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REVIEWS

Life history trade-offs are influenced by the diversity, availability and interactions of dietary antioxidants

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The expression of most life history traits, such as immunity, growth and the development of sexual signals, is negatively affected by high levels of oxidative stress. Dietary antioxidants can reduce oxidative stress and have therefore been the focus of numerous studies in behavioural and evolutionary ecology in the last few decades. Most of this research has focused on carotenoids, neglecting a number of more common, more potent, and thereby potentially more important, antioxidants, such as polyphenolic antioxidants. However, the effects of several classes of antioxidants on different life history traits have been thoroughly investigated in medical and animal-breeding studies. We suggest that behavioural and evolutionary studies will benefit from incorporating these advances. By reviewing the literature on the effects of antioxidants on life history traits in fish, birds and mammals, we develop a broad framework for dietary antioxidants. Fundamental properties of antioxidants, in particular their biochemistry, their potency and the interactions between them affect their relative relevance for life history traits. Based on tissue affinity, we distinguish between two categories of dietary antioxidants: focal antioxidants that are intrinsically important for a given trait and nonfocal antioxidants that influence traits only indirectly. Furthermore, we show how temporal and spatial environmental variability in antioxidant availability, as well as individual variation in food selection, may generate interindividual differences in the expression of life history traits. Finally, we suggest future research lines and experimental designs that may provide basic information needed to advance our knowledge of the ecological and evolutionary relevance of dietary antioxidants.

Keywords: ascorbate; carotenoids; food selection; life history traits; oxidative stress; polyphenol; senescence; sexual selection; tocopherol; vitamin E

Many physiological functions depend on a balance between reactive species (e.g. reactive oxygen and nitrogen compounds) and antioxidant defences (Halliwell & Gutteridge 2006). Reactive species are metabolic by-products essential for energy supply, chemical signalling and detoxification (Halliwell & Gutteridge 2006). However, overexposure to reactive species leads to oxidative stress causing cell and tissue damage and, finally, premature aging and eventually degenerative diseases (Finkel & Holbrook 2000). Oxidative stress is reduced by a complex network of antioxidants, among which dietary antioxidants play a fundamental role (reviewed in Vertuani et al. 2004). In the last two decades, a wealth of studies in medicine and animal health has demonstrated that dietary antioxidants may increase immunocompetence (Hughes 1999a), slow down the process of ageing (Ames

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et al. 1993), and reduce the occurrence of chronic diseases such as cancer or Alzheimer's (Brash & Havre 2002).

These effects make dietary antioxidants ideal candidates to influence key traits in life history (von Schantz et al. 1999). The same may be true for endogenous antioxidants, such as superoxide dismutase or uric acid (Vertuani et al. 2004). However, little is known about their interindividual variation and their relevance for behavioural traits. We thus focus our review exclusively on dietary antioxidants.

Dietary antioxidants comprise a group of several hundred different compounds. Although medical studies have investigated the effects of several antioxidants on various traits, behavioural ecologists have, with a few recent exceptions (e.g. de Ayala et al. 2006; Hõrak et al. 2007; Pike et al. 2007b; Catoni et al., in press), mostly focused on a single class of antioxidants, carotenoids. In the last two decades, carotenoid-based signalling has become a model system in sexual selection theory to analyse the role of oxidative stress in life history trade-offs such as those between self-maintenance and reproduction (McGraw & Ardia 2004). However, the relevance of carotenoids as antioxidants might have been overestimated, at least in birds (Hartley & Kennedy 2004; Costantini & Møller 2008). Consequently, although the focus on carotenoids has generated many valuable insights into animal physiology and the evolution of animal signals, it has, at the same time, limited our understanding of the general relevance of antioxidants in evolutionary ecology and physiology.

In this review, we aim to rejoin the progresses in medical and veterinary science with those from behavioural ecology and thereby develop an encompassing framework for the ecological and evolutionary significance of dietary antioxidants. To this end, we first consider the basic characteristics of the most common antioxidant classes, their bioavailability, their tissue distribution and their interactions. Based upon this information, we discuss the relevance of single antioxidants for various life history traits of mammals, birds and fish. Furthermore, we show how behaviourally and environmentally induced variations in antioxidant intake may affect the expression of life history traits. Finally, we identify critical gaps in our current knowledge and briefly outline methods and experiments to address them.

