

The role of bright plumage in male–male interactions in the ring-necked pheasant

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Abstract. The brightness and colour of birds' plumages have been considered sexually selected traits, indicating health, condition or parasite resistance. However, recent studies with pheasants, *Phasianus colchicus*, suggest they are not signals used by females in mate choice. Instead, males might rely on plumage when assessing the quality of competitors. In this study, bright and experimentally dulled males were presented to a group of captive male pheasants to determine the response to differences in plumage brightness of the intruder. Males in the group directed more aggression to the experimentally dulled males than they did to any other males. This may be partly because they considered the dull males as novel males. When the bright and the dull males were both unknown, both still received more aggression than the average for any individual in the group, but dull males were attacked by more males. Bright males were attacked more by the dominants and dull males by the subordinates. The results show that plumage brightness may affect individual recognition, but also that it is used by males to assess the quality of competitors. Male–male interactions, therefore, may have played a role in the evolution of plumage brightness, either in the context of competition for mates or for resources when males gather into unisexual groups.

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The adaptive function of sexual dimorphism of some bird plumages, and their possible evolutionary origin and maintenance, remain contentious. Although several hypotheses may provide alternative explanations (see reviews in Butcher & Rohwer 1989; Andersson 1994), it is generally assumed that mate choice and contest competition may be important selection factors for many conspicuous and coloured bird plumages. On the one hand, plumages of males might indicate health, condition, parasite resistance or ability to acquire resources, thus providing potential cues in female mate choice (e.g. Andersson 1982; Hamilton & Zuk 1982; Grafen 1990; Hill 1991). On the other hand, males might rely on plumage when assessing the quality of competitors. Many studies on bird plumages indicate that selection for male competitive ability and aggression might favour the evolution of conspicuous conventional signals or 'badges' of status in male plumages (Rohwer 1977, 1982; Rohwer & Ewald 1981;

Studd & Robertson 1985; Evans & Hatchwell 1992; Guilford & Dawkins 1995).

Recent studies on Galliformes confirm that females prefer less parasitized, more resistant males (e.g. Hillgarth 1990; Zuk et al. 1990a), but do not seem to indicate that the signals used in female choice were the colour and brightness of the male plumage (red junglefowl, *Gallus gallus spadiceus*: Zuk et al. 1990b; Ligon & Zwartjes 1995; wild turkey, *Meleagris gallopavo*: Buchholz 1995) and the same applies to the ring-necked pheasant, *Phasianus colchicus* (Mateos & Carranza 1995). For this species, we already know that some male ornaments, such as the red wattles, and even the small feathers in the ear tufts, are signals on which males rely during agonistic contests (Mateos & Carranza 1997). Similarly, other plumage features, such as brightness, might be used by males to indicate the quality of the opponent.

Male ring-necked pheasants are polygynous, defend mating territories and do not contribute to parental care. Male competition to acquire territories is quite high (Cramp & Simmons 1980; Hill & Robertson 1988; Biadi & Mayot 1990).

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Pheasant plumage is dichromatic all year. Some features of current variability in plumage coloration between individuals may be the result of cross-breeding between subspecies (Biadi & Mayot 1990). However, the brightness and pigmentation of plumage in Galliformes are susceptible to diseases and parasite load (Manetti 1980; Zuk et al. 1990a). Also, in the pheasant, males gather into unisexual groups after the mating season, where aggression is frequent (Cramp & Simmons 1980; Hill & Robertson 1988). In these circumstances, males should be aware of any indicator of the quality of the opponent, such as quality of the plumage, at any time of year. Although healthy males probably enjoy higher reproductive success (see Hillgarth 1990), it is not known whether males take plumage brightness into account during male-male contests. In this study, we investigated the role of plumage brightness in male-male interactions in captive ring-necked pheasants.

METHODS

Subjects

We carried out the study in two periods (after the mating seasons of 1990 and 1991), with a group of males maintained in captivity, and as part of a broader study on sexual selection in the ring-necked pheasant conducted over 3 years. Our subjects were initially 41 males of the same age, hatched in April and May of 1989 on a breeding farm and introduced into our yards in October 1989. This yard consisted of an outdoor enclosure, 10 × 6 m and 2.5 m high (1 m of wall and 1.5 of wire mesh). The ground was covered with sand and small gravel, with areas of shadow, shelter places, branches for perching and areas with fine sand for care of the plumage. A set of 18 independent small cages (1.5 × 2.5 × 1.3 m), visually isolated, with an area of shadow and a perch, was also built for keeping isolated males. The animals were fed ad libitum by automatic troughs which delivered commercial feed for pheasants. Diet was complemented by fresh plants (*Urtica* sp. and *Cichorium intibius*) and a mixture of wheat and oats scattered directly on the ground. Before the birds arrived, they were vaccinated against Newcastle disease, avian pox and Pullorum disease. Faeces were periodically collected and checked for parasites (coccidia, nematodes

and cestodes) and affected individuals were treated.

