



# Condition dependence of iridescent wing flash-marks in two species of dabbling ducks

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## ABSTRACT

Growing empirical evidence supports the hypothesis of male mate choice for female ornaments which are thought to reflect individual quality and future breeding ability. While structural colors are clearly used in mate choice and pairing, the condition dependence of such traits is less obvious, particularly in females. We present spectral measurements of wing flash-marks in two species of dabbling ducks during the pairing period and evaluate color and brightness contrasts as seen through the mallard's (*Anas platyrhynchos*) visual system. We tested for possible relationships between body size (and condition) and feather measurements both on captive and wild individuals. By analyzing reflectance spectra of semi-captive mallards soon after the molting period, we found that brightness was condition related. Color contrast was positively related to body size, but only in females. In wild ducks, color contrast was positively related to body size in the common teal *A. crecca* only for females. These results suggest that female color traits are likely to be used by males for mate choice, and support the hypothesis that the structural color is condition-dependent. Finally, brightness contrast decreased over time in both duck species. Natural abrasion or the effect of keratinolytic bacteria could explain such pattern.

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## 1. Introduction

Animal coloration is thought to evolve as a compromise between two antagonistic selection pressures (Endler, 1978): sexual selection that leads signals towards maximal conspicuousness of mates and rivals (Andersson, 1994), and natural selection, through communication with prey (Rohwer and Paulson, 1987) or predators (Baker and Parker, 1979) and selecting for maximal crypsis. Under sexual selection, because females are expected to be the choosy sex, conspicuous plumage coloration is more likely to evolve in males than in females (Andersson, 1994; Hill, 2006a). Courtship and coloration have traditionally been viewed as means for the male to convey information about himself to the female (Hamilton and Zuk, 1982; Andersson, 1994). This may include information on species identity and individual quality. Among birds, ducks (family Anatidae) display some of the most complex behaviours and brightest plumage (Lorenz, 1978), involving both pigments and feather microstructure.

Cues in mate choice such as courtship activity (Bossema and Kruijt, 1982; Holmberg et al., 1989), hormonal status (Sorenson et al., 1997), body condition (Holmberg et al., 1989) and bill or plumage coloration (Holmberg et al., 1989; Omland, 1996a,b; Peters et al., 2004), have been investigated in ducks. However, as pointed out by Davis (2002), little attention has been paid to female phenotype. While it is well established that females prefer to pair and mate with brighter and/or more colorful males (review by Hill, 2006a), there is also growing evidence that males too make pairing and mating choices, leading to conspicuous female signals at least in some species (review in Amundsen and Pärn, 2006). Even in such highly sexually dichromatic species, both males and females possess wing flash-marks.

The information content of these wing flash-marks is unclear (Omland, 1996a,b; Sorenson and Derrickson, 1994). The wing flash-marks in dabbling ducks come from iridescent feathers that diffract ambient light and compose a structural color trait (Hill, 2006b). Nutritional condition of an individual during molt might be reflected in the expression of structural coloration (review in Hill, 2006b). Previous studies on mallard and other closely related dabbling duck species have suggested that breeding ability was related with body condition (e.g. Heitmeyer, 1995; Blums et al., 2005). Moreover, nutrient reserves on the wintering grounds affect survival as well as pairing success, hence future reproductive success (e.g. Pawlina et al., 1993; Guillemain et al., 2008). Generally,

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ducks pair in fall and winter (Hepp and Hair, 1983), which is also when they exhibit courtship behaviours. In ducks, reflectance spectrometry has been used to study bill color in the mallard (Peters et al., 2004) and wing flash-marks in the common eider, *Somateria mollissima* (Hansen et al., 2006, 2008), while other male ornaments have only been investigated using human vision (Holmberg et al., 1989; Omland, 1996a,b). By using recent spectrometry techniques, our aims are twofold:

- (1) With mallards fed *ad libitum* held in semi-captivity, we investigated reflectance intensity delivered by the flash-marks at the beginning of the pairing period and soon enough after molting to avoid feather degradation after growth. We investigated the possibility of condition dependence of the wing flash-mark coloration and tested the relationships between body size (or condition, two individual phenotypic measures known to modulate breeding performance in Anatidae) and feather reflectance. We expect a positive relationship between body condition and flash-mark reflectance for both sexes.
- (2) Compare the signal obtained when individuals came from natural habitats (killed by hunters in autumn and winter, i.e. during the pairing period of these species; Hepp and Hair, 1983). Same predictions on sex and condition (or size) listed in point 1 are expected for wild individuals. We also expect wild individuals to display lower quality plumage than semi-captive individuals due to a more constraining environment in nature (i.e. less food availability, Hill, 2006b).

Finally, we hypothesize that, overall structural plumage gradually fades due to the abrasion mediated by keratinolytic bacteria (Burt and Ichida, 1999; Shawkey et al., 2007) or to natural abrasion, and therefore expect a decrease of plumage coloration over time.

