

# 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

daylight CIE D65, and the visual background was the reflectance of black feathers surrounding the wing flash-marks. We measured the reflectance of the black feathers on a subsample ( $N = 63$ ) of individuals and found that black feathers always reflected less than our black reference. We thus assumed perfect absorption, and calculated the brightness and color contrast using the same value of black color. The black background was chosen because wing flash-mark appears as a color signal surrounded by black and white patches belonging to the same feathers or to other secondary remiges. This particularity enhances the shape and amplifies conspicuousness of the visual signal (Hailman, 1977). Color contrast, that provides information about object color under variable illumination, is likely to be used at a shorter distance than brightness contrast that is used for detection at longer range (Osorio et al., 1999).

We assessed repeatability of measurements by comparing three reflectance spectra taken on the same feather in 20 mallard males. Because neither color nor brightness contrasts were normally distributed, we estimated repeatability by using Kendall coefficient of concordance, following the calculation described in Siegel and Castellan (1988). This coefficient is used as a nonparametric estimate of the repeatability (De Rosa et al., 2003). After ranking individuals within a series of color measurement, we estimated the relatedness between the three series of rankings. A high coefficient indicates a high similarity between the three rankings given to one individual. Both variables were found highly repeatable:  $W = 0.993$ ,  $df = 19$ ,  $P < 0.001$  for brightness contrast and  $W = 0.991$ ,  $df = 19$ ,  $P < 0.001$  for color contrast.

### 2.3. Data analysis

On captive birds, data were analyzed with ANOVAs to test the effect of body size and body condition on spectral measures. The variable responses were brightness and color contrast. Note that brightness and brightness contrast were closely related ( $F_{1,1094} = 13,800$ ,  $P < 0.0001$   $AdjR^2 = 0.93$  in teal) and chroma or hue were related to color contrast ( $F_{1,1094} = 1144$ ,  $P < 0.0001$   $AdjR^2 = 0.51$ ;  $F_{1,1094} = 1928$ ,  $P < 0.0001$   $AdjR^2 = 0.64$ , respectively). On wild individuals, we used the same approach using the following explanatory covariates: age, sex, years, body mass and wing length and date (in days since 1st September). We used a backwards stepwise model selection procedure, starting with the most satu-

rated model and subsequently removing all non-significant terms. Non-significant interaction terms were removed when they did not significantly improve the fit of a model.

We used non-transformed data since DeltaS and DeltaQ were normally distributed. All Kolmogorov–Smirnov tests  $< 0.15$ ;  $P > 0.78$  and all constant variance tests passed;  $P > 0.42$ .

## 3. Results

For both species, reflectance spectra of dabbling ducks wing flash-marks showed both a peak in the UV and a peak in the visible wavelengths (Fig. 1). In mallards, the UV peak occurred on average at  $346.9 \text{ nm} \pm 25.5 \text{ SD}$  for wild ( $N = 339$ ) and  $342.3 \text{ nm} \pm 18.4 \text{ SD}$  for captive mallards ( $N = 42$ ). The blue color peak occurred on average at  $463.6 \text{ nm} \pm 9.06 \text{ SD}$  for wild individuals and at  $470.0 \text{ nm} \pm 8.4 \text{ SD}$  for captive ones. In teal ( $N = 1167$ ), the UV peak occurred on average at  $340.8 \text{ nm} \pm 41.8 \text{ SD}$  and the green at  $547.6 \text{ nm} \pm 48.2 \text{ SD}$ .

Brightness and color contrasts were negatively related:  $F_{1,1084} = 125.9$ ;  $P < 0.001$ ;  $AdjR^2 = 0.10$  for wild teal;  $F_{1,329} = 63.7$ ;  $P < 0.001$ ;  $AdjR^2 = 0.16$  for wild mallards;  $F_{1,40} = 27.8$ ;  $P < 0.001$ ;  $AdjR^2 = 0.40$  for captive mallards.