On their arrival, we randomly divided the males into two groups: 18 males (group A) were maintained in visual isolation in individual outdoor cages, and 23 males (group B) were simultaneously introduced and kept together in the large enclosure.

Dominance Measurement

We marked group males with an individual combination of colour rings for identification. We used five colours, allowing 20 variations with two colours plus three individuals that were marked with a single colour. There was no effect of band colour on male-male interactions, that is, no significant differences in rank between animals with one particular colour and the remaining males (Mann-Whitney *U*-test: $U=41-63$, $N_1=9$, $N_2=14$, NS in all five tests for each colour of band versus any other colour), and rank distances between pairs of individuals with the same two colours (in different order) did not differ from those of pairs of individuals taken at random (Mann-Whitney *U*-test: $U=56.5$, $N_1=1$, $N_2=10$, NS).

From December 1989, we monitored agonistic interactions between group males daily and periodically (every 3 months) calculated dominance rank. The agonistic interactions recorded were: (1) displacing: an individual, the loser, withdraws when another one, the winner, approaches him without showing any apparent aggressive behaviour; (2) threatening: three types of threats were considered, referred to in the literature as Walk threat in which the male approaches the opponent with head and tail held high, Peck threat in which the male intermittently pecks at the ground, and Lateral strut in which the side of the body and the plumage, tail and head ornaments are directed towards the opponent (Hill & Robertson 1988); (3) pecking: aggression with the bill usually directed at the head of the opponent; (4) chasing: the aggressor runs towards a retreating opponent.

We observed the males in periods of 30-60 min, throughout the day, seasons and years. The size of the aviary allowed the simultaneous observation of the whole group, and we can assume that every dyadic interaction that took place during observation periods was recorded. We noted 10 624 interactions, for which we recorded the identity of

both aggressor and recipient, and the outcome of the encounter. Most interactions occurred out of the context of direct competition for resources, but they were consistent with those occurring at feeding and drinking sites, perches or sand baths.

We calculated dominance using the cardinal index of Clutton-Brock (ICB) which takes into account the success of opponents, so that the rank of an individual is determined by the ranks of the defeated individuals and the ranks of those individuals defeating him (Clutton-Brock et al. 1979; Boyd & Silk 1983):

$$(B + \Sigma b + 1) / (D + \Sigma d + 1)$$

For a given male, B is the number of males he defeated, and Σb is the total number of males that these defeated males in turn defeated (excluding the given male). D is the total number of males that defeated the given male, and Σd is the total number of males that defeated the males that defeated him (excluding the given male). Using the RagTime spreadsheet we calculated ICB for each winner-loser matrix every 3 months from the observations over this period. Individuals with $ICB > 1$ were considered dominants, and those with $ICB < 1$ were considered subordinates. Values of exactly 1 are extremely unlikely because of the features of this index.

For isolated males (group A), we recorded the frequency with which every male maintained the swollen wattle and erected ear tufts (wattle display). Every day during the breeding season (from February to July), two persons noted at regular intervals (30 min) the identity of males in wattle display, and periodically (every 3 months) we calculated its average value for this period. This measure proved to be a strong correlate of dominance rank for group males (group B), and a good predictor of the outcome of agonistic encounters between unknown males without social contact (Mateos & Carranza 1997).

Experiments

We conducted the first experiment in late June and early July of 1990. We took two similar males from group B ($N=22$), matching them for weight, tarsus length, wattle size, length of ear tufts, tail length, spur size, frequency of wattle display and rank (ICB), because these features are potentially important in male-male competition (Mateos

& Carranza 1996, 1997). We made one of the males duller with transparent make-up powders (MASKOA transparent powder, Laukrom, Prod. Bell. Lavrendor, Barcelona, Spain) applied on the surface of the plumage from head to tail, with a hair brush. These powders are used in television for removing the brightness of human faces without modifying the colour. The appearance thus obtained for the male pheasant was quite similar to that of an ill animal (personal observation). We handled the other male of the pair in the same way and for the same time, but the make-up powder was applied only on his armpits, where it was covered by the wing and so was not visible to other males. After 20 min, the males were simultaneously released back into the same aviary and flock, and two observers recorded for 30 min the agonistic interactions (threatening, pecking and chasing) in which either of the two birds took part. We performed this experiment with six different pairs of males, all of them from group B. In each trial, the member of the pair to be made duller was chosen at random, and there were no significant differences between bright and dull males for any of the variables considered (Table I).