All our predictions are tested according to two different measures of the feather reflectance spectra: color and brightness contrasts (see Section 2).

## 2. Materials and methods

### 2.1. Feather collection and body measurements

We collected one feather from the wing color flash-mark (also termed “speculum”, i.e. the distal side of secondary remiges) of each individual killed by hunters or reared in our laboratory.

In the laboratory, feather collection took place in September for semi-captive mallards ( $N = 19$  female and 23 male mallards) fed *ad libitum* with a mix of wheat and corn grains. Adult ducks descended from individuals caught in the wild.

We measured body mass, flattened wing length, tail length (length of the longest rectrice), and bill length, height and width. A Principal Components Analysis (PCA) was performed on all measurements (except body mass), so that the scores of the first principal component (PC1) provided an index of body size (Table 1).

**Table 1**

Morphological measurements for 23 male and 19 female mallards raised in the lab and fed *ad libitum* until measurements in September, right after the molting period. Shown are means  $\pm$  SD and coefficients for two principal components (PC1 and PC2) of morphological variation. The PC1 scores were used to derive a body-size index.

Variable	Measurements (mean $\pm$ SD)		Principal component scores <sup>a</sup>	
	Females	Males	PC1	PC2
Bill length (mm)	52.3 $\pm$ 2.4	53.9 $\pm$ 1.7	0.31	0.82
Bill width (mm)	21.7 $\pm$ 0.7	23.1 $\pm$ 0.9	0.47	-0.11
Bill height (mm)	17.8 $\pm$ 0.9	18.9 $\pm$ 1.0	0.31	-0.24
Tarsus length (mm)	47.1 $\pm$ 1.9	49.0 $\pm$ 2.1	0.42	0.28
Wing length (mm)	269.1 $\pm$ 5.0	287.1 $\pm$ 6.4	0.44	-0.20

<sup>a</sup> PC1 and PC2 accounted for 57% and 14% of the variation in measurements, respectively.

To obtain an index of body condition, we used the residuals from the regression between body mass and PC1.

Feather collection from shot mallards and teal occurred from September to January during four years (2001–2005) in France. Teal feathers ( $N = 1096$  individuals) were collected from individuals hunted in France in 82 localities. Mallard feathers ( $N = 373$  individuals) all came from the Brenne area (Western France, see Legagneux et al., 2009). In Brenne, mallards are mainly non-migratory probably because of massive hand-raised releases (Legagneux et al., 2009). Moreover, ducks in Brenne are largely fed with wheat and corn deposited on lakes from July to February (Legagneux, 2007). Cultivated grains can thus represent a very large share of duck diet in Brenne (Legagneux, 2007). Therefore, captive and “wild” mallards had access to broadly the same sources of food, though *ad libitum* only for captive ones.

We used the same body size and condition indices calculation for wild mallards (see above) and because only wing length and body mass were available for teal, we kept these two rough measures in our analyses. Birds were also aged as adults or juveniles (hatch year birds) using wing feather criteria (Baker, 1993). The sex-ratio (males on males + females) was 0.55 for teal, 0.51 for wild mallard and 0.45 for captive mallards.

### 2.2. Color measurements and spectral data analysis

Recent technical developments allow the investigation of animal signaling through the visual system of conspecifics or predators in relation to ambient light and background colors (e.g. Théry and Casas, 2002). Duck wing flash-marks are surrounded by black feathers, which are thought to reinforce signaling (Hailman, 1977). The color contrast between black and flashy feathers thus appears as a biologically relevant measure to study such iridescent traits.

We measured wing flash-mark reflectance with a portable spectrometer (Avantes AVASPEC-2048 calibrated from 290 to 840 nm) and a deuterium-halogen light source (Avantes DH-2000 emitting from 215 to 1500 nm) connected with a 1.5-mm diameter sensor inserted in a miniature black chamber (Théry et al., 2005). Reflectance spectra were taken at 90° incidence relative to a 99% reflectance standard (300–700 nm Spectralon) and to dark current (black velvet background). A reference and dark current calibration were taken before measuring the feather of each individual. For each individual bird, after sampling the whole feather to detect the maximum reflectance area of the feather, a measure was taken.

From these spectrum measurements, we first extracted hue, chroma and brightness as response variable to assess variation in true coloration (see Loyau et al., 2007 for a full description of these color variables). To account for photoreceptor sensitivity of the mallard visual system, we used the physiological visual model of Vorobyev and Osorio (1998) with the visual sensitivities measured by Jane and Bowmaker (1988) and computed color and brightness contrasts with the visual background. The model was used with neural noise and photoreceptor relative densities from Håstad et al. (2005). Computations were conducted with the Avicol software (Gomez, 2006). The ambient light irradiance was diffuse

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