



# Body mass and immune function, but not bill coloration, predict dominance in female mallards



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## ABSTRACT

Competition over indivisible resources is common and often costly. Therefore, selection should favor strategies, including efficient communication, that minimize unnecessary costs associated with such competition. For example, signaling enables competitors to avoid engaging in costly asymmetrical contests. Recently, bill coloration has been identified as an information-rich signal used by some birds to mediate aggressive interactions and we evaluated this possibility in female mallards *Anas platyrhynchos*. Specifically, we conducted two rounds of competitive interactions among groups of unfamiliar adult female ducks. By recording all aggressive behaviors exhibited by each individual, as well as the identity of attack recipients, we were able to assign dominance scores and evaluate links between numerous physiological, morphological, and experimental variables that we predicted would influence contest outcome and dominance. Contrary to our predictions, dominance was not linked to any aspect of bill coloration, access to dietary carotenoids during development, two of three measures of immune function, or ovarian follicle maturation. Instead, heavier birds were more dominant, as were those with reduced immune system responses to an experimentally administered external immunostimulant, phytohemagglutinin. These results suggest that visual signals are less useful during the establishment of dominance hierarchies within multi-individual scramble competitions, and that immune function is correlated with contest strategies in competitions for access to limited resources.

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## 1. Introduction

Intraspecific competition for food, space, or mates drives the evolution and elaboration of traits that increase the likelihood of winning aggressive interactions and securing resources (Hardy and Briffa, 2013; Huntingford and Turner, 1987). For example, armaments may allow individuals to physically dominate competitors, increasing the likelihood of gaining access to contested resources (e.g., Emlen, 1997; Plard et al., 2011). However, because engaging in fights is energetically expensive and bears risk of injury, evolution frequently favors the production of signals that mediate aggressive or competitive interactions via information transfer, thus potentially avoiding the risks associated with physical combat (Searcy and Nowicki, 2005). Such status signals aid conflict participants by providing them with additional information about their oppo-

nents, allowing individuals that are likely to lose an encounter to avoid injuries inflicted by markedly superior animals, and enabling individuals that are likely to win encounters to avoid expending energy in unnecessary escalation (Rohwer, 1975). Though status signals have typically been examined in males (Briefer et al., 2008; Ligon and McGraw, 2013; Ord and Evans, 2003; Rick and Bakker, 2008), females of many species can be territorial (Murphy et al., 2009a,b), compete for mates (Chancellor et al., 2009; Pryke, 2007), and produce signals related to dominance status (Murphy et al., 2009b). Examining the role of female ornaments in modulating intraspecific, female–female competition may facilitate new insights regarding the evolution of these characters, specifically whether such traits evolved as socially selected signals within females or as by-products of sexual selection on males (Amundsen, 2000; Clutton-Brock, 2009; LeBas, 2006).

Status signals frequently manifest as visual signals, often in the form of colorful patches of integument. Animal coloration is produced by several mechanisms, including pigment deposition (Hill and McGraw, 2006) or physical arrangement of nanostructures (i.e., structural colors; Prum, 2006). Among pigmentary colors,

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two frequently studied modes of animal coloration are melanin-based coloration (McGraw, 2006a) and carotenoid-based coloration (McGraw, 2006b). Melanins, large molecules that can be synthesized *de novo* in many vertebrate species, produce many of the black, grey, and rufous colors in vertebrate skin, hair, scales, and feathers (McGraw, 2006a). In contrast, carotenoids must be acquired from the diet and are responsible for many of the vibrant yellow, orange, and red colors in vertebrate integuments (McGraw, 2006b). Both melanin- and carotenoid-based coloration have been linked to social status in males (Ardia et al., 2010a; Liker and Barta, 2001), and several mechanisms linking coloration and behavior have been investigated, including putative links between circulating levels of testosterone and melanin-based coloration in both males (Lindsay et al., 2011) and females (Muck and Goymann, 2011). Because testosterone can increase aggressive behaviors (Ardia et al., 2010a), the same hormone that drives aggression can also increase melanin-based coloration, allowing for such colorful patches to honestly signal status. Similarly, testosterone levels in males have been linked to increased bioavailability of carotenoids (Blas et al., 2006) and expression of carotenoid-based ornaments (Martínez-Padilla et al., 2010), suggesting a similar potential for honest signaling.

To date, most studies linking coloration and behavior have focused on relationships between adult body condition and the concurrent expression of colorful ornaments (e.g., Hill and Montgomerie, 1994; Weiss, 2006). However, conditions experienced during development can also shape adult phenotype, a phenomenon termed developmental plasticity (Monaghan, 2008). While a variety of dietary manipulations (e.g., access to protein; Ohlsson et al., 2002) can affect adult phenotype, developmental access to dietary carotenoids in particular can shape carotenoid physiology (e.g., the ability to assimilate, circulate, or mobilize carotenoids; Blount et al., 2003), immune function (Butler and McGraw, 2012a,b), and even the color of eggshells laid at adulthood (Butler and McGraw, 2013a). Carotenoid supplementation during development can also affect behavior, with carotenoid-supplemented individuals exhibiting increased pecking behaviors (Fenoglio et al., 2002) and improved song performance (Van Hout et al., 2011). Thus, it seems plausible that carotenoid access during development may shape adult coloration or dominance status because individuals that consume high quantities of carotenoids during development may be able to produce more colorful bills and may also be in better overall health or condition.

