



Behavioural antioxidant strategies to cope with high temperatures: a study in a tropical butterfly



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Exposure to high temperatures can disrupt the balance between the production of reactive oxygen species (ROS) and antioxidant defences. Animals may be able to correct such an imbalance physiologically by up-regulating endogenous antioxidant defences. They may also respond behaviourally by increasing the intake of dietary antioxidants (e.g. polyphenols) and/or by reducing physical activity (thereby decreasing ROS production). The use of a given antioxidant strategy is expected to depend on its associated cost/benefit ratio relative to that of other strategies. We found that captive *Bicyclus anynana* butterflies almost doubled polyphenol intake under hot conditions and reduced flight activity, while temperature did not affect endogenous antioxidant defences (as measured by superoxide dismutase activity) and did not increase oxidative damage. These results suggest that butterflies primarily respond to hot conditions by adjusting their behaviour, thereby avoiding an imbalance between ROS production and antioxidant defences (i.e. oxidative stress). Interestingly, butterflies increased polyphenol intake in the morning when they also consumed energy resources (sugar). Increasing polyphenol intake on hot mornings subsequently led to decreased sugar intake in the middle of the day, which may have contributed to reducing flight activity at that time. Overall, this suggests that *B. anynana* butterflies prioritized polyphenol intake over energy intake (and its associated benefits) under hot conditions. This prioritization might be risky under natural conditions where energy intake is more critical than in captivity. Therefore, further studies should examine whether animals also prioritize the behavioural adjustments that we observed here under conditions where the benefits associated with high energy intake are increased.

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When facing challenging conditions, animals may alleviate the costs related to physiological adjustments by modifying their behaviour, thereby promoting homeostasis despite variable environmental conditions (Huey, Hertz, & Sinervo, 2003). This so-called 'Bogert effect' may also be of primary importance for animals with limited physiological plasticity (Gunderson, Stillman, & Gunderson, 2015). This notion has received most attention in studies examining the response of ectothermic animals facing challenging thermal conditions (Marais & Chown, 2008; Marais, Terblanche, & Chown, 2009; Mitchell, Sinclair, & Terblanche, 2013). These studies showed that behavioural variation could indeed influence thermal tolerance and survival, but the associated physiological mechanisms remain unclear.

High temperatures can alter the oxidative status of an animal by increasing its production of reactive oxygen species (ROS) due to

elevated metabolic rate (Ju, Wei, Wang, Zhou, & Li, 2014; Lin, De Vos, Decuyper, & Buyse, 2008; Tumminello & Fuller-Espie, 2013). To counterbalance increased ROS production, which can result in critical levels of oxidative damage to biomolecules, animals can activate endogenous antioxidant defences, such as superoxide dismutase, catalase or glutathione peroxidase (Jia, Dou, Hu, & Wang, 2011; Ju et al., 2014; Yang, Huang, & Wang, 2010). This physiological response, however, is likely to incur costs to the organism, which may limit its capacity to sustain such an antioxidant defence system (Monaghan, Metcalfe, & Torres, 2009). Interestingly, recent studies have highlighted interrelationships between individual behaviour and oxidative status (i.e. the balance between the production of ROS and antioxidant defences; Arnold, Herborn, Adam, & Alexander, 2015; Costantini, Carere, Caramaschi, & Koolhaas, 2008; Garratt & Brooks, 2014; Isaksson et al., 2011; Rammal, Bouayed, & Soulimani, 2010). This suggests that animals could adjust some aspects of their behaviour to alleviate the costs related to the use of endogenous antioxidant defences or to compensate for limited physiological plasticity when experiencing hot conditions.

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The first obvious behavioural adjustment that may enable animals exposed to hot conditions to avoid resorting to physiological antioxidant defences is to find habitats with more favourable thermal conditions. A prerequisite for such a behavioural adjustment is that the environment can provide animals with thermal refuges, such as shaded sites or burrows. This may be problematic in some habitats, such as tropical forests, where thermal variability is low (Huey et al., 2012). In that case, instead of increasing activity to find better conditions, it may be more advantageous for animals to reduce activity (Bregazzi & Naylor, 1972; Galloway & Maughan, 1999; Gannon et al., 2014; Tucker & Gilliland, 2007). Because physical activity generates ROS (Banerjee, Mandal, Chanda, & Chakraborti, 2003), such a behavioural response may indeed allow animals to compensate for higher ROS production (and higher energy requirements) due to an elevated basal metabolism at high temperatures (Clarke & Fraser, 2004; Halsey, Matthews, Rezende, Chauvaud, & Robson, 2015; Ju et al., 2014; Lin et al., 2008; Tumminello & Fuller-Espie, 2013). Decreasing activity at high temperatures may therefore allow animals to limit the recourse to endogenous antioxidant defences, while avoiding oxidative damage (Fig. 1). This behavioural response may be directly initiated by high ROS levels that decrease muscle contractility and increase muscle fatigue (Full & Tullis, 1990; Lawler, Hu, & Barnes, 1998; Segal, Faulkner, & White, 1986). Decreasing physical activity should be particularly important in flying animals for which the energetic cost of flight is high relative to the cost of basal metabolism (Reinhold, 1999). Accordingly, the effect of ambient temperature on longevity in house flies, *Musca*

domestica, strongly depends on temperature-associated variation in physical activity (Ragland & Sohal, 1975), and these effects appear to be mediated by variation in oxidative status (Sohal, Agarwal, Dubey, & Orr, 1993).