To control for the possibility that making a male dull affected individual recognition, making the dull male look novel, we conducted a second experiment in late June of 1991 with different pairs of males, from the individual cages, which were, therefore, unknown to all the males in the aviary (there were then 14 males in the aviary in group B). In the isolated cages (group A) we had 11 males in 1991. We chose three pairs of males with similar within-pair frequency of wattle display (see above for the procedure for measuring this variable). In each pair, the male to be dulled was chosen at random and we followed exactly the same manipulation process as in the first experiment. The experimental pairs were simultaneously placed in group B and the observers recorded for 30 min the agonistic interactions (threatening, pecking and chasing) in which either of the two birds took part. Two weeks after the first three trials (once the effect of the make-up powder had completely disappeared), we performed the remaining three trials with the same pairs of males but they were manipulated in the opposite way, that is, the formerly bright individual was now made dull. By this procedure we controlled the potential influence on the results of

Table 1. Characteristics ($\bar{X} \pm \text{SE}$) considered for matching the males in experiment 1

Variable	Bright male	Dull male	t_5	P
Weight (g)	1350 \pm 43	1408 \pm 65	0.746	NS
Tarsus length (cm)	9.34 \pm 0.11	9.41 \pm 0.10	0.897	NS
Tail length (cm)	17.50 \pm 3.34	22.25 \pm 3.80	1.350	NS
Spur length (cm)	1.35 \pm 0.15	1.26 \pm 0.03	0.640	NS
Wattle size (cm)	3.71 \pm 0.09	3.71 \pm 0.11	0.000	NS
Ear-tuft length (cm)	1.13 \pm 0.16	1.11 \pm 0.13	0.069	NS
Wattle display	0.23 \pm 0.02	0.24 \pm 0.03	0.086	NS
Dominance index	0.35 \pm 0.05	0.40 \pm 0.08	0.688	NS

Paired t -test of difference in the six trials between bright and dull males ($N=6$), and two-tailed P . Wattle display: arcsine transformation of the frequency of wattle display. Dominance index: square root and logarithmic transformation of the cardinal index (ICB).

any differences (other than brightness) between experimental males.

We conducted all the trials in both experiments in the afternoon peak of activity (between 1700 and 1800 hours, Universal Time Coordinates). To compare with the interactions observed during the experiments, we recorded the mean rate for the same agonistic interactions in normal conditions in the aviary. This was done during six periods of 30 min each on non-experimental days (to avoid the disturbance caused by the experimental manipulation) and at hours corresponding to the experimental hours. For the analysis of results we used the total number of aggressive acts (threats, pecks and chases) received by each male.

Ethical Note

Pilot tests and an experiment previously conducted on plumage brightness and female choice (Mateos & Carranza 1995) showed that aggression directed at experimental dull males or novel males was never severe. The choice of sample size (six pairs of males) was based on the minimum sample size for significance in the tests we used (Wilcoxon tests). The trial length (30 min) was the minimum for the objectives of the study. A slightly shorter duration would probably have sufficed to test for differences in the number of aggressive acts received, but would not have allowed the comparisons of number and rank of males interacting with the experimental males (see Results).

The conditions in the aviary (see above) allowed us to carry out the experiments with minimal

impact on the subjects. Seventy-four per cent of aggressive acts directed to the manipulated males were brief chases and males had the opportunity to escape (to perches or shelter sites, and there was enough space for runs and short flights); 15% were threatening and only 11% fell into the category we called pecking. These were mostly only attempts at pecking, and in only a few cases was the recipient pecked. In no case was a male injured, even slightly. Should it have been necessary, the observer and an assistant were continuously ready to take action in the case of severe aggression. We had a special hand net to remove any individual quickly with minimal disturbance. After the trial experimental males did not show any sign of stress (e.g. weight loss, changes in their activity rhythm, lower frequency of wattle display or presence of stereotyped behaviours).

