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The importance of white on black: unmelanized plumage proportion predicts display complexity in birds

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Abstract Animal ritualized displays have been classically viewed as behavioral characters that decrease signal ambiguity or that facilitate the evaluation of costly exhibitions. It has been shown that their prevalence and level of complexity across species can reflect phylogenetic relationships between them, but the adaptive function of these behavioral traits is poorly known. Here, I hypothesize that, given that the efficacy of visual displays basically depends on conspicuousness and level of performance, species with low levels of conspicuousness may be forced to perform more complex varieties of a given display to get the same signal efficiency than other more conspicuous species. Thus, the evolution of display complexity, considered as the level of exaggeration of ritualized movements, may be explained as an adaptive trait and not only by phylogenetic inertia. I illustrate and test this hypothesis with the case of black-and-white plumage patches of pelecaniform birds. As predicted, there was a negative correlation between level of complexity and species conspicuousness (proportion of unmelanized plumage) for two different social displays. This indicates that classical ideas on the adaptiveness of ritualized displays should be considered to understand the present variation in signal form across species, which sheds light on the evolution of multiple signals.

Keywords Melanin · Multiple signals · Pelecaniformes · Plumage color · Ritualization

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Introduction

Animal displays comprising ritualized movements were one of the subjects that captured the attention of early ethologists (e.g., Huxley 1914). The classical explanation for the function of these signals, from a tactic point of view (sensu Rowe and Skelhorn 2004), was that they serve to reduce message ambiguity (Cullen 1966). Zahavi (1979) later applied his "handicap principle" to these behaviors arguing that ritualized displays facilitate the evaluation by receivers of the costs that ensure their reliability. At an interspecific perspective, Lorenz (1941) proposed that the prevalence of this type of displays can reflect phylogenetic relationships, which has been demonstrated more recently by showing that these traits are not more convergent than biochemical or morphological characters (Kennedy et al. 1996). However, interspecific studies have rarely taken into account ideas made from intraspecific perspectives that consider the adaptive function of ritualized displays like those of Cullen (1966) or Zahavi (1979; see Bókony et al. 2003; Ord and Blumstein 2002 for examples testing adaptive hypotheses). Interspecific variation in prevalence or complexity of ritualized displays may be explained not simply by phylogenetic inertia (i.e., the effects of ancestors on descendents) but also by variation in phenotypic traits that affect the tactic aspects of displays and also reflect phylogenetic relationships.

The efficacy of visual displays in eliciting a response from a receiver depends on two elements: conspicuousness and level of performance (Zahavi 1979; Hasson 1991; Aragonés et al. 1999). "Conspicuousness" refers to the capacity of a color patch to stand out against the background (e.g., Livingstone 2002). In the case of displays composed of ritualized movements, the terms "performance" or "complexity" refer to the level of exaggeration

of such movements, given that they evolve from simple movements resembling an initially unritualized act (e.g., intention movements to fly away or to copulate) to more complex stereotyped movements (see for example Zahavi 1979; Kortlandt 1995). Hence, among a group of species that share a given display but that differ in the level of performance with which it is made, the most conspicuous species may be less constrained to communicate efficiently through their displays. These species should therefore need lower levels of performance to get the same signal efficiency (i.e., should be less complex) than less conspicuous species. I hypothesized that variation in the expression of phenotypic traits that confer animals with varying levels of conspicuousness could explain variation in the level of display performance. In addition to conspicuousness, the exaggeration of movements reflects the motivation of the senders and affects the efficacy with which visual displays are perceived (Wachtmeister 2001; Lander and Chuang 2005; Ord et al. 2007; Peters 2008). In fact, performance level is often related to copulation or breeding success (Grønstøl 1996; Blomqvist et al. 1997; Torres and Velando 2003).

An example of such phenotypic traits could be the unpigmented (i.e., white) patches that can be observed in several species of birds and mammals whose body integuments are otherwise covered by dark colors conferred by melanins. As white is created by reflectance through all wavelengths, these achromatic patches are very conspicuous when exhibited over dark structures such as terrestrial backgrounds (Bókony et al. 2003; Beauchamp and Heeb 2001) or the melanized surface of the body itself (Kenward et al. 2004; Wüster et al. 2004; Ljetoff et al. 2007). Several authors that have studied white plumage or hair patches have shown that they often function as signaling devices that transfer many types of information, mainly the presence of signalers or predators (e.g., Alvarez et al. 1976; Beauchamp and Heeb 2001; Alvarez 2004; Ellis and Lish 2006; Ljetoff et al. 2007; Penteriani et al. 2007b; Caro 2008) or signaler quality (Ferns and Hinsley 2004; Doucet et al. 2005; Ljetoff et al. 2007; Penteriani et al. 2007a, b). These patches are also involved in other signaling functions such as sensory exploitation (Jabloński 2001), countershading (Ruxton et al. 2004), predator confusion (Kamler and Ballard 2006), or deceptive attraction of prey (Negro et al. 2007).