Although reducing activity under hot conditions conveys direct benefits (reduced energy requirements and ROS production), it can also have indirect negative effects. Indeed, it increases predation risk (Avery & Krebs, 1984), impairs foraging capacity (Corbet et al., 1993) and decreases the probability of finding a mate (Larsson, 1991). To circumvent these negative effects, animals may vary their activity budget by restricting activity to periods when the cost/benefit ratio of activity is low. For instance, being active may be more important in the morning (to find food after fasting at night) than during the rest of the day. Alternatively, to alleviate the negative effects of low activity, animals can use a second behavioural strategy by exploiting antioxidant compounds of dietary origins (e.g. vitamin C, vitamin E, carotenoids, polyphenols). This behavioural strategy is expected to limit the use of endogenous defences, reduce oxidative damage and/or keep physical activity unchanged (Beaulieu & Schaefer, 2013; Catoni, Peters, & Schaefer, 2008). For example, supplementing budgerigars, *Melopsittacus undulatus*, with dietary antioxidants can either reduce oxidative damage or improve flight capacity (Larcombe, Coffey, Bann, Alexander, & Arnold, 2010; Larcombe et al., 2008). This suggests that animals can allocate dietary antioxidants either to the regulation of oxidative status or to increasing physical activity. Such allocation is likely to depend on the benefits of optimizing oxidative status relative to remaining active under given conditions.

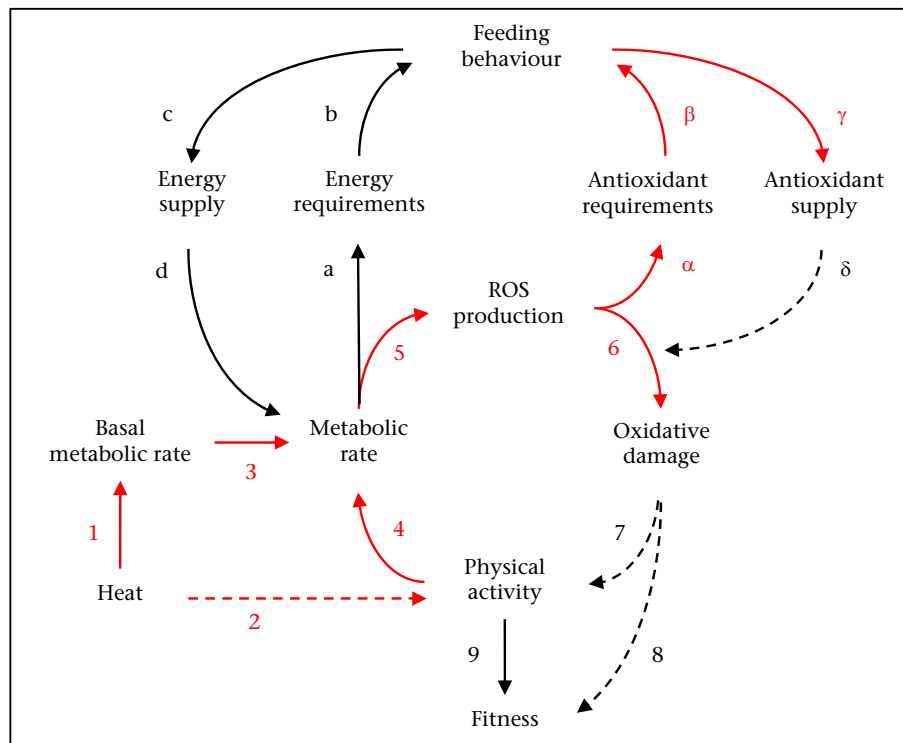


Figure 1. Schematic view showing the interplay between physical activity, oxidative status and feeding behaviour in animals exposed to hot conditions. Solid and dashed lines symbolize positive and negative effects, respectively. Exposure to hot conditions increases basal metabolic rate (1), which may increase overall metabolic rate (3). Physical activity also increases metabolic rate (4) but is reduced under hot conditions (2). Physical activity can also be reduced because of higher ROS production (6, 7) resulting from higher metabolic rate (5). If reduced activity is not sufficient to compensate for increased basal metabolic rate and keep metabolic rate stable, energy requirements increase (a). At the same time, requirements for antioxidants also increase (α) to counteract the action of higher ROS levels (6). Animals therefore have to adjust their feeding behaviour to respond to higher energetic (b, c) and antioxidant (β , γ) requirements, which may ultimately alleviate the effects of heat exposure on metabolic rate (d), oxidative damage (δ), physical activity (7) and fitness (8, 9). Red lines symbolize the most probable scenario occurring in our study: heat increased basal metabolic rate (1) and decreased activity (2). Decreased activity was sufficient to keep metabolic rate stable or even reduced it (4), as energy requirements remained stable (a) and oxidative damage decreased (5, 6). However, metabolic rate and ROS production must have temporarily increased to some extent, as antioxidant requirements appeared to be elevated (α). This was reflected by higher antioxidant intake (β), which resulted in higher antioxidant defences (γ).

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