In experiment 1, manipulated males remained in the aviary after the trial, but the level of aggression received by dull males was not very high (see Results), and decreased during the trial. The rate of aggression received on the following day by these individuals ($\bar{X} \pm \text{SE} = 1.66 \pm 0.33$, $N=6$) was not different from that received by any other member of the group (1.76 ± 0.14 ; Mann-Whitney U -test: $U=16$, $N_1=N_2=6$, NS).

RESULTS

Experiment 1

The mean rate of aggression received per male in the aviary at this season $\pm \text{SE}$ was 1.76 ± 0.14 acts per 30 min ($N=6$). This rate did not differ

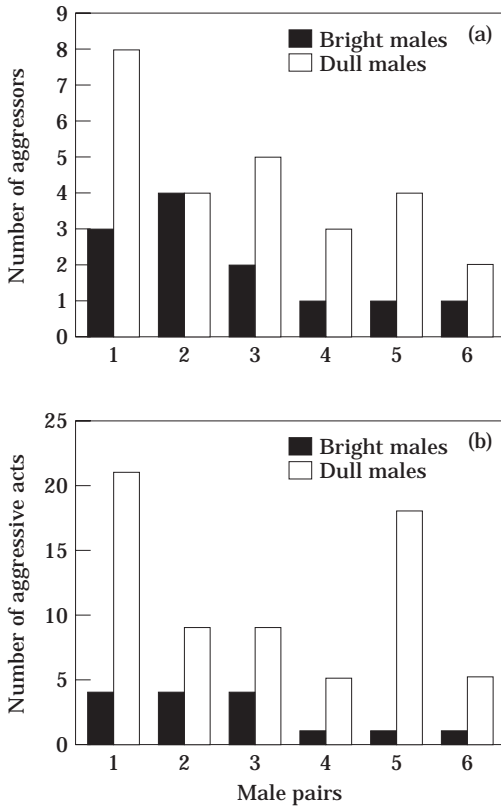


Figure 1. Experiment 1: (a) number of males directing aggression to, and (b) number of aggressive acts received by, the bright and the dull member of six male pairs known to the rest of the group.

from the mean received by bright males in the six trials (2.50 ± 0.67 ; Mann-Whitney U -test: $U=18$, $N_1=N_2=6$, ns), but was significantly lower than that received by dull males (11.16 ± 2.76 ; Mann-Whitney U -test: $U=36$, $N_1=N_2=6$, $P<0.01$). Individuals with dull plumage received aggression from more males in the six trials ($\bar{X} \pm SE = 4.33 \pm 0.84$ for dull males, 2.00 ± 0.51 for bright males; two-tailed Wilcoxon test: $Z=2.03$, $N_1=N_2=6$, $P<0.05$; Fig. 1a) and also received more aggressive acts than the bright males ($\bar{X} \pm SE = 11.16 \pm 2.76$ for dull males, 2.50 ± 0.67 for bright males; two-tailed Wilcoxon test: $Z=2.214$, $N_1=N_2=6$, $P<0.05$; Fig. 1b). Regarding the hierarchical order of aggressors, there were no significant differences between the status of males interacting with dull or bright males (two-tailed Wilcoxon test: $Z=0.105$,

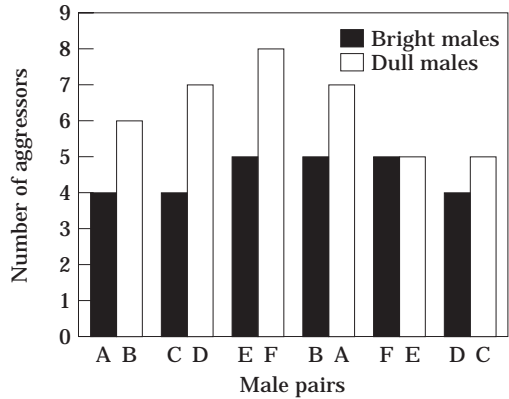


Figure 2. Experiment 2: number of males in an established group directing aggression at the bright and the dull member of a newly introduced pair of males. Letters under the histogram indicate individual males.

$N_1=N_2=6$, ns). Dull males received more aggressive acts from dominant males than the bright ones ($\bar{X} \pm SE = 6.00 \pm 1.34$ for dull males, 1.00 ± 0.25 for bright males; two-tailed Wilcoxon test: $Z=2.207$, $N_1=N_2=6$, $P<0.05$) and also from subordinate males, although in this case the difference did not reach significance ($\bar{X} \pm SE = 5.16 \pm 1.79$ for dull males, 1.50 ± 0.56 for bright males; two-tailed Wilcoxon test: $Z=1.826$, $N_1=N_2=6$, $P<0.1$).

