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The frontal shield of the moorhen: sex differences and relationship with body condition

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Moorhens *Gallinula chloropus* have a conspicuous frontal shield, which is used in competitor assessment, and whose size and colour is testosterone-dependent in both sexes. During 2 months in winter we examined sex-related differences in size and colour of the red or red-orange shield and the yellow-tipped bill of free-living adult moorhens, as well as their relationship with indices of body condition (body size, tarsi fluctuating asymmetry, fat index, serum lutein carotenoid concentration, and a number of blood parameters). Shield area was greater in males and more red in females. In females, area and colouration intensity of the shield were positively correlated, respectively, to body size and concentration of circulating lutein. In males, area and intensity of red colouration of the shield were positively correlated, respectively, to albumin/globulin ratio and body size, while shield colour saturation was negatively related to the leukocyte index. Our results suggest that shield area and colour of male and female moorhens may provide cues to their opponents for assessment of body size and health status, and therefore of their competitive ability.

KEY WORDS: body condition, competitive ability, *Gallinula choropus*, moorhen, sex differences, shield and bill colouration.

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INTRODUCTION

Participants in competitive aggression benefit from being able to assess the probability of winning or losing a fight (Parker 1974, Enquist & Leimar 1983, Keeley & Grant 1993, Pryke & Andersson 2003). In birds, success in aggressive encounters may depend to some extent on body size (Birkhead 1981) and condition (Carrascal et al. 1998). Conspicuous colouration in birds (either more intense or larger coloured areas) often appears to act as an honest signal of body condition (Hamilton & Zuk 1982, Rohwer 1982, Dufva & Allander 1995, Thompson et al. 1997, Figuerola et al. 1999, Blount et al. 2003, Faivre et al. 2003), because only the more healthy individuals can afford the costs of developing such colouration. Under this hypothesis we can expect conspicuous colouration to provide information for assessment of competitive ability during agonistic encounters (Pryke et al. 2001, 2002), and to find a positive relationship of signal size and colour with body size and health.

Since it is difficult to identify a single index of health that summarizes all aspects of body condition (Blem 1990, Norris & Evans 2000), a variety of indices should be considered when trying to find the physiological correlates of signals.

Among morphological traits, body size and fluctuating asymmetry (FA) are the more utilized, and while the former is an important factor of the biology of each species (Kooijman 1986), the latter appears to be a valid indicator of environmental and genetic stress (Leary & Allendorf 1989, Parsons 1992, Swaddle & Witter 1994, Yang et al. 1997). The extent of body fat reserves is another factor to consider, as it is known to affect fitness (Blem 1990).

Blood composition is a good indicator of an animal's condition during the period preceding blood sampling (Brown 1996). Among haematological parameters, packed cell volume (PCV) or haematocrit relates to efficiency of oxygen uptake and transport to tissues, and reflects the level of metabolic activity (Nelsen & Brandl 1988, Ots et al. 1998). Leukocyte number also reflects body condition, and high levels are often related to inflammatory processes (Siegel 1985, Hõrak et al. 1998). In particular, the heterophil to lymphocyte ratio increases in response to infectious disease and other stressors, resulting from a decrease in the lymphocyte number and a simultaneous increase in the heterophil number (Gross & Siegel 1983, Maxwell 1993).

Low plasma albumin level is a symptom of many pathological states (malnutrition, liver disorders, inflammation), while high levels of immunoglobulins (Ig) are seen in chronic infections. Accordingly, the albumin to globulin (Alb/Glo) ratio can be used as a reliable index of health (Ots et al. 1998).

In birds, red, orange and yellow colours are produced mostly by carotenoids, which also play important immune and detoxification functions, and must be acquired in the diet. Carotenoid-dependent coloration has been shown to signal condition, playing a role in intraspecific communication (Hill 1994, 1996; Wolfenbarger 1999; Blount et al. 2003).

In birds, fleshy ornaments have received much less attention than plumage, although they have been found to be associated with intrasexual competition and are sometimes used as signals (Brodsky 1988, Ligon et al. 1990, Zuk et al. 1990, Buchholz 1997). On the other hand, fleshy ornaments are more apt than feathers (which may have grown a long time before they are displayed) to signal short-term body conditions.