Even if animals use the color per se of stimuli, the contrast of the color may be more important than the color per se in detection (Osorio et al. 1999; Schmidt et al. 2004). In theoretical and empirical studies carried out with humans, it has been shown that patterns of contrasting colors facilitate the perception of size (Berglund 2000) and of the direction of movement (Delicato and Derrington 2005; Lenoir et al. 2005). Animals also seem to have sensory biases towards contrasting colors (Jabloński 2001), perhaps because visual perceptions such as motion exhibit

greater sensitivity to abrupt than to gradual color change (Linvingstone 2002). Given these properties, the presence of white color patches on melanized body structures could be of particular importance in sexual and social displays in which stereotyped movements are performed, as they may improve the perception of such movements or simply the presence of the attracting signaler. In fact, it has been suggested that this signal design could have evolved as an amplifier of individual quality because "odd" individuals would stand out during the course of displays (Barber and Folstad 2000; Ljetoff et al. 2007).

Therefore, I predicted that, in species that perform terrestrial displays, the higher the proportion of white, the more conspicuous the body surface and, hence, the more efficient the visual displays in transferring information or in carrying out any other function (e.g., sensory exploitation or deception; see references above). A negative linear relationship between the proportion of white plumage and display complexity was thus expected if this possibility is true.

It must be noted here that the negative relationship is predicted irrespective of the type of information transferred by visual displays (i.e., presence or individual quality; see above). In the first case (i.e., if signals are "notices"), such a relationship would indicate that selection is favoring the use of either exaggerated movements or white color patches because there would be only a certain amount of information that needs to be conveyed (e.g., Dale 2006). In the second case (i.e., if signals are "advertisements") a negative relationship would indicate that the honesty of displays is maintained because of the costs of repetitive exaggerated costs (e.g., Zahavi 1979) or of white plumage patches (e.g., Kose et al. 1999), and, thus, selection would be favoring one or the other honest indicator, but not both since the cost would be prohibitive (Pryke et al. 2001).

As these hypotheses deal with the interaction of two potentially signaling traits (i.e., ritualized movements and plumage color), the results could be worthy for our understanding of the evolution of multiple signals, an issue that is aim of current research from both theoretical and empirical approaches (e.g., Badyaev et al. 2002; Candolin 2003).

I tested this prediction by carrying out a comparative study on the relationship between the proportion of unmelanized plumage and display complexity in the order Pelecaniformes. These birds constitute a good study model because (a) their plumage is entirely composed of melanized and unmelanized feathers that create black- (or brown) and-white patches, with the exception of red tail feathers in red-tailed tropicbirds *Phaethon rubricauda* and iridescent tones in some cormorants (del Hoyo et al. 1992; Harrison 1996) and (b) the complexity of their social displays has been studied in detail (van Tets 1965; Kennedy et al. 1996).

Materials and methods

Measurement of display complexity

I used the study of Kennedy et al. (1996) to obtain information on the complexity of the social displays of Pelecaniformes. These authors compiled detailed information on the different displays for 20 pelecaniform taxa obtained by van Tets (1965) and showed that the prevalence and complexity level of displays reflect the phylogenetic relationships between the studied taxa. With the exception of "locomotion on land", all of them are social displays performed by the sitting or perching birds (i.e., terrestrial displays), some of them during the breeding season only, and others all year round (Kennedy et al. 1996).

I used the information for the only two displays for which different degrees of complexity were established: "male advertising" and "threat" (Kennedy et al. 1996). While "male advertising" is a sexual display that serves to attract females towards single males, the "threat display" is performed by both males and females to frighten other animals away and thus maintain the individual distance (van Tets 1965). For the former display, there are five levels of complexity: (0) absent, (1) sky pointing, (2) alternate wings waved, (3) slow rate wing waving, (4) rapid flutter wing waving, and (5) darting and throwback, while there are eight levels for the latter one: (1) pecking and screaming; (2) pointing or wagging bills; (3) move towards intruder; (4) snapping and waving open bills; (5) raise, open, and wave bills; (6) S-shaped expanded neck, open bill; (7) head repeatedly thrown forward; and (8) repeated head darting followed by head shake and gargling sound. Although van Tets (1965) and Kennedy et al. (1996) did not explicitly mention that these gradations correspond to variations in display complexity because they were "only" interested in how these categories are distributed among taxa and it is difficult to make textual descriptions of exaggeration levels, it can be inferred from these descriptions that the higher the score, the higher the exaggeration of movements: There is a "default" stereotyped posture that is subsequently complemented with additional exaggerations of movements like higher waving velocities or strengthments of the neck. For example, van Tets (1965) indicated that, in the case of the "male advertising display", the extent to which the tail is raised appears to be related to the intensity of the display. A detailed description of postures and movements performed during the different display categories is shown in "Appendix". Thus, it must be pointed out that the terms "complexity" and "performance" refer here to variations in the ritualization of displays and not to display repertoire size like in other studies (e.g., Ord and Blumstein 2002).