While coloration may be linked to dominance status via shared physiological processes (e.g., high testosterone levels), color could also signal other aspects of phenotype that contribute to variation in dominance hierarchies. For example, carotenoid- and melanin-pigmented ornaments can signal immune function (Butler and McGraw, 2011), parasite load (Mougeot et al., 2010), or nutritional history (Ohlsson et al., 2002), and behavioral tests have shown that such factors can affect dominance hierarchies (Dolnik and Hoi, 2010; Royle et al., 2005). Thus, dominance may be associated not only with carotenoid- or melanin-based coloration, but may be more strongly influenced by, and correlated with, other aspects of phenotype. Here, we tested whether carotenoid- and melanin-pigmented bill coloration is related to dominance status in female mallards *Anas platyrhynchos* and whether dietary carotenoid manipulation during development influenced the expression of aggressive behavior. However, despite our initial predication that developmental access to carotenoids would influence adult beak coloration, no such relationship was detected (these results are described in detail in Butler and McGraw, 2013b). This absence of a developmental influence on adult beak coloration thus allowed us to separately assess how developmental diet and adult beak coloration relate to adult aggressive behavior and dominance.

The carotenoid-pigmented bill of male mallards is used as a signal during mate choice (Omland, 1996a, 1996b), but the potential signaling function of the female bill is currently unknown. Because female bills contain dark, putatively melanin-pigmented patches in the center, surrounded by orange, carotenoid-pigmented coloration (Butler and McGraw, 2013b), it is possible that female bill coloration may have a signaling function similar to the social signaling function of male bill coloration. To test this possibility, we conducted a series of behavioral tests using adult female mallards to assess the relative influence of bill coloration, developmental nutrition, immune function-based indicators of quality, body mass, and reproductive status on female aggressive behavior and dominance.

## 2. Methods

### 2.1. Husbandry and experimental protocol

This study was conducted in accordance with the Institutional Animal Care and Use Committee at Arizona State University under protocol 10–1094R. We acquired 48 one-day-old female ducklings from Metzger Farms (Gonzales, CA) in December 2009 and housed them as described in Butler and McGraw (2009). Ducklings were reared indoors in randomly selected groups of five ducklings per cage (60 × 60 × 60 cm) until they were two weeks old, three per cage until they were four weeks old, and two per cage until they were seven weeks old, at which point all birds were moved outside and individually housed in these same cages to allow for normal sexual maturation (Butler and McGraw, 2009). Light:dark regime was 13L:11D when ducklings were housed indoors, and natural photoperiod thereafter (10.5L:13.5D at 7 weeks old to 13.5L:10.5D at 20 weeks old). Individuals received *ad libitum* access to a base diet that contained low levels of carotenoids (described below) unless otherwise specified.

Individuals were randomly assigned to one of four developmental treatment groups that varied in dietary carotenoid content (none of which had any detectable influence on adult bill coloration; Butler and McGraw, 2013b). Per Butler and McGraw (2013b), individuals received carotenoid-supplemented diets during either the period of maximal growth (EARLY; 3–6 weeks old; N=10), minimal growth and nuptial plumage acquisition (MIDDLE; 8–11 weeks old; N=12), or nuptial plumage acquisition (LATE; 13–16 weeks old; N=12). CONTROL (N=12) birds did not receive carotenoid-supplemented diets at any point during the study. The sample size for the EARLY treatment was 10 instead of 12 because two ducklings had their diets mistakenly switched and were removed from the study. We prepared diets by mixing a base diet of dry food (Mazuri Waterfowl Starter; Richmond, IN, USA, weeks 0–7; Mazuri Waterfowl Maintenance thereafter) with ORO-GLO dry pigmenter (2% carotenoids by mass, predominately lutein; Kemin AgriFoods North America, Inc., Des Moines, Iowa, USA) suspended in sunflower oil to achieve concentrations of 25 µg/g of carotenoids (upper quartile of carotenoids in mallard duckling diets in the wild; Butler and McGraw, 2010). Circulating levels of carotenoids in mallards receiving non-supplemented diets were in the lower range of those found in wild ducklings, while supplemented levels were in the higher range (Butler and McGraw, 2010; Butler and McGraw, 2013b). Whenever any particular treatment group was receiving carotenoid-supplemented diets, all other individuals received food mixed with sunflower oil as a sham control.

We measured body mass to the nearest gram immediately prior to each of two rounds of dominance trials (21–22 weeks). We calculated the average of these two body mass values to determine adult mass for each bird. For immune assessment, conducted two weeks before dominance trials, we quantified primary and secondary antibody response to the benign antigen keyhole limpet hemo-

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