In the Moorhen *Gallinula chloropus* the male is slightly larger than the female. This species is monogamous (sometimes polyandrous) and sexually monomorphic, and shows partial sex-role reversal, the males performing most of the incubation (Siegfried & Frost 1975; Ripley 1977; Petrie 1983a, 1983b, 1988; del Hoyo et al. 1996).

Moorhens possess a yellow-tipped bill and a bright red frontal fleshy shield, which extends onto the forehead from the upper mandible. It is displayed to the opponent during pre-fight challenges before fighting, while it is less obvious in courtship, because the head is bowed (Wood 1974). The frontal shield increases in size and turns bright red at the time of most intense competition, after the period of courtship and mate selection, and declines at the time when birds copulate (Petrie 1988). Both sexes use their frontal shields in competitor assessment, females fighting for acces to males of good quality (Petrie 1983a, 1983b), and males for the defence of territories (Petrie 1984).

Fenoglio et al. (2002a, 2004) found a positive relationship between brightness of the yellow bill patch and adult body mass, the haematocrit, the heterophil to lymphocyte ratio, and the immune reaction to PHA injection, while the colour of the red part of the bill was related to cloacal bacterial presence, confirming that the bill colours can be an honest signal of health status.

Following Lozano's (1994) argument, if carotenoids are a finite resource, and are used both to enhance immune functions and to give colour to display structures, these might signal immunocompetence, and only the most healthy individuals would be able to produce maximally-pigmented ornaments. A trade-off between intensity of carotenoid-based bill colour and immune function has been demonstrated in male Zebra Finches *Taeniopygia guttata* and Blackbirds *Turdus merula* (Blount et al. 2003, Faivre et al. 2003). According to the immunocompetence–handicap hypothesis (Folstad & Karter 1992), a testosterone-mediated trade-off would control the investments in the ornamental traits and in the immune system.

Since the shield size and colour of male and female moorhens are testosterone-dependent (Eens et al. 2000), we would expect the immunocompetence handicap hypothesis to also operate in this species, as an explanation of the evolutionary stability of the honest signalling system.

Previous studies in moorhens have revealed a decrease in gonad weight and shield size following experimental reduction of food supply (Huxley 1976), and mass loss (Acquarone et al. 1998) during the pre-reproductive winter period. These findings led us to try to investigate (a) the relationship between the colour and size of both bill and shield and the birds' health during the winter period in free-living conditions, and (b) whether or not intersexual differences in these features exist.

METHODS

The study was carried out at La Lantejuela (SW Spain, 37°21'N, 5°13'W) in November and December of 2002, on 156 adult moorhens captured in barley-baited funnel wire traps at the shores of fresh water pools, in the early morning. Immediately after capture, the subjects were individually marked with metal rings. Before and after obtaining measurements and blood samples from each subject, the colouration of the shield (central lower area) and bill (upper dorsal yellow area) of 88 subjects was recorded (always in the morning, by the

same person, outdoors and in the shade) with the aid of the Munsell Book of Color (Munsell 1976).

The Munsell system identifies colour according to three attributes or dimensions of colour: hue, value and chroma. Hue is the attribute according to which a colour is perceived as red, yellow, green, blue, purple or intermediate. Value indicates the lightness (i.e., the amount of white) or darkness of a colour sample. Chroma indicates the degree of saturation. The three attributes are arranged in a spherical array of colour samples, and each colour occupies a particular site in the three dimensions (actually a paper card in the Munsell Book of Color).

Since there is no obvious limit between the shield and the bill, shield length was considered to be bill plus shield length (from tip of bill to top of shield) minus bill length. Shield area was calculated as the product of shield length by its widest width (Petrie 1988, Eens et al. 2000).

The subjects were weighed to the nearest gram on a portable electronic balance, and both tarsi were measured with a digital calliper to the nearest 0.01 mm. According to Petrie (1983a), tarsus length was used as an index of body size, and body mass × tarsus length^{-3} was used as an index of fat reserves. The measurements were taken twice, and always by the same person. Fluctuating asymmetry (FA) of length of tarsi was computed as length difference (|Right-Left|), since it did not change with length (Palmer 1994). The two values obtained for these measures were used to calculate the repeatability correlation coefficients, as well as to obtain the mean values used in calculations.