BASIC CHARACTERISTICS OF DIETARY ANTIOXIDANTS

Dietary antioxidants are mainly secondary metabolites that plants synthesize to protect themselves against oxidative stress. According to their chemistry, they may be grouped into four classes: vitamin C (ascorbic acid); vitamin E (tocopherols); carotenoids (e.g. α- and β-carotenes, lycopene, lutein); and polyphenolic antioxidants. The latter are a very diverse group among which phenolic acids and flavonoids such as anthocyanins and quercetin are the most important antioxidants. The four classes of dietary antioxidants differ dramatically in their mean antioxidant potency, absorbability and environmental availability. Flavonoids and phenolic acids are the antioxidants with the highest environmental availability, being most concentrated in all food categories (Table 1). Flavonoids also have the highest antioxidant potency in vitro, followed by carotenoids, vitamin E and vitamin C. We expect these fundamental differences to shape the relative importance of each antioxidant for consumers as outlined below.

Biochemistry and Tissue Distribution

The biochemistry of antioxidants is fundamental to understanding their possible physiological roles. Biochemistry affects not only the potency (Table 2) but also the mechanism of action (see below) and the tissue

Table 1. Antioxidant content of major food items

Antioxidants	Seeds	Fruits	Leaves	Arthropods*
Vitamin E[1] (tocopherols and tocotrienols)	0.9 (0.007−1.21)	0.4 (0.1−0.9)	1.3 (0.3−3.1)	0.04 (0.01−0.07)
Carotenoids[2] (e.g. β-carotene, lutein, lycopene, canthaxanthin)	0.008 (0.002−0.03)	1.0 (0.0008−2.2)	0.1 (0.02−0.3)	0.2 (0.002−0.4)
Vitamin C[3]† (ascorbate and derivates)	?	18.0 (0.3−113.6)	2.3 (0.2−5.1)	?
Anthocyanins[4]‡ (e.g. cyanidin 3-glucoside)	1.6 (1.3−1.8)	19.3 (1.3−59.2)	1.0 (0−2.6)	?
Polyphenolic antioxidants (e.g. quercetin, catechin, caffeic acid)[5]	0.5 (0.5−0.6)	1.4 (0.1−3.2)	34.1 (10.9−105.8)	7.5 (5.4−9.6)

Mean antioxidant concentration in fruits, leaves, seeds and arthropods in μmol/g (range indicated in parentheses). Question marks denote lack of information. Source: (1) Bramley et al. (2000); Marconi et al. (2002); Gomez-Coronado et al. (2004); Konyahoglu et al. (2005); Sivakumar & Bacchetta (2005); Sanchez-Machado et al. (2006); U.S. Department of Agriculture (2007); (2) Hudon (1994); Marconi et al. (2002); Konyahoglu et al. (2005); U.S. Department of Agriculture (2007); (3) U.S. Department of Agriculture (2007); (4) Kähkönen et al. (2001); Czerwinski et al. (2004); Jaakola et al. (2004); (5) Burghardt et al. (2001); Konyahoglu et al. (2005); Määttä-Riihinen et al. (2005).

*The concentration of antioxidants in arthropods is probably dependent on their trophic level, with content decreasing with increasing trophic levels. The data shown here refer only to caterpillars (Lepidoptera) which are in the second trophic level (herbivores). The information available, although probably not representative of all taxa, may still give a gross estimation of the range of variation in antioxidant contents in arthropods relative to that of other food categories. Further studies are needed to investigate the antioxidant content of more arthropod taxa.

†Although vitamin C can be synthesized by many vertebrate taxa (e.g. amphibians, reptiles and most mammals; Chatterjee 1973), a far greater number of species lack this ability, e.g. all teleost fishes (Dabrowski 1990), many birds (Chaudhuri & Chatterjee 1969; Martinez del Rio 1997), and a few mammalian taxa, such as guinea pigs, monkeys, apes and bats (Chatterjee 1973). Therefore, we treat vitamin C here as a regular dietary antioxidant.

‡Owing to their distinctive distribution in plant tissues, anthocyanins are listed separately from other polyphenolic antioxidants. Thus, the sum of both rows indicates total polyphenolic antioxidant contents.