### 3.1. Colors of captive mallards

The spectra did not differ between age classes, but did so between sexes for both color and brightness contrasts. Females showed lower color contrast and greater brightness contrast than males ( $F_{1,40} = 6.44$ ,  $P = 0.015$  and  $F_{1,40} = 8.15$ ,  $P = 0.007$ , respectively). Brightness contrast decreased with increasing body condition in both sexes ( $F_{1,21} = 6.82$ ,  $P = 0.016$ ,  $AdjR^2 = 0.21$  and  $F_{1,17} = 6.89$ ,  $P = 0.018$ ,  $AdjR^2 = 0.25$  for males and females, respectively; Fig. 2). A similar relationship between brightness and body size was found in females ( $F_{1,17} = 7.48$ ,  $P = 0.014$ ,  $AdjR^2 = 0.26$ ), but not in males ( $P = 0.19$ ). In females, nearly significant positive relationships between color contrast and body condition or body size were found ( $F_{1,17} = 3.36$ ,  $P = 0.084$ ,  $AdjR^2 = 0.12$  and  $F_{1,17} = 3.42$ ,  $P = 0.082$ ,  $AdjR^2 = 0.12$ , respectively, Fig. 2), as well as a significant positive relationship between color contrast and wing length ( $F_{1,17} = 6.96$ ,  $P = 0.017$ ,  $AdjR^2 = 0.25$ ). All relationships between color contrast and body condition or size were far from significant in males (all  $P > 0.12$ ).

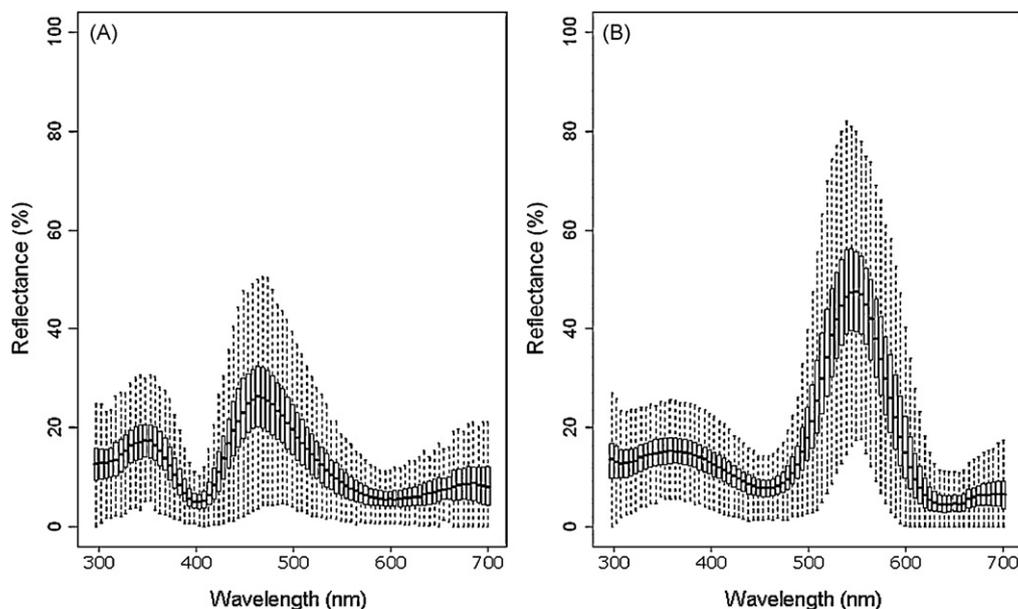
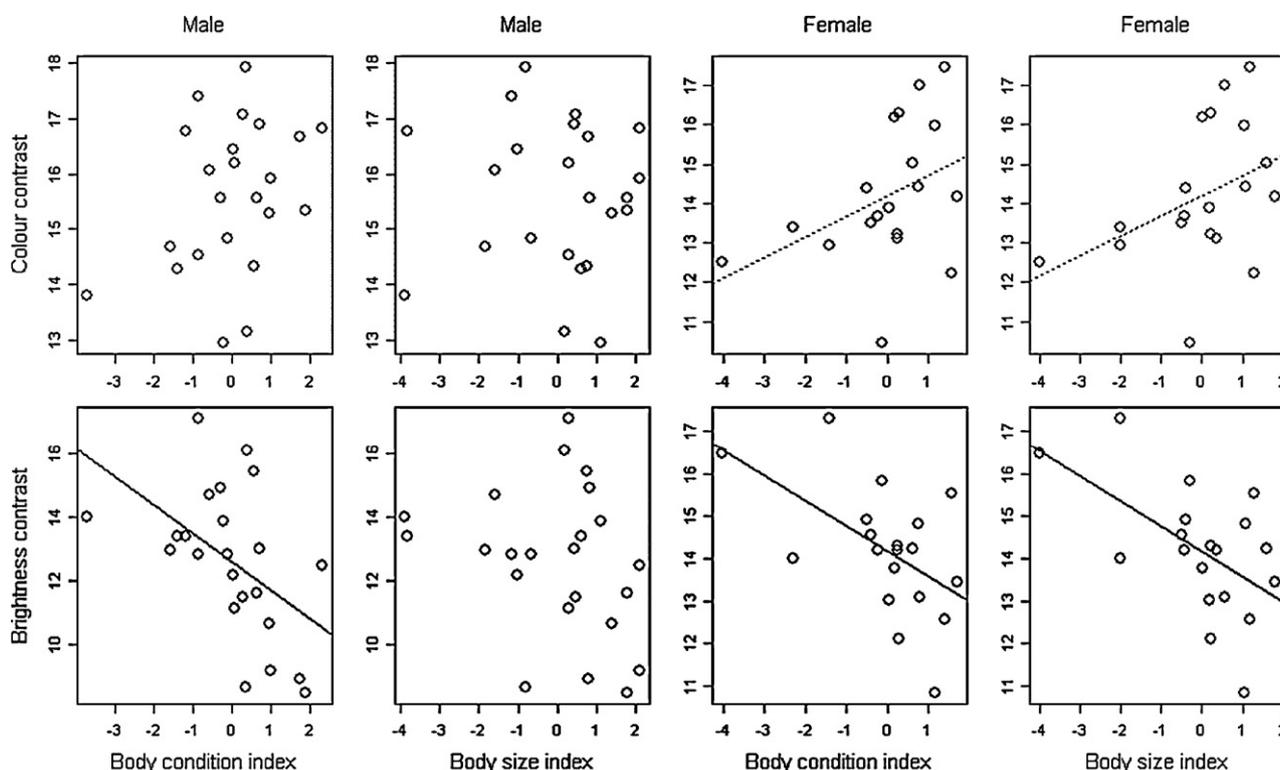