Quantification of unmelanized plumage patches

As the displays of pelecaniforms imply stereotyped postures in which practically all body parts are involved (van Tets 1965), I quantified the proportion of white plumage parts by examining illustrations of pelecaniforms in del Hoyo et al. (1992) and Harrison (1996). Illustrations of both resting and flying birds were examined. I did not consider neither iridescent plumage patches or colored bare parts. I followed the method used by Beauchamp and Heeb (2001) to obtain estimates of the proportion of white present in the plumage of each species, assigning scores that ranged from 0 (total lack of white) to 5 (all white).

The 20 taxa of van Tets (1965) corresponded to three genera and 17 species, so in the three genera reported, I examined the proportion of unmelanized plumage for each component that composed them and then assigned the mean value to the genus for the analyses. Only illustrations corresponding to adult birds in breeding plumage of the nominate subspecies were examined, even when subspecies differed in the degree of white (e.g., the great cormorant). In the case of the red-footed booby *Sula sula*, which is highly polymorphic, I only considered the white morph, as this is the most common along the species' range (Baião et al. 2007). I only considered two species of darters (*Anhinga anhinga* and *Anhinga melanogaster*) as reported by del Hoyo et al. (1992). Sexual dichromatism is almost absent in pelecaniforms (del Hoyo et al. 1992; Harrison 1996; Nelson 2006), but male and female frigatebirds and darters differ in the proportion of white plumage. In those cases, I assigned to each species the mean unmelanization score of male and female. When the presence of white in a certain body part was not composed of well-defined plumage patches but limited to loose white flecks (double-crested cormorant *Phalacrocorax auritus*) or filoplumes (Brandt's cormorant *Phalacrocorax penicillatus*) that gave the birds a "whitish look", I assigned an unmelanization score of 1. Although all whiteness scores assigned to individual species were discrete values that ranged from 0 to 5, I assigned a score of 1.5 to the great cormorant, as this species presents an intermediate proportion of white between those species only presenting white flecks or filoplumes and those with a higher proportion of white like the brown booby *Sula leucogaster*. The whiteness scores obtained for each taxon are shown in Table 1.

Comparative analyses

The scores obtained for both display complexity and unmelanized plumage were log transformed (adding 1 in the case of "male advertising" and plumage whiteness), and the Pearson's correlation coefficient between these two

Table 1 Proportion of unmelanized plumage (whiteness), complexity of two different displays (male advertising and threat) for the species considered in the study

Species	Whiteness score		Male advertising complexity	Threat complexity
	Male	Female		
Phaeton aethereus	4	4	0	1
Phaeton rubricauda	5	5	0	1
Phaeton lepturus	4	4	0	1
Fregata aquila	0	0	0	4
Fregata andrewsi	1	2	0	4
Fregata magnificens	0	2	0	4
Fregata minor	0	2	0	4
Fregata ariel	1	2	0	4
Pelecanus onocrotalus	4	4	0	5
Pelecanus rufescens	4	4	0	5
Pelecanus philippensis	4	4	0	5
Pelecanus crispus	5	5	0	5
Pelecanus conspicillatus	3	3	0	5
Pelecanus erythrorhynchos	4	4	0	5
Pelecanus occidentalis	3	3	0	5
Sula sula	4	4	1	2
Sula leucogaster	2	2	1	2
Sula dactylatra	4	4	1	2
Sula nebouxii	3	3	1	2
Sula variegata	3	3	1	2
Morus capensis	4	4	0	2
Morus serrator	4	4	0	2
Morus bassanus	4	4	0	2
Anhinga anhinga	1	1	2	3
Anhinga melanogaster	1	3	2	3
Phalacrocorax penicillatus	1	1	4	7
Phalacrocorax carbo	1.5	1.5	3	6
Phalacrocorax olivaceus	1	1	3	6
Phalacrocorax varius	3	3	3	6
Phalacrocorax auritus	0	0	3	6
Phalacrocorax aristotelis	0	0	5	7
Phalacrocorax pelagicus	1	1	4	8
Phalacrocorax urile	1	1	4	8

In the analyses, the mean values for the genera *Phaeton*, *Fregata*, *Pelecanus*, and *Anhinga* were used because van Tets (1965) did not provide information on complexity and prevalence of displays for each of the species belonging to those genera

variables was then calculated. An inspection of residuals confirmed that the normality assumption was fulfilled.

In the case of "male advertising" display, the first category of complexity (0) corresponded to an absence of display (see above). Thus, I performed a correlation analysis for the entire dataset and another for only taxa with categories >0 in order to determine if the consideration of the absence of display as the minimum complexity level could affect the results.