Blood samples (about 1.5 ml) of 95 subjects were taken from the leg vein. From each sample two capillaries were used to obtain haematocrit values. The capillaries were kept on ice for 3-4 hr before processing. Blood samples were centrifuged for 8 min at 11500 rpm in a portable centrifuge (Bayer M 1101), and haematocrit was expressed as volume of the part of the capillary occupied by blood cells / total blood volume in the capillary. The two samples for each bird were used to assess repeatability, and the average of the two values was used in calculations.

We used two blood smears from each sample for leukocyte and parasite counts. For each smear, a drop of blood was collected in a microcapillary tube, and then transferred to a glass slide, air dried, and fixed in absolute methanol for 10 min. The blood smears were then stained following the May Grünwald-Giemsa technique. Leukocytes were counted by an experienced person on 100 fields under oil, using magnification of × 100. Although we looked for blood parasites, we did not find any in the samples. The counted leukocytes were classified as lymphocytes, monocytes, eosinophils, heterophils, and basophils, and the heterophil to lymphocyte (H/L) ratio was used as an index of health. A leukocyte index was obtained by multiplying each subject's leukocyte count by its observed PCV (Campbell 1995, modified). In order to obtain repeatability values, a third of the samples was examined twice.

Two drops of blood preserved in absolute ethanol at ambient temperature were used for sex determination. Following Griffiths et al. (1998), we used the polymerase chain reaction (PCR) amplification of CHD1 genes with primers P2 and P8. Females were identified by the amplification of two PCR products of 380 and 340 base pairs, corresponding to CHD1-Z and CHD1-W genes, respectively, while males yielded only the longer fragment. Blind tests of ten subjects were repeated and yielded the same results. In all, 77 and 79 of the subjects were classified as females and males, respectively.

Part of the samples was used for plasma protein assays. Plasma samples for protein electrophoresis were obtained after centrifugation of blood for 5 min at 4000 rpm (vials contained gel aiding the separation of plasma from clots) and then stored at 4 ºC. Capillarity-zone electrophoresis with Parangon CZE 2000 system was used for detection of protein groups, and from the values of the areas in the densitometric profile the relative abundance of albumin and of immunoglobulins (alpha-, beta-, and gamma-globulins) (Alb/Glo ratio) was obtained. In order to assess repeatability, two samples were obtained from a third of the subjects.

Finally, two 30 µl blood samples were used for carotenoid analysis. Spectrophotometry was utilized to assess plasma carotenoid concentration (Tella et al. 1998). As lutein is one of the most abundant carotenoids that birds accumulate (Møller et al. 2000), we limited the analysis to the lutein. To determine lutein concentration in plasma, the samples were kept in

darkness and transported in coolers to the laboratory on the day of collection and centrifuged at 4 ºC for 10 min at 3000 rpm to separate blood cells from plasma, which was then frozen at – 20 ºC for subsequent analyses. Three volumes of acetone were added to the plasma samples, and the mixture was centrifuged at 13000 rpm for 10 min at 4 ºC. Carotenoid concentration was measured automatically in the Ultraspec 2000 UV/Vis spectrophotometer (Pharmacia Biotech), recording absorbance at 476 nm. A standard curve of lutein was used to estimate its concentration.

Statistical analysis

Since values of all the variables related to bill and shield coloration deviated significantly from a normal distribution ($P < 0.01$, Kolmogorov-Smirnov test) except chroma of the shield colouration for the males ($P > 0.20$), non-parametric tests were used (SIEGEL & CASTELLAN 1988, SOKAL & ROHLF 1995). The repeatability of all recorded variables was high (coefficient of intraclass correlation: $0.430 < r_1 < 0.982$, $19 < df < 140$, $P < 0.001$).

RESULTS

Sex differences and relationship among the shield and bill variables

Mean values for the shield and bill parameters of moorhens of both sexes are shown in Table 1. Among the shield parameters, the area was greater in males than in females, and colour hue was redder in females than in males. No other significant differences in colour were observed between the sexes.

Correlations among the shield variables are presented in Table 2. The sign of each of the correlations was the same for both sexes, although the level of significance may differ. Larger shields were redder, lighter and more saturated, the effect

Table 1.

Comparison of male and female shield and bill measurements of moorhens (Mann-Whitney U test).