Fig. 1. Typical median reflectance spectra ( $\pm$ lower and upper hinges and whiskers) of wild mallards (A) and teal (B) wintering in France, measured with reflectance spectrometry.



**Fig. 2.** Relationships between brightness (bottom line of graphs) or color (top line of graphs) contrast (relative to black surrounding feathers) and body condition (residuals from the regression of body-size index and body mass) and body size (estimated with the 1st scores of a PCA on body measurements) per sex, from semi-captive mallards ( $N = 19$  females and 23 males). Dotted line, nearly significant relationships  $0.05 < P < 0.08$ . Plain line, significant regressions ( $P < 0.05$ ).

### 3.2. Colors of wild mallards and teal

To compare the signals between mallards from the wild and kept in semi-captivity, we subsampled wild individuals from September only ( $N = 70$  females and 65 males). Color contrast was greater for captive mallards (both sexes combined) than for wild ones ( $F_{1,133} = 7.99, P = 0.005$ ). Brightness contrast was greater for captive females than for wild ones ( $F_{1,68} = 4.57, P = 0.036$ ), while no significant difference was found for males ( $F_{1,63} = 0.33, P = 0.568$ ).

The results of the ANOVA that included color and brightness contrasts as dependent variables revealed a strong sexual dimorphism in wing flash-mark signaling (Table 2). Color contrast increased with teal wing length (see Table 2 and Fig. 3). The positive relationship between wing length and color contrast was mainly due to females ( $F_{1,650} = 5.448, P = 0.021$ ) rather than males ( $F_{1,519} = 0.288, P = 0.59$ ). An age effect was also found in wintering teal: the color of adults was more contrasted than that of juveniles (Table 2). In mallards, an age effect was found for the brightness (Table 2) where adults were brighter than juveniles. Wing flash-mark reflectance greatly differed among years. In teal, the 13 individuals collected in 2005 showed lower color contrasts which may partly explain the strong year effect. Interestingly, in both species, an effect of date was also recorded (Table 2): brightness contrast decreased over time in both species, but only after a certain date in teal (Fig. 4), while color contrast increased only for teal. More specifically, in mallard, brightness decrease over time varied between years. In 2001, brightness contrast increased over time.