I did not control for factors such as body size because there are no a priori reasons to expect a relationship between this variable and plumage whiteness. In fact, Beauchamp and Heeb (2001) found that the level of whiteness is not associated with body size across several species of birds. Sexual dichromatism could be a confounding factor, but its occurrence among pelecaniform birds is very low, limited to frigatebirds and darters, and in these cases, its degree is also low (del Hoyo et al. 1992; Harrison 1996; Nelson 2006). There are other possible confounding variables. For example, cormorants might be selected to be black because this helps to dry their feathers quickly (Burtt and Ichida 2004), an effect of habitat or diving lifestyle that might also affect their display performance (e.g., through predation pressure, see Johnson 2000). However, it is likely that such a large birds as cormorants are not under strong predation risk. On the other hand, tropicbirds have a more aerial lifestyle: They catch fish by hovering, so white plumage might give them better hunting camouflage (Götmark 1987). Although several possibilities may exist, only analyses between pairs of variables were performed in the present study, thus increasing the degrees of freedom and power of the tests.

The effect of common ancestry among taxa can lead to an overestimation of degrees of freedom if phylogenetic relationships are not taken into account (see Garland et al. 2005 for a recent review). Thus, I calculated a critical value for the correlation coefficient from data simulated on the basis of the phylogeny of taxa and following a particular model of evolution. For this purpose, I introduced the phylogenetic relationships and the values of both variables in the module PDTREE of the software PDAP and then used this information to generate 1,000 Monte Carlo computer simulations with PDSIMUL (Garland et al. 1993). The branch lengths were set equal to unity, and the simulations were made according to a speciational Brownian motion model of evolution (Garland et al. 1993).

The phylogenetic hypothesis used (Fig. 1) was obtained from different phylogenies inferred from mitochondrial DNA sequences. The phylogeny obtained by Kennedy et al. (2000) was used to determine relationships among *Phalacrocorax* species. Phylogenetic relationships between *Sula* species were determined from Friesen et al. (2002). The results reported by Friesen and Anderson (1997) were used to determine relation-

ships between *Morus* species. Finally, relationships between *Phaeton*, *Pelecanus*, *Morus*, *Anhinga*, *Phalacrocorax*, and *Fregata* were inferred from the phylogeny obtained by Kennedy and Spencer (2004) and relationships between *Morus* and *Sula* from Kennedy et al. (2000).

I set the correlation between the traits to simulate as zero in order to contrast the analyses with data on the traits having evolved independently with those performed with real data. I simulated the data adding a lower bound of 0 to the evolution of all traits (see Lovegrove 2001 for an example of bounded simulations) and upper bounds corresponding to the logarithm+1 of the maximum values obtained for all variables. The "replace" algorithm of PSIMUL (Garland et al. 1993) was used during the course of simulations. Thus, I calculated a correlation coefficient for each set of simulated data, considering the 95th percentile of the absolute values of this distribution as the phylogenetically correct critical value. The P value was then calculated as the number of absolute values of coefficients that were higher than the absolute value of the empirical coefficient divided by the number of simulations performed (Garland et al. 1993). As a different

simulated distribution of correlation coefficients was used for each analysis, it was not necessary to apply corrections for multiple tests.

Results

I obtained a negative and significant correlation between the complexity of male advertising display and proportion of white plumage without controlling for phylogeny ($r=-0.66$, $n=20$, $P=0.002$; Fig. 2a). The critical value from conventional tables was a coefficient of -0.44 and was increased up to -0.54 when calculated from the phylogenetically correct distribution of correlation coefficients. Thus, the relationship remained significant when the effect of common ancestry was considered, with an exact P value of 0.012. The same relationship was found when data on taxa in which male advertising is absent were removed from the analysis (conventional tables—$r=-0.76$, $n=14$, $P=0.001$; phylogenetically correct distribution—critical $r=-0.66$, $P=0.015$).