	Females		Males	
Variables	Mean ± SD	(n)	Mean ± SD	(n)
Shield				
Area (mm^2)***	93.62 ± 33.15	(71)	122.31 ± 36.85	(63)
Hue*	7.44 ± 0.26	(44)	7.87 ± 1.22	(44)
Value^{NS}	3.71 ± 0.60	(44)	3.86 ± 0.66	(44)
Chroma^{NS}	11.30 ± 2.70	(44)	11.02 ± 2.51	(44)
Bill				
Hue	27.50 ± 0.00	(44)	27.50 ± 0.00	(44)
Value^{NS}	8.02 ± 0.30	(44)	7.88 ± 0.48	(44)
Chroma^{NS}	9.23 ± 1.68	(44)	9.13 ± 1.68	(44)

^{NS} : not significant, * : $P < 0.05$, *** : $P < 0.001$.

Table 2.

Spearman rank correlation between area and colour indices of the shields of male and female moorhens.

	Hue				Value				Chroma			
	females		males		females		males		females		males	
	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)
Area	-0.045^{NS}	(42)	-0.355^{*}	(36)	0.158^{NS}	(42)	0.366^{*}	(36)	0.389^{*}	(42)	0.739^{***}	(36)
Hue					0.083^{NS}	(44)	0.190^{NS}	(44)	-0.384^{**}	(44)	-0.202^{NS}	(44)
Value									0.500^{***}	(44)	0.516^{***}	(44)

^{NS} : not significant, * : $P < 0.05$, ** : $P < 0.01$, *** : $P < 0.001$.

being more pronounced in males than in females. The shield colouration was also more saturated when more red (especially in females) and lighter (in both sexes).

Hue of the yellow portion of the bill showed no variance. With respect to the two other attributes of yellow colour, a lighter colour (i.e., a higher value) was more saturated, although the correlation was significant only for females (females: $r_s = 0.487$, n = 44, $P < 0.001$; males: $r_s = 0.135$, n = 44, $P = 0.381$).

Value, and especially chroma of the red shield and of the yellow bill were positively correlated in both sexes (value; females: $r_s = 0.177$, n = 44, $P = 0.251$; males: $r_s = 0.303$, n = 43, $P = 0.048$; chroma; females: $r_s = 0.425$, n = 44, $P = 0.004$; males: $r_s = 0.498$, n = 43, $P < 0.001$).

Relationship with body condition

The correlations of the shield and bill parameters with the indices of body condition (body size, tarsi FA, fat index, carotenoid concentration, haematocrit, leukocyte index, H/L ratio, and Alb/Glo ratio), are reported in Table 3 (females) and Table 4 (males). There were significant relationships for three of the shield parameters (area, hue and chroma), and for none of the yellow bill.

In the case of females, shield size was positively related to body size, while its chroma was positively related to the concentration of circulating lutein (Fig. 1), and negatively to the fat index.

In males, the shield size was negatively related to the leukocyte index (Fig. 2), and positively to the albumin/globulins ratio. Male shield colouration was related to condition too: hue was negatively related to body size (larger males were more red, smaller males were more orange), while chroma was negatively related to the leukocyte index (leukocytosis would accompany low colour saturation) (Fig. 2).

DISCUSSION

We found a pattern of variation of shield appearance in which at one end the shield would be larger, redder and more saturated, and at the other it would be smaller, with an orange tinge, and less saturated.

Table 3.

Spearman rank correlation between the variables of the shield and bill of female moorhens and the parameters of body condition during autumn and winter at La Lantejuela (Spain).

	Shield								Bill					
	area		hue		value		chroma		hue		value		chroma	
	rs	(n)	rs	(n)	rs	(n)	rs	(n)	rs	(n)	rs	(n)	rs	(n)
Body size	0.392*	(70)	– 0.215^{NS}	(44)	0.022^{NS}	(44)	0.212^{NS}	(44)	—	(44)	0.145^{NS}	(44)	0.114^{NS}	(44)
Tarsi FA	– 0.069^{NS}	(68)	– 0.228^{NS}	(44)	0.015^{NS}	(44)	– 0.093^{NS}	(44)	—	(44)	– 0.094^{NS}	(44)	– 0.194^{NS}	(44)
Fat index	– 0.178^{NS}	(68)	0.196^{NS}	(43)	– 0.106^{NS}	(43)	– 0.441*	(43)	—	(43)	– 0.038^{NS}	(43)	– 0.202^{NS}	(43)
Carotenoid	– 0.013^{NS}	(37)	– 0.312^{NS}	(38)	0.386^{NS}	(38)	0.456*	(38)	—	(38)	– 0.214^{NS}	(38)	0.116^{NS}	(38)
Haematocrit	– 0.399^{NS}	(49)	0.120^{NS}	(44)	0.024^{NS}	(44)	– 0.020^{NS}	(44)	—	(44)	– 0.351^{NS}	(44)	– 0.301^{NS}	(44)
Leukocyte index	– 0.318^{NS}	(36)	– 0.078^{NS}	(37)	– 0.086^{NS}	(37)	– 0.354^{NS}	(37)	—	(37)	– 0.045^{NS}	(37)	– 0.253^{NS}	(37)
H/L ratio	0.068^{NS}	(36)	– 0.146^{NS}	(37)	0.039^{NS}	(37)	0.375^{NS}	(37)	—	(37)	0.260^{NS}	(37)	0.242^{NS}	(37)
Alb/Glo ratio	0.091^{NS}	(31)	0.020^{NS}	(31)	0.211^{NS}	(31)	0.387^{NS}	(31)	—	(31)	– 0.208^{NS}	(31)	– 0.040^{NS}	(31)

