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Exploratory behavior is associated with plasma carotenoid accumulation in two congeneric species of waterfowl

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ABSTRACT

Recently, carotenoid pigments have received considerable attention as modulators of animal health and performance. While studies show that elevated carotenoid intake and accumulation can influence activities like parental care and escape-flight performance, little is known of how carotenoid status influences the expression of animal personality traits, which can be energy-demanding and entail survival costs but also rewarding in the context of foraging and mating. We experimentally investigated the effects of carotenoid availability on exploratory behavior and activity level, using adult males and females of two species of waterfowl: mallard (*Anas platyrhynchos*) and northern pintail (*Anas acuta*). We assessed behavior using a novel-environment test designed to measure an individual's response to novel objects and a potential predator threat (fox urine scent). We found that carotenoid availability was positively associated with some aspects of exploratory behavior: birds with higher concentrations of circulating carotenoids entered the test arena sooner and approached and entered predator-scented bedding material more frequently than birds with low carotenoid concentrations. These results suggest that the availability of carotenoid resources can influence personality traits in waterfowl, and we discuss putative physiological mechanisms underlying this effect.

1. Introduction

In many species, individuals exhibit consistent differences in a range of behavioral traits (e.g., boldness, aggressiveness, and exploration). Furthermore, such traits are frequently correlated (Verbeek et al., 1996; Dingemanse et al., 2007; Kortet and Hedrick, 2007) and are therefore regarded as aspects of an individual's personality (Gosling, 2001; Réale et al., 2007, 2010; Stamps and Groothuis, 2010). Exploratory behavior (i.e., an individual's reaction to new environmental situations; Réale et al., 2007) is a commonly measured personality trait that has been studied in a range of captive and wild organisms (e.g., Verbeek et al., 1994; Dingemanse and de Goede, 2004; Carere et al., 2005; Boon et al., 2007; Dingemanse et al., 2007; Jones and Godin, 2010; Butler et al., 2012). Animals may benefit from acquiring information about their environment that permits them to make quick, informed decisions about mate choice, habitat or food selection and predator avoidance, and one way to gather such information is exploration. However, while exploratory behavior can be rewarding in the context of foraging and mating, it can also be energy-demanding and entail survival costs. As individuals vary considerably in their propensity to approach and explore new situations or objects (Verbeek et al., 1994), recent studies have aimed at understanding the mechanisms driving inter-individual variation in exploratory behavior (e.g., Carere et al., 2005; Careau et al., 2008; Butler et al., 2012). These studies have shown that exploratory behavior is heritable (Dingemanse et al., 2002), with further variation driven by a range of environmental factors, including current abiotic/biotic conditions, prior and early life experience and social context (Dingemanse et al., 2004; Carere et al., 2005; Schuett and Dall, 2009; Biro and Stamps, 2010; Ward, 2012).

Among the possible environmental factors contributing to variation in exploratory behavior, the nutritional status of individuals (e.g., diet quantity and composition) remains relatively understudied. Moreover, the few studies that have examined the influence of diet on personality traits more generally have focused on nutritional conditions during ontogeny. For example, nutritional deprivation and diet deficiencies early in life have been shown to

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influence exploratory behavior in a range of taxa, including birds (*Parus major* (Carere et al., 2005); *Taeniopygia guttata* (Krause et al., 2009)), fish (*Kryptolebias marmoratus* (Edenbrow and Croft, 2012)), rats (*Rattus norvegicus* (Fraňková and Barnes, 1968; Weinberg et al., 1980; Enslen et al., 1991)), mice (*Mus musculus* (Ishii et al., 2005)) and monkeys (genus *Cebus* (Elias and Samonds, 1974)). In contrast, while there is good reason to expect a link between adult nutritional status and an energy-demanding activity like exploration, investigations into the influence of variation in adult dietary intake on an individual's propensity to explore new environments are lacking. Moreover, attempts to tie particular nutrients to aspects of exploratory behavior are limited.

Carotenoid pigments have received considerable attention of late as dietary modulators of animal health and performance (Vinkler and Albrecht, 2010). In addition to their provitamin activity and role in pigmentation, carotenoids can serve as immunostimulants (e.g., Blount et al., 2003; McGraw and Ardia, 2003). Carotenoids may also serve as antioxidants by mitigating oxidative damage through the quenching of free radicals and break down of lipid peroxidation chain events (Burton and Ingold, 1984; Krinsky, 1989; Miki, 1991; Krinsky, 1998); though the importance of carotenoids relative to other antioxidant molecules (e.g., vitamins) remains unclear (Hartley and Kennedy, 2004; Costantini and Møller, 2008) and carotenoids can become pro-oxidants under certain conditions (Palozza et al., 2003; Hurst et al., 2005). Importantly, elevated carotenoid intake has been found to enhance various animal behaviors, including reproduction (Blount et al., 2004), parental effort (Pike et al., 2007; Ewen et al., 2008), song output (Van Hout et al., 2011) and escape-flight performance (Blount and Matheson, 2006). Because high carotenoid resources are associated with enhanced immunocompetence, antioxidant activity and health of individuals in a range of species (e.g., Blount et al., 2003; McGraw and Ardia, 2003 but see Costantini and Møller, 2008), including mallards (*Anas platyrhynchos* (Butler and McGraw 2012)), we hypothesized that exploratory behavior and activity level may be influenced by the availability of carotenoid resources. More specifically, since activity-induced increases in reactive oxygen species (ROS) production can lead to muscle fatigue (Powers et al., 2004), we suggest that carotenoids may influence physiological performance at the behavioral level if they provide antioxidant protection to muscles (Ji, 1999; Powers et al., 2004) or other body tissues relevant to animal movement (e.g., eyes, brain). Additionally, since recent studies have linked the past or current immune status of individuals to exploratory behavior and activity level (Butler et al., 2012; Grindstaff et al., 2012; Männiste et al., 2013), we suggest that high levels of circulating carotenoids may also promote exploration and activity behavior via their effects on overall immunocompetence or general health.