Fig. 1 Phylogenetic hypothesis for the 20 taxa used in the study
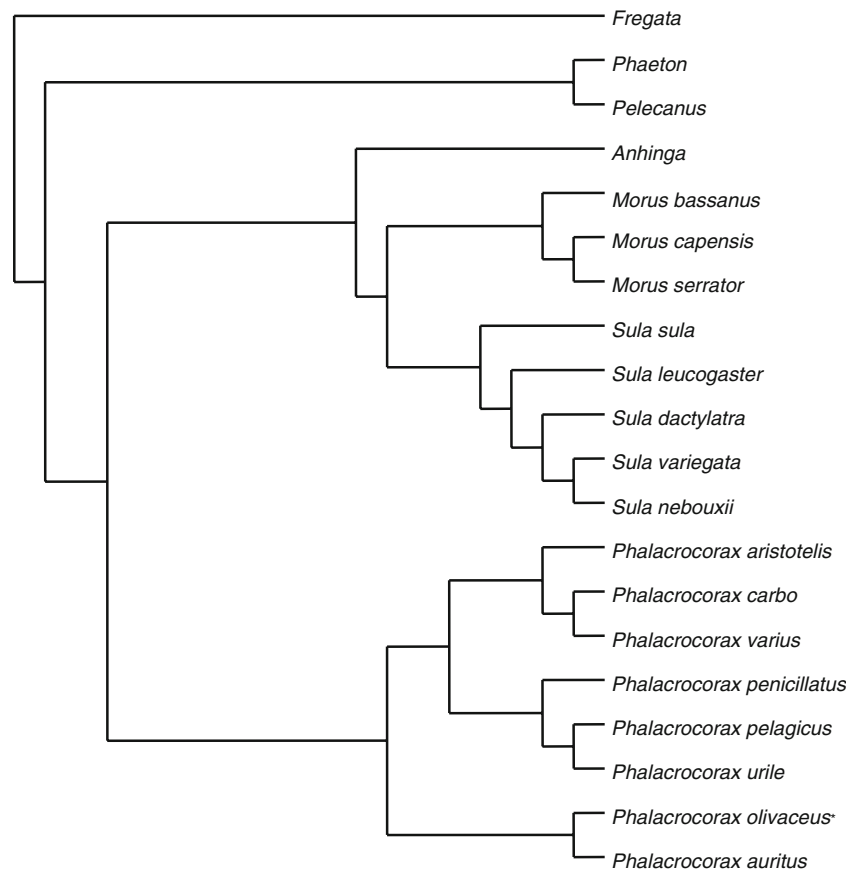
*: as *Phalacrocorax brasilianus* in Kennedy et al. (2000).
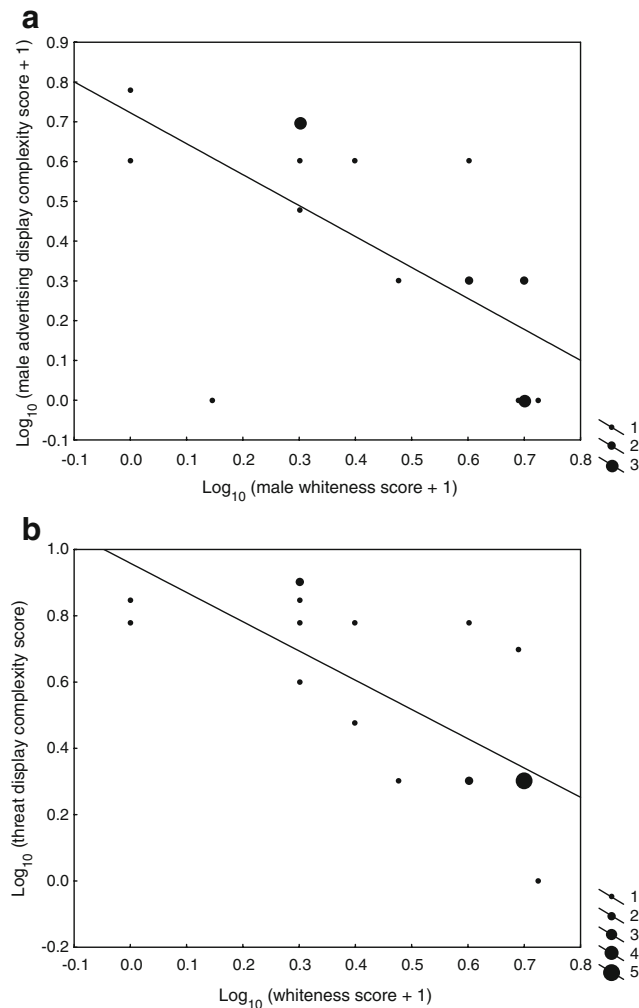
Fig. 2 a Relationship between male advertising display complexity and male plumage whiteness. **b** Relationship between threat display complexity and plumage whiteness. The *size of the points* indicates the number of overlapping taxa. *Lines* are regression lines

When the complexity of the threat display was considered, the correlation with the proportion of unmelanized plumage was also significant (conventional tables—$r=-0.74$, $n=20$, $P<0.001$; phylogenetically correct distribution—critical $r=-0.53$, $P=0.005$; Fig. 2b). Therefore, the complexity of displays decreased across taxa as the proportion of white color on plumage increased.

Discussion

As predicted by the hypothesis that dark-and-white contrasts increase the efficacy of visual displays because they enhance the perception of movements or the presence of the signalers (see "Introduction"), the complexity of two

stereotyped displays (male advertising and threat display) decreased as the proportion of unmelanized plumage increased across 20 taxa of pelecaniform birds. These displays are shared by the members of the order, but the level of performance varies between species in a manner that reflect the phylogenetic relationships between them (Kennedy et al. 1996). The results of the present study show that this variation can be also explained by a phenotypic trait whose evolution may have been favored, at least in part, by the benefits reported to signalers during the course of displays, whatever their function is.