Experiment 2

As expected, the introduction of two unknown males into a stable group of 14 individuals, very well ranked in a highly linear hierarchy (Mateos & Illanes, in press), resulted in a high rate of aggression to the intruders, so that both males received more aggressive acts than the other males in the group ($\bar{X} \pm SE$ rate of aggressive interactions in June 1991 = 2.14 ± 0.34 aggressive acts received per male in the group in 30 min; received by novel dull males: 36.66 ± 4.52 , Mann-Whitney U -test: $U=42$, $N_1=N_2=6$, $P<0.01$; received by novel bright males: 40.50 ± 5.74 , Mann-Whitney U -test: $U=42$, $N_1=N_2=6$, $P<0.01$).

These results support those from experiment 1: dull males, compared with bright ones, received aggression from more males in the six trials ($\bar{X} \pm SE = 6.33 \pm 0.49$ for dull males, 4.50 ± 0.22 for bright males; two-tailed Wilcoxon test: $Z=2.041$, $N_1=N_2=6$, $P<0.05$; Fig. 2), although in this case there were no significant differences in the total

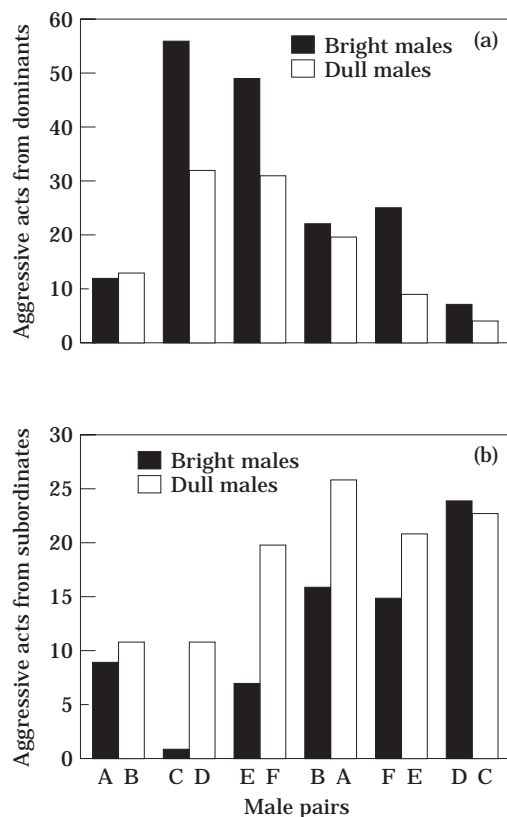


Figure 3. Experiment 2: number of aggressive acts directed by (a) dominant and (b) subordinate males in an established group at the bright and the dull member of a newly introduced pair of males. Letters under the histograms indicate individual males.

number of aggressive acts received by dull and bright males ($\bar{X} \pm SE = 36.66 \pm 4.52$ for dull males, 40.50 ± 5.74 for bright males; two-tailed Wilcoxon test: $Z = 1.153$, $N_1 = N_2 = 6$, ns). These figures resulted from the differences in behaviour of dominants and subordinates when strange males were introduced into the aviary, since:

(1) the mean dominance index of aggressors of the bright male was higher than that of the aggressors of the dull male, in the six trials (two-tailed Wilcoxon test: $Z = 1.992$, $N_1 = N_2 = 6$, $P < 0.05$);

(2) bright males received more aggressive acts from dominant males than did dull males ($\bar{X} \pm SE = 28.50 \pm 8.09$ for bright males, 18.00 ± 4.71 for dull males; two-tailed Wilcoxon test: $Z = 1.997$, $N_1 = N_2 = 6$, $P < 0.05$; Fig. 3a) and dull

males received more aggressive acts from subordinate males than did bright males ($\bar{X} \pm SE = 18.66 \pm 2.56$ for dull males, 12.00 ± 3.28 for bright males; two-tailed Wilcoxon test: $Z = 1.997$, $N_1 = N_2 = 6$, $P < 0.05$; Fig. 3b); and

(3) the novel bright male received more aggressive acts from the alpha male than the novel dull male ($\bar{X} \pm SE = 24.33 \pm 8.30$ for bright males, 12.16 ± 3.71 for dull males; two-tailed Wilcoxon test: $Z = 2.207$, $N_1 = N_2 = 6$, $P < 0.05$). In particular, the alpha male was the aggressor