In some of the only comparable literature, (Costantini et al., 2008) found that another personality trait in mice (i.e., aggressiveness) was associated with serum antioxidant status. Similarly, plasma antioxidant capacity was positively associated with greater exploration in European greenfinches (*Carduelis chloris* (Herborn et al., 2011)). Neither of these studies, however, singled out the potential contributions from carotenoids. Here, we investigated the effect of carotenoid availability on exploratory behavior and activity level in two congeneric species of dabbling duck – mallard and northern pintail (*Anas acuta*). We selected a phylogenetically matched pair of species, where one taxon exhibits carotenoid-based integumentary coloration and the other does not, because it allowed us to examine whether differing carotenoid allocation strategies are associated with different behavioral responses. Male mallards in nuptial plumage have a yellow, carotenoid-based bill (Butler et al., 2011), whereas female mallards exhibit less colorful bills (predominately brown with some orange coloration). In contrast, neither male nor female northern pintails display carotenoid-based integumentary coloration. Female mallards prefer to mate with males having yellower bills (Omland, 1996), whereas female pintails show a preference for males with whiter breast coloration and more colorful scapular feathers (Sorenson and Derrickson, 1994). The species and sexes also show differences in general behavior: pintails are generally considered to be largely nonaggressive and sociable, and appear to be subordinate to mallards when foraging (Bailey and Batt, 1974). Conversely, mallards tend to be more aggressive, in both feeding and mating contexts, relative to other waterfowl species (Bailey and Batt, 1974), including a congener, the American black duck (*Anas rubripes* (Brodsky and Weatherhead, 1984)). Additionally, in both species, males tend to be more aggressive than females (Bailey and Batt, 1974; Hepp and Hair, 1984), and at least in pintails, males spend more time moving relative to females (Kaminski and Prince, 1981).

We generated predictions related to carotenoid-dependent behavioral responses within two alternate frameworks linked to variation in carotenoid ornamentation and physiology. We also predicted a number of general species- and sex-specific differences in exploratory behavior and considered how these predictions may be modulated by each of the physiological frameworks. Our first framework was based on the assumption that the investment of carotenoids into integumentary coloration reduces carotenoid availability for other functions (sensu carotenoid trade-off hypothesis; Lozano, 1994). Within this framework, and under the assumption that carotenoids enhance immune function or reduce oxidative stress (see Butler and McGraw, 2012 for evidence in mallards), we predicted that birds with greater carotenoid resources (i.e., higher concentrations of circulating carotenoids) would be more exploratory and more active than those with low carotenoid levels. Moreover, given that pintails, unlike mallards, do not invest in carotenoids into integumentary coloration, we predicted that pintails with high carotenoid levels might exhibit relatively greater increases in exploratory behavior and activity level compared to mallards. Similarly, we predicted that female mallards might benefit more from high carotenoid resources than male mallards because females exhibit less colorful bills (and thus, for a given carotenoid level, should have comparatively more resources available in the body for physiological functions).

Given the biology of these two species and because of aggressiveness and exploratory behavior are correlated in a range of species (Verbeek et al., 1996), we generally expected pintails to be less exploratory than mallards due to their less aggressive nature. Similarly, we expected the typically more aggressive males of both species to be more exploratory and show greater activity levels relative to females. However, within the framework of reduced carotenoid availability when integumentary coloration is carotenoid-dependent, we expected these species- and sex-specific differences might be reduced. This is because carotenoid resources would be more available to pintails (male and female) and female mallards as these groups lack carotenoid-dependent ornamentation, and these additional resources would remain in circulation and thus be available for boosting activity levels and exploratory behaviors.

Our second framework is built on the assumption that birds displaying carotenoid-based coloration possess physiological adaptations that allow them to absorb or accumulate more carotenoids (McGraw, 2005). Under this framework, it is expected that individuals with high carotenoid resources would exhibit increases in both exploratory behavior and activity level, but that mallards would show relatively greater increases in behavioral responses compared to pintails. Following this same logic, male mallards were expected to show the greatest increases in exploratory behavior and activity level when carotenoid-replete, as they exhibit the most elaborate form of carotenoid-based coloration compared to pintails and female mallards. Finally, in terms