Conspicuousness and level of performance are two elements that determine the efficacy with which visual displays act on receivers (see "Introduction"). Therefore, species in which natural selection has led to the conservation of highly melanized forms because of any of the adaptive benefits reported by melanins to birds (mainly related to an increase of stiffness and resistance to abrasion, thermoregulation, protection against UV radiation, and different tasks of visual signaling; Bortolotti 2006; McGraw 2006; Prum 2006) may have been forced to develop varieties of displays with high levels of performance. This may explain why a stereotyped display, whose presence is conserved throughout a phylogeny, can vary in complexity across species. This interpretation could fit well with the classic explanation of Cullen (1966) that ritualized displays serve to decrease ambiguity. Of course, the reversed direction (i.e., that the presence of white patches has been favored because of constraints on performance displays) is also possible. In any case, these results agree with the idea that multiple signals can evolve because the expression of one of the traits increases as a compensation for a decrease in the expression of other trait (Badyaev et al. 2002).

Another question that now arises is if the relevant character for displaying birds is the contrast of melanized and unmelanized plumage patches per se or the contrast that the white plumage patches create against the environmental background. This latter possibility is likely because all the displays analyzed here are performed on the ground, which is generally dark and thus contrasts with the white color of birds (e.g., Bókony et al. 2003; Beauchamp and Heeb 2001), or on perchs that can be seen against the ground. Indeed, it has been shown that white color per se increases the conspicuousness of birds and thus has been favored in species that benefit from communal foraging (Beauchamp and Heeb 2001; but see Green and Leberg 2006). However, the fact that there are no entirely white pelecaniforms, even when there are white feathers on all body parts, and all of them present melanized patches, means that there are always black-and-white contrasts between body parts, and this may suggest that these contrasts on the same body structure may have evolved in part to precisely increase

conspicuousness (Barber and Folstad 2000; Ljetoff et al. 2007). Future empirical studies should resolve this question by determining if the location of melanized plumage patches in pelecaniforms and other groups of birds with dark-and-white contrasts depends on natural selection or on (in addition to) signal selection effects.

It is noteworthy that theoretical studies have shown that, when two different signals coevolve together with a receiver system, they tend not only to be different but to be opposed to each other as well (Hurd et al. 1995), and this may explain the high prevalence of black-and-white contrasts in nature. The present study shows that colored patches that increase conspicuousness may have coevolved together with ritualized movements, and the "opposing" nature of black and white colors could make them one of the best alternatives to increase the efficacy of stereotyped displays, especially in species limited to generate other types of colorations through different pigments or structures. This interaction between color and movement opens a novel field to explore and suggests that these two elements are probably essential to understand animal visual communication.

Appendix

Table 2 Descriptions of the different levels of complexity for "male advertising" and "threat" displays of Pelecaniformes, following van Tets (1965)

Display type	Display complexity	Description
Male advertising	Absent	No display observed
	Sky pointing	The head and neck are in a vertical position, while the body axis is in a horizontal position. The wings are raised by humera rotation up and outwards. The tail is raised
	Alternate wings waved	Head, neck, and tail in a position similar to that in the "sky-pointing" display. It starts with both wings moving up and down together as in the "sky-pointing" display, but the wings are then raised alternately as a repetitive movement at a faster rate, two or more cycles per second
	Slow rate wing waving	The wing tips are raised simultaneously up and outwards with the primaries folded behind the secondaries. The wings are waved less than twice per second. Head, neck, and tail in a vertical position as in the "sky-pointing" display, but the head is held above the back with the bill pointing upwards and forwards during the wing waving and is moved up and down at the same rate as the wing tips. The head moves down as the wing tips move up and vice versa
	Rapid flutter wing waving	As in the "slow rate wing-waving display", but the wings are waved faster than twice per second
	Darting and throwback	As in the "slow rate wing-waving display", but the head is moved rapidly up and down with more emphasis, while it is held above the back close to the base of the tail
Threat	Pecking and screaming	The birds peck and scream at opponents
	Pointing or wagging bills	Closed bills are pointed, open bills are wagged, or birds lunge and snap at opponents
	Move towards intruder	The birds walk or hop with the wings slightly spread and the bill open towards the opponent. Snapping movements are made at intervals
	Snapping and waving open bills	The birds snap at opponents and wave open bills
	Raise, open and wave bills	
	S-shaped expanded neck, open bill	The neck is S-shaped, the throat is expanded and the mouth is open. The head is moved irregularly from side to side and back and forth, while the bill is pointed towards the opponent
	Head repeatedly thrown forward	The head is repeatedly thrown forward in a rapid and irregular fashion
	Repeated head pointing followed by head shake and gargling sound	The head is repeatedly darted back and forth, then the head is shaked in the withdrawn position

References

Alvarez F (2004) Black and white tail markings in Rufous Bush Chats *Cercotrichas galactotes*: size, symmetry and the extent of seasonal abrasion. Ardeola 51:169–175

Alvarez F, Braza F, Norzagaray A (1976) The use of the rump patch in the fallow deer (*D. dama*). Behaviour 56:298–308

Aragonés J, Arias de Reyna L, Recuerda P (1999) Visual communication and sexual selection in a nocturnal bird species, *Caprimulgus ruficollis*, a balance between crypsis and conspicuousness. Wilson Bull 111:340–345

Badyaev AV, Hill GE, Whittingham LA (2002) Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. Evolution 56:412–419

Baião PC, Schreiber EA, Parker PG (2007) The genetic basis of the plumage polymorphism in red-footed boobies (*Sula sula*): a Melanocortin-1 receptor (MC1R) analysis. J Hered 98:287–292

Barber I, Folstad I (2000) Schooling, dusk flight and dance: social organisations as amplifiers of individual quality? Oikos 89:191–194

Beauchamp G, Heeb P (2001) Social foraging and the evolution of white plumage. Evol Ecol Res 3:703–720

Berglund A (2000) Sex role reversal in a pipefish: female ornaments as amplifying handicaps. Ann Zool Fenn 37:1–13

Blomqvist D, Johansson OC, Unger U, Larsson M, Flodin L (1997) Male aerial display and reversed sexual size dimorphism in the dunlin. Anim Behav 54:1291–1299

Bókony V, Liker A, Székely T, Kis J (2003) Melanin-based plumage coloration and flight displays in plovers and allies. Proc R Soc B 270:2491–2497

Bortolotti GR (2006) Natural selection and coloration: protection, concealment, advertisement, or deception? In: Hill GE, McGraw KJ (eds) Bird coloration, vol II. Function and evolution. Harvard University Press, Cambridge, pp 3–35

Burtt EH Jr, Ichida JM (2004) Gloger's rule, feather-degrading bacteria, and color variation among Song Sparrows. Condor 106:681–686

Candolin U (2003) The use of multiple cues in mate choice. Biol Rev 78:575–595

Caro T (2008) Leaping in impala. Afr J Ecol 46:105–106

Cullen JM (1966) Reduction of ambiguity through ritualization. Philos Trans R Soc Lond B 251:363–374

Dale J (2006) Intraspecific variation in coloration. In: Hill GE, McGraw KJ (eds) Bird coloration, vol II. Function and evolution. Harvard University Press, Cambridge, pp 36–86

del Hoyo J, Elliott A, Sargatal J (1992) Handbook of the birds of the world, vol 1. Lynx Edicions, Barcelona

Delicato LS, Derrington AM (2005) Coherent motion perception fails at low contrast. Vision Res 45:2310–2320

Doucet SM, Mennill DJ, Montgomerie R, Boag PT, Ratcliffe LM (2005) Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. Behav Ecol 16:218–222

Ellis DH, Lish JW (2006) Thinking about feathers: adaptations of Golden Eagle rectrices. J Raptor Res 40:1–28

Ferns PN, Hinsley SA (2004) Immaculate tits: head plumage pattern as an indicator of quality in birds. Anim Behav 67:261–272

Friesen VL, Anderson DJ (1997) Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of evolution. Mol Phylogenet Evol 7:252–260

Friesen VL, Anderson DJ, Steeves TE, Jones H, Schreiber EA (2002) Molecular support for species status of the Nazca Booby (*Sula granti*). Auk 119:820–826

Garland T Jr, Bennett AF, Rezende EL (2005) Phylogenetic approaches in comparative physiology. J Exp Biol 208:3015–3035

Garland T Jr, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292

Götmark F (1987) White underparts in gulls function as hunting camouflage. Anim Behav 35:1786–1792

Green MC, Leberg PL (2006) Sociality among foraging Ardeidae: does plumage coloration influence nearest-neighbor spacing? Ame Midl Nat 156:344–352

Grønstøl GB (1996) Aerobatic components in the song-flight display of male lapwings *Vanellus vanellus* as cues in female choice. Ardea 84:45–55

Harrison P (1996) Seabirds: an identification guide, revised edition. Helm, London

Hasson O (1991) Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. Behav Ecol 2:189–197

Hurd PL, Wachtmeister C-A, Enquist M (1995) Darwin's principle of antithesis revisited: a role for perceptual biases in the evolution of intraspecific signals. Proc R Soc B 259:201–205

Huxley JS (1914) The courtship-habits of the great crested grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. Proc Zool Soc Lond 35:491–562

Jabłoński PG (2001) Sensory exploitation of prey: manipulation of the initial direction of prey escapes by a conspicuous 'rare enemy'. Proc R Soc B 268:1017–1022

Johnson KP (2000) The evolution of courtship display repertoire size in the dabbling ducks (Anatini). J Evol Biol 13:634–644

Kamler JF, Ballard WB (2006) Ear flashing behavior of black-tailed jackrabbits (*Lepus californicus*). Am Midl Nat 155:402–403

Kennedy M, Spencer HG (2004) Phylogenies of the Frigatebirds (Fregatidae) and Tropicbirds (Phaethonidae), two divergent groups of the traditional order Pelecaniformes, inferred from mitochondrial DNA sequences. Mol Phylogenet Evol 31:31–38

Kennedy M, Spencer HG, Gray RD (1996) Hop, step and gape: do the social displays of the Pelecaniformes reflect phylogeny? Anim Behav 51:273–291

Kennedy M, Gray RD, Spencer HG (2000) The phylogenetic relationships of the shags and cormorants: can sequence data resolve a disagreement between behavior and morphology? Mol Phylogenet Evol 17:345–359

Kenward B, Wachtmeister C-A, Ghirlanda S, Enquist M (2004) Spots and stripes: the evolution of repetition in visual signal form. J Theor Biol 230:407–419

Kortlandt A (1995) Patterns of pair-formation and nest-building in the European Cormorant *Phalacrocorax carbo sinensis*. Ardea 83:11–25

Kose M, Mänd R, Møller AP (1999) Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. Anim Behav 58:1201–1205

Lander K, Chuang L (2005) Why are moving faces easier to recognize? Vis Cogn 12:429–442

Lenoir M, Vansteenkiste J, Vermeulen J, de Clercq D (2005) Effects of contrasting colour patterns of the ball in the volleyball reception. J Sport Sci 23:871–879

Livingstone M (2002) Vision and art: the biology of seeing. Abrams, New York

Ljetoff M, Folstad I, Skarstein F, Yoccoz NG (2007) Zebra stripes as an amplifier of individual quality? Ann Zool Fenn 44:368–376

Lorenz KZ (1941) Vergleichende Bewegungsstudien an Anatinen. J Orn 89:194–294

Lovegrove BG (2001) The evolution of body armor in mammals: plantigrade constraints of large body size. Evolution 55:1464–1473

McGraw KJ (2006) Mechanics of melanin-based coloration. In: Hill GE, McGraw KJ (eds) Bird Coloration, vol I. Mechanisms and measurement. Harvard University Press, Cambridge, pp 243–294

Negro JJ, Bortolotti GR, Sarasola JH (2007) Deceptive plumage signals in birds: manipulation of predators or prey? Biol J Linn Soc 90:467–477

Nelson JB (2006) Pelicans, cormorants, and their relatives. Oxford University Press, Oxford

Ord TJ, Blumstein DT (2002) Size constraints and the evolution of display complexity: why do large lizards have simple displays? Biol J Linn Soc 76:145–161

Ord TJ, Peters RA, Clucas B, Stamps JA (2007) Lizards speed up visual displays in noisy motion habitats. Proc R Soc B 274:1057–1062

Osorio D, Jones CD, Vorobyev M (1999) Accurate memory for colour but not pattern contrast in chicks. Curr Biol 9:199–202

Penteriani V, Delgado MM, Alonso-Alvarez C, Sergio F (2007a) The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. Behav Ecol 18:143–147

Penteriani V, Delgado MM, Alonso-Alvarez C, Viqueira Pina N, Sergio F, Bartolommei P, Thompson LJ (2007b) The importance of visual cues for nocturnal species: eagle owl fledglings signal with white mouth feathers. Ethology 113:934–943

Peters RA (2008) Environmental motion delays the detection of movement-based signals. Biol Lett 4:2–5

Prum RO (2006) Anatomy, physics, and evolution of structural colors. In: Hill GE, McGraw KJ (eds) Bird coloration, vol I. Mechanisms and measurement. Harvard University Press, Cambridge, pp 295–353

Pryke SH, Andersson H, Lawes ML (2001) Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. Evolution 55:1452–1463

Rowe C, Skelhorn J (2004) Avian psychology and communication. Proc R Soc B 271:143–1442

Ruxton GD, Speed MP, Kelly DJ (2004) What, if anything, is the adaptive function of countershading? Anim Behav 68:445–451

Schmidt V, Schaefer HM, Winkler H (2004) Conspicuousness, not colour as foraging cue in plant-animal signalling. Oikos 106:551–557

Torres R, Velando A (2003) A dynamic trait affects continuous trait assessment in the blue-footed booby, *Sula nebouxii*. Behav Ecol Sociobiol 55:65–72

van Tets GF (1965) A comparative study of some social communication patterns in the Pelecaniformes. Ornithol Monog 2:1–88

Wachtmeister C-A (2001) Display in monogamous pairs: a review of empirical data and evolutionary explanations. Anim Behav 61:861–868

Wüster W, Allum CSE, Bjargardóttir IB, Bailey KL, Dawson KJ, Guenioui J, Lewis J, McGurk J, Moore AG, Niskanen M, Pollard CP (2004) Do aposematism and Batesian mimicry require bright colors? A test, using European vipper markings. Proc R Soc B 271:2495–2499

Zahavi A (1979) Ritualization and the evolution of movement signals. Behaviour 72:77–81