advertise territory ownership (Bradbury & Vehrencamp, 2011). In theory, the same traits could also serve as indicators of territorial fighting ability that help individuals assess opponents and avoid unnecessary escalated fights. For that to work, there needs to be an unbreakable link between the trait and fighting ability; otherwise 'cheaters' would be favoured by selection and the trait would eventually cease to be predictive of fighting ability (Maynard Smith & Harper, 1995). While it is theoretically possible for condition-dependent traits to be reliable indicators of fighting ability merely because they are costly for survival (Grafen, 1990; Penn & Számadó, 2020), in the best-documented empirical examples, signal expression is constrained by the same factors that affect fighting ability itself, such as energy reserves and body size (Bradbury & Vehrencamp, 2011). Classic examples include the frequency of roaring in red deer and the pitch of croaking in toads (Clutton-Brock & Albon, 1979; Davies & Halliday, 1978).

The red wing spots of male American rubyspot damselflies have long been thought to be indicators of territorial fighting ability (Grether, 1996a, 1997), but the mechanism that prevents males from producing deceptively large wing spots is unknown. G-Santoyo et al. (2021) provide compelling evidence for a new hypothesis that they refer to as detoxifying ability signalling. Other insects detoxify the metabolic by-products of the amino acid tryptophan by converting them to non-toxic ommochrome pigments, which are then excreted. By contrast, the damselflies deposit ommochromes in their wings, which G-Santoyo et al. (2021) suggest makes the wing spots honest signals of male nutritional status. In addition to using state-of-the-art methods to characterize the wing pigments, G-Santoyo et al. (2021) show that the ommochrome precursor 3-hydroxy-kynurenine (3-Hk) is toxic to the damselflies and that

mature males injected with 3-Hk had more ommochromes in their wing spots at the time of death, compared to sham-manipulated and unmanipulated controls.

It had already been established that artificial augmentation of wing spot size enhances the ability of males to hold territories but reduces their survival in the field (Grether, 1996a, 1997). Under natural conditions, wing spot size correlates positively with both territory tenure and survival (Grether, 1996b), as well as with indices of immune system strength and physiological condition (Contreras-Garduno et al., 2008; Contreras-Garduño et al., 2006, 2007). Thus, wing spots have all the hallmarks of a condition-dependent sexually selected trait (Andersson, 1994). G-Santoyo et al.'s (2021) confirmation that the red pigments have a dietary origin suggests that the final size of a male's wing spots depends on his hunting success during the adult maturation period. While the maximum wing spot area is fixed at adult emergence, the proportion of the area that actually fills in with pigment is quite variable (Grether, 1996b). G-Santoyo et al.'s (2021) hypothesis could be tested further by temporarily placing immature males in field enclosures stocked with different levels of prey. Males with greater access to prey should develop proportionally larger wing spots, and be more likely to win territorial fights after they reach maturity.

Adding to previous experimental evidence that the colour of the wing spots is affected by immunological challenges (Contreras-Garduno et al., 2008) and oxidative stress (Martínez-Lendech et al., 2018), G-Santoyo et al.'s (2021) discovery that the chroma (colour saturation) of the wing spots can be increased by injecting mature males with tryptophan metabolites suggests that the colour of the wings spots might be a dynamic indicator of a male's physiological condition well beyond the age when wing spot size is developmentally fixed. Escalated damselfly territorial fights are highly

energetic and males have to replenish their energy reserves through hunting to remain competitive (Marden & Waage, 1990). Thus, if the chroma of the wing spots is affected by prey consumption throughout a male's life, wing spot chroma is likely to be a better indicator of the fighting ability of older males than wing spot size. Whether the damselflies perceive these differences in chroma, and adjust their responses to rivals accordingly, remains to be tested. It has been shown that territory holders use wing spot chroma to discriminate between mature and immature male intruders (Grether et al., 2015), and the same method could be used to determine whether males discriminate between the smaller differences in chroma seen in mature males.

Beyond providing experimental evidence for a new honesty-enforcing mechanism in animal signalling, G-Santoyo et al. (2021) raise intriguing questions about the evolution of sexual dichromatism. Female rubyspot damselflies consume the same tryptophan-rich insects as males do, but instead of red wings spots, females have amber-coloured wing patches (Figure 1) that probably help them blend in with the background vegetation while hunting (Grether & Grey, 1996) and also when they are most vulnerable to homeothermic predators such as birds (Switzer & Grether, 1999). A diagnostic chemical property of red ommochromes is that they can be converted to yellow pigments through reduction or oxidation (Linzen, 1974). Indeed, differences in ommochrome redox state are known to be the basis of sex differences in the body coloration of some dragonflies (Futahashi et al., 2012). This raises the exciting possibility that males and females dispose of tryptophan metabolites in precisely the same way, but over evolutionary time, have repurposed the ommochrome waste products for opposite functions, that is, males for enhancing conspicuousness and females for enhancing crypsis. If so, this would parallel the recent discovery that female tanagers have the same amounts of carotenoid pigments in their feathers as males do, although the striking sex difference in tanager coloration results not from redox but instead from sex differences in feather microstructure (McCoy et al., 2019).

Ommochromes have some interesting properties from a signal evolution standpoint, and despite being common in insects (Futahashi et al., 2012; Linzen, 1974), are vastly understudied compared to carotenoid, melanin and pteridine pigments. G-Santoyo et al. (2021) have opened a new window on the evolution of animal

coloration filled with highly tractable subjects for behavioural ecology field research.

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FIGURE 1 Female (left) and male (right) American rubyspot damselflies. (The male, photographed while defending his territory, was colour marked on the abdomen for individual identification in a behavioural study.)



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