^{NS}: not significant, * Correlation significant at $P < 0.05$ after a sequential Bonferroni correction for multiple comparisons.

Table 4.

Spearman rank correlation between the variables of the shield and bill of male moorhens and the parameters of body condition during autumn and winter at La Lantejuela (Spain).

	Shield								Bill					
	area		hue		value		chroma		hue		value		chroma	
	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)	r_s	(n)
Body size	0.302^{NS}	(63)	– 0.421*	(44)	0.366^{NS}	(44)	0.325^{NS}	(44)	—	(44)	0.369^{NS}	(44)	0.131^{NS}	(44)
Tarsi FA	– 0.075^{NS}	(63)	0.025^{NS}	(44)	0.182^{NS}	(44)	0.261^{NS}	(44)	—	(44)	0.023^{NS}	(44)	0.095^{NS}	(44)
Fat index	– 0.148^{NS}	(63)	0.401^{NS}	(44)	– 0.307^{NS}	(44)	– 0.388^{NS}	(44)	—	(44)	– 0.307^{NS}	(44)	– 0.250^{NS}	(44)
Carotenoid	0.359^{NS}	(37)	– 0.130^{NS}	(39)	0.164^{NS}	(39)	0.311^{NS}	(39)	—	(39)	– 0.045^{NS}	(39)	0.255^{NS}	(39)
Haematocrit	0.167^{NS}	(38)	– 0.036^{NS}	(40)	0.141^{NS}	(40)	0.312^{NS}	(40)	—	(40)	0.164^{NS}	(40)	– 0.082^{NS}	(40)
Leukocyte index	– 0.462*	(38)	0.205^{NS}	(40)	– 0.139^{NS}	(40)	– 0.424*	(40)	—	(40)	– 0.243^{NS}	(40)	– 0.025^{NS}	(40)
H/L ratio	0.052^{NS}	(38)	– 0.308^{NS}	(40)	– 0.028^{NS}	(40)	0.165^{NS}	(40)	—	(40)	0.301^{NS}	(40)	0.005^{NS}	(40)
Alb/Glo ratio	0.481*	(34)	– 0.362^{NS}	(34)	0.090^{NS}	(34)	0.298^{NS}	(34)	—	(34)	0.281^{NS}	(34)	0.133^{NS}	(34)

^{NS}: not significant, * Correlation significant at $P < 0.05$ after a sequential Bonferroni correction for multiple comparisons.

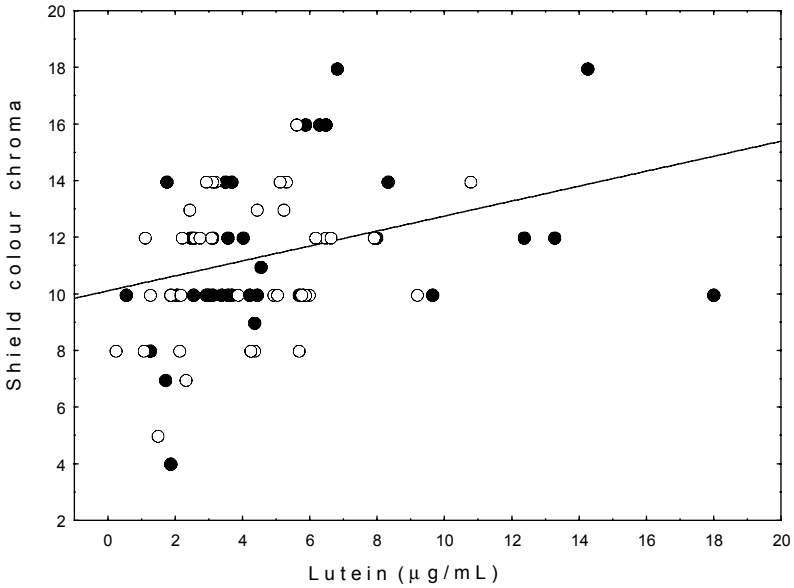

Fig. 1. — Relationship between concentration of circulating lutein and chroma of shield colour of female (filled dots) and male (empty dots) moorhens. The effect was statistically significant only for the females (linear fit shown).

As happens with other body dimensions, shield size is greater in males than in females. Less expected was the redder shield colour of females. The stronger relationship between shield and body size (itself probably directly related to fighting ability) in females as compared to males may be related to the higher aggressiveness of females in the winter flocks, and their more active role in pair formation (Petrie 1983a, 1983b, 1988). The females may therefore have a greater need to provide cues to opponents for assessment of their fighting ability (Zahavi 1981). Accordingly, the positive relationship between shield area, body size and their more conspicuous (redder) colour would make females more able in this respect.

The lack of any important relationship between body condition and bill yellow colour points to the red shield as the likely base for the signals of competitive ability in our population. These results contrast with the findings of Fenoglio et al. (2002b, 2004) in Italy on the same species of a positive relationship between the colouration of the yellow portion of the bill with health, and of a negative correlation between frontal shield redness and bacterial presence, but not with any other health index. The disagreement between the results on the Italian and Spanish populations can be explained in different ways. Firstly, the two populations may be different with respect to shield and bill colouration. Also, perhaps the low variance observed in the yellow bill colouration of the Spanish population has prevented the detection of any relationship. It is also possible that the sexing procedure in the present study has brought to light the stronger effects of health on the females' shield colouration. In connection with this, future research on monomorphic bird species could benefit of molecular sexing.