### 4. Discussion

Our results revealed that body size (and condition to a lesser extent) and structural signals were related in ducks. This was especially true for semi-captive birds, measured soon after molting. The positive relationships were significant in females but not in males, a

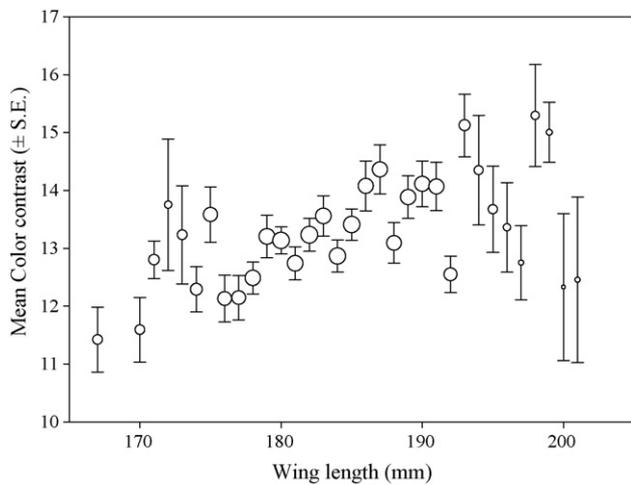
result consistent with what was found for wild teal on wing length. Wild birds were less bright and colored than semi-captive birds fed *ad libitum*. *In natura*, we first found an age effect indicating that adults were more colored than juveniles. Secondly, as expected, we found that plumage brightness decreased over time while color contrast was more constant.

Although condition dependence of pigment coloration has been largely demonstrated during the past decade (e.g. Hill, 1999; Alonso-Alvarez et al., 2004; Peters et al., 2004, 2007), relatively few

**Table 2**

ANOVA results for the linear models based on the color and brightness contrast with degrees of freedom (df), Sum of squares (Sum sq),  $F$ -values, and  $P$ -values for variables retained in the model after a backward stepwise selection procedure. Significant  $P$ -values are shown in bold.

	df	Sum sq	$F$ -value	$P$ -value
<b>Mallard</b>				
Response: color contrast				
Sex	1	65.0	13.648	<b>&lt;0.001</b>
Response: brightness contrast				
Age	1	100.4	8.49	<b>0.004</b>
Date	1	21.9	1.85	0.17
Year	2	70.9	2.99	<b>0.05</b>
Date*year	2	114.0	4.82	<b>0.009</b>
<b>Teal</b>				
Response: color contrast				
Wing length	1	49.3	7.68	<b>0.006</b>
Date	1	84.6	14.73	<b>&lt;0.001</b>
Year	4	90.3	3.52	<b>0.007</b>
Age	1	74.2	11.57	<b>&lt;0.001</b>
Sex	1	221.9	34.57	<b>&lt;0.0001</b>
Response: brightness contrast				
Date	1	45.0	9.26	<b>&lt;0.01</b>
Year	4	128.2	6.59	<b>&lt;0.0001</b>
Sex	1	59.5	12.23	<b>&lt;0.001</b>



**Fig. 3.** Relationship between color contrast and wing length in the green-winged teal shot by hunters in France. Dot size is proportional to the number of individuals. Data presented here include both sexes.