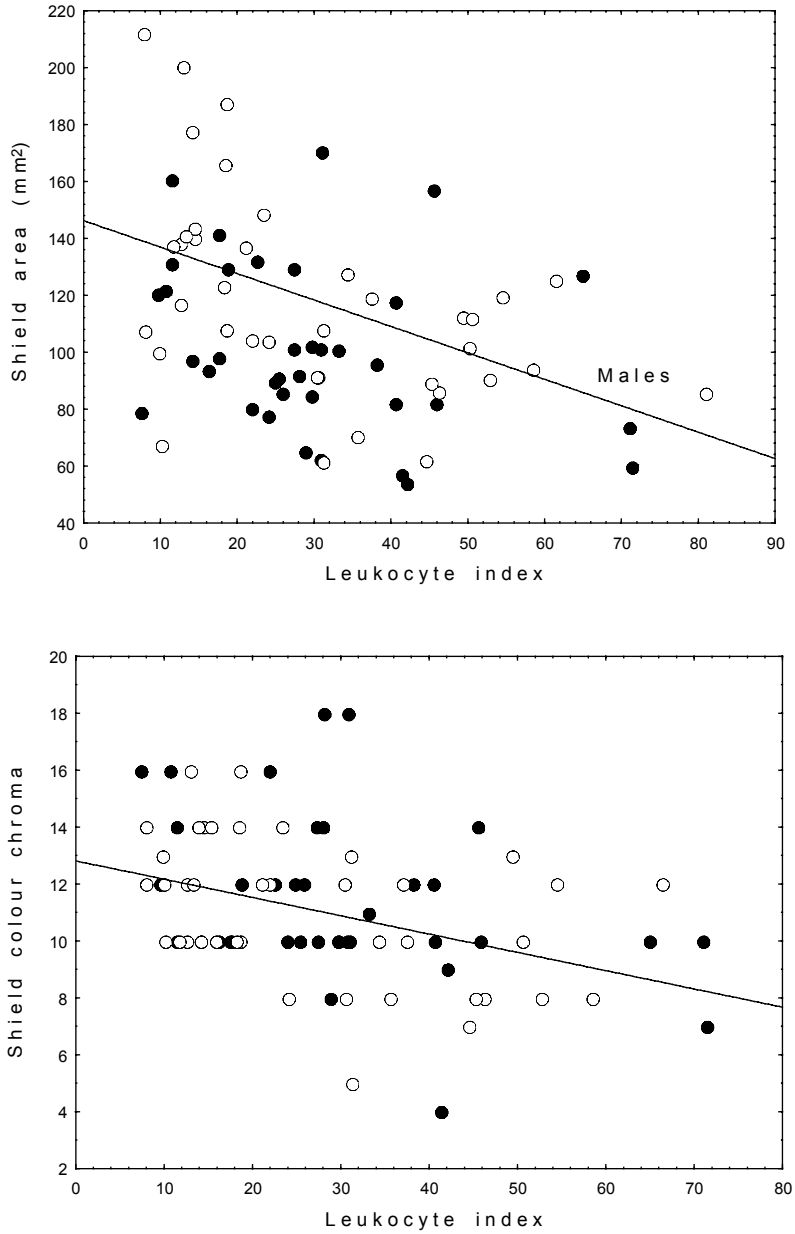

Fig. 2. — Relationship between leukocyte index (leukocyte count × PCV) and shield area (above) and chroma (below) of female (filled dots) and male (empty dots) moorhens. In both cases the effect was statistically significant only for the males (linear fit shown).

Several shield parameters were found to be related to condition. The relationship between a larger shield size and a better Alb/Glo ratio and leukocyte index in

males would suggest that shield size would be acting in their case more as a signal of health (Gross & Siegel 1983, Ots et al. 1998), which could be only indirectly related to competitive ability. Concerning shield colour, the redder shield of larger males would also point to signalling fighting ability (Petrie 1984), while the greater saturation of their shield colour accompanying lower leukocyte numbers could be a signal of good health.

As seen in other bird species (Hill 1995, Negro et al. 2000, Blount et al. 2001), shield colour in our study was related to the concentration of circulating lutein carotenoid. However, the relationship was present only in females, whose more active role in intraspecific aggression could make them more inclined to provide cues for the evaluation of their fighting ability.

The finding that females with higher fat deposits showed less saturated shield colour agrees with reports of subordinates of some dominance-structured bird flocks storing more fat than dominants (Ekman & Lilliendahl 1993, Witter & Swaddle 1995, Gosler 1996). Subdominant moorhens may store more fat as insurance for periods when sufficient food cannot be obtained (Blem 1990, Gosler 1996). After pair formation, perhaps the more dominant birds of the winter flocks hold the best territories and leave the worse habitat to subdominants, whose access to food would thus be limited. As heavy fat loads are detrimental in front of predators, then dominant individuals could hold less fat reserves than subordinates, as a response to perceived predation risk (Gentle & Gosler 2001). Because individuals of different dominance classes may show different foraging strategies (Pöysä 1988), and, consequently, be subject to different levels of predation risk, the strategy of fat storage may also differ.

For the features of the shield to be honest signals of competitive ability, they must be associated with a cost, otherwise individuals unable to win fights could cheat. But because fighting ability is likely to be challenged by other moorhens, weak individuals have to be honest, thus avoiding the costs associated with fighting superior opponents (Pärt & Qvarnström 1997).

Shield size and colour are testosterone-dependent in male and female American coots *Fulica americana* and moorhens (Gullion 1951, Eens et al. 2000), and testosterone is known to often increase aggression in birds (Beach 1961, Moss et al. 1979). According to Folstad & Karter's (1992) immunocompetence-handicap hypothesis, honest signalling by shield display in moorhens would be guaranteed by a testosterone-mediated trade-off between investment in the expresion of the trait, and the investment in the immune system (via the immunosuppressive effects of testosterone, Grossman 1985, Ligon et al. 1990, Puerta et al. 1995, Eens et al. 2000). Furthermore, carotenoid pigments per se, by being scarce or toxic (Gray 1996, Olson & Owens 1998), may add a guarantee to signal honesty. The costs associated with shield traits, especially during periods of higher testosterone production, would guarantee that only healthy individuals would bear large and colourful frontal shields.

In conclusion, shield size and colour conspicuousness in our population of moorhens are related to body size and condition, and colour appears to be dependent on concentration of circulating carotenoid. Since the effect is especially pronounced in females, and they are more aggressive in the winter flocks and play a more active role in pair formation, shield size and coloration in females are probably signals for assessment of their fighting ability.

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