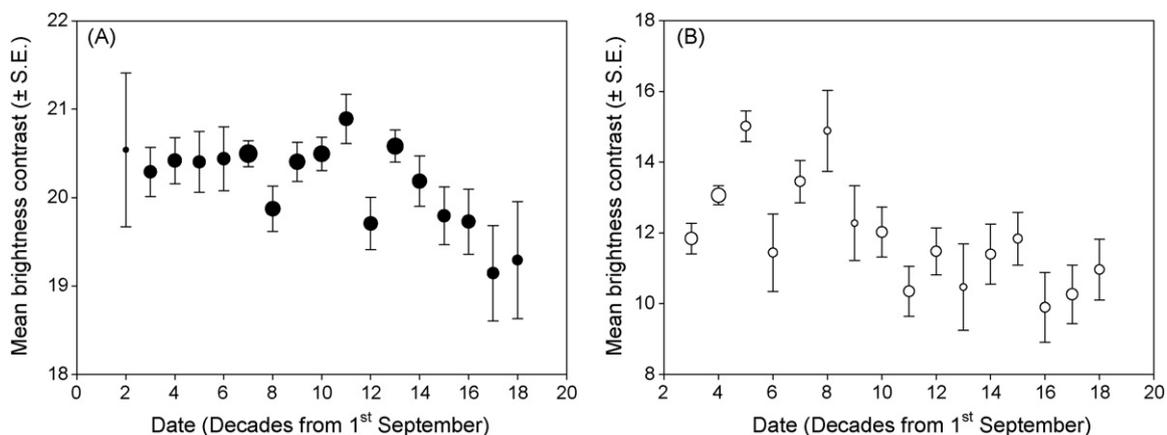
studies have investigated such condition dependence in structural colors (McGraw et al., 2002; Shawkey et al., 2003; Siefferman and Hill, 2005; Madsen et al., 2007; Siitari et al., 2007).

In captive mallards, body condition was negatively related to brightness contrast. However, this was not the case in wild individuals. This discrepancy may be related to the reduction of potential environmental constraints such as food limitation or predation risk in the lab. Individuals raised in semi-captivity and fed *ad libitum* were indeed more colored than wild birds. This is likely to reflect the importance of the amount of food available during the molting period, as pointed out by McGraw et al. (2002) even if other factors such as parasites, degree of social interactions, light environment, and temperature might also be invoked here. Conversely, we did not find any difference in brightness contrast between wild and captive mallards, which suggests a less flexible component of feather coloration. We found a positive relationship between color contrast and body size or wing length in both captive female mallards and wild female teal. Brightness contrast also decreased over time. However, the decrease phase occurred later in the season for teal compared to mallards. This discrepancy may be due to different migratory regimes. Mallards are known to be more sedentary than teal in France, the latter being a typical long-distance migrant (Guillemain et al., 2005). In addition, hand-reared mallards are released each year in Brenne before the hunting season (Legagneux et al., 2009), and this could enhance sedentary behaviour. In teal,

different individuals belonging to different breeding areas are likely to have been sampled throughout the hunting season. Repeated measures on the same individuals would have allowed determining the temporal pattern of feather degradation, though this was obviously impossible with hunter-shot birds. However, we are confident that whatever the mechanism explaining feather degradation (i.e. bacteria attack, UV rays from daylight, abrasion when flying or landing), brightness contrast is more likely to decrease over time than color contrast (slight increase in teal). In winter, during the mating period, color contrast appears to be more preserved than brightness contrast, and may therefore constitute a reliable indicator of condition or body size.

However, we found that brightness contrast and condition were negatively related in semi-captive mallards. In females, the relationship between condition and brightness contrast was dominated by the strong size-brightness relationship, while in males the condition index was dominated by body mass. Larger (or in better condition) females are more likely to be darker and to some extent more colored, especially in teal. Since color and brightness contrasts are negatively related (i.e. more colorful individuals have a darker plumage), the combination of both brightness and color might be integrated as a “quality indicator”. For instance, females that present lower brightness would tend to maximize crypsis, a crucial factor affecting reproductive success in ducks (Kreisinger and Albrecht, 2008). Color contrasts would be used by birds at a short distance and provide information about object color under variable illumination; whereas brightness contrast would be used for detection at longer range (Osorio et al., 1999). It is worth noting that Doutrelant et al. (2008) found that brightness rather than color (Chroma, UV) was positively related to laying date and survival in blue tit. Differences in migration regimes, timing of pairing, etc. may be involved in explaining these differences. Moreover, further experiments are definitely needed to investigate which part of the spectra is devoted to pairing attractiveness.

Interestingly, relationships between body size (or condition) and color traits were found only in females. Duck female contrast with males that present multiple ornaments to signal themselves, including bill color (a carotenoid-based signal, Peters et al., 2004), a predominant factor in female mallard attraction (Omland, 1996a,b). Most studies on mate choice have focused on female preferences and comparatively, less attention has been given to the study of male choices (Davis, 2002). However, a growing number of empirical studies demonstrate male mating preferences in bird species (Amundsen, 2000; Griggio et al., 2005; Amundsen and Pärn, 2006). Such condition-dependent structural traits in females were found on different studies involving passerines (Amundsen et al., 1997; Siefferman and Hill, 2005; Doutrelant et al., 2008). For exam-



**Fig. 4.** Relationship between brightness contrast and date (in decades) for green-winged teal (A) or mallard (B) shot in France. Dot size is proportional to the number of individuals. Data presented here include both sexes.

ple, by combining experimental and field approaches, Siefferman and Hill (2005) were able to demonstrate the importance of structural coloration on female reproductive output. Females that were given *ad libitum* access to food displayed more ornamented structural coloration than females on a food-restricted diet. The structural coloration of bluebird females predicted first egg date, maternal provisioning rates, and measures of reproductive success.

Yet, to our knowledge, such studies that investigate male choice in relation to female plumage coloration and body size or condition in ducks are still lacking. In Goldeneye, *Bucephala clangula*, females with wing patches with more white than black of the female bred earlier and had a better reproductive success (Ruusila et al., 2001). In the common eider, *S. mollissima*, Hansen et al. (2006) found that size and purity of the female wing white patch was related with immune functions during breeding. Our results suggest that the color of structural feathers is size and condition-dependent in females. The main factors involved in the breeding ability of female Anatidae are hatching date (Ruusila et al., 2001; Blums et al., 2005), body condition (Blums and Clark, 2004; Blums et al., 2005) and body size (Larsson et al., 1998). We found significant relationships between plumage coloration and a fitness-related trait in females in both wild teal and captive mallards. Such link would suggest that female characteristics may be under sexual selection, as for males (Muma and Weatherhead, 1989; Møller, 1993) and that bi-directional mate choice should be expected (see Sorenson and Derrickson, 1994; Heitmeyer, 1995). However, such links were not found in wild mallards and testing this through behavioural experiments remained to be done.

We found that adults were more colored than juveniles in teal, a long-distant migrant. Since only adult males replace their flight feathers on distinct molting grounds, molting location differences are not likely to explain such differences. Another explanation is that ducklings have to allocate most of their energy to growth. Adults may be better able to allocate resources to (presumably) secondary sexual characters than juveniles. On the contrary, we found no significant differences between age classes and strong variation among years in mallards. Here again, the fact that mallards in our study site are non-migratory could explain such result. Because dabbling ducks are sexually mature the year after hatching (Cramp and Simmons, 1977), juveniles should develop a plumage coloration very similar to that of adults right in the first winter. The additional energetically cost of migration in teal would prevent young to reach adult color scores. This idea is reinforced by the fact that no age effect was found in captive mallards raised without nutritional stress. This may reflect the ability of juveniles to grow feathers of similar quality to adults when necessary nutrients are readily available. In addition, our results underline a strong inter-annual variation of the wing flash-marks coloration of wild individuals. This likely reveals a direct effect of environmental conditions, which fluctuate from year to year, on duck feather quality. To investigate which environmental factor (e.g. flooding levels, food availability and quality) is the main driver of plumage quality, long-term studies comparing environmental variables and feather reflectance at the molting grounds would be necessary.

## 5. Conclusion

This study suggests that brightness and color contrasts are involved in different signaling functions. Sexual differences in speculum coloration are related to color contrast while the brightness contrast is more influenced by time. Individuals able to produce more colorful structural feathers, well discriminated at short distance, would be less conspicuous to predators using brightness contrast from a longer range. Mediated by both natural and sexual selection, colorful individuals should be selected. The

present study appears as a necessary step in the understanding of duck signaling and the function of structural signals. Because ducks are easy to hold and to reproduce in captivity, it also offers great experimental perspectives to test for the existence of directional male mate choice and assess the importance of wing flash-mark reflectance as an honest signal during pairing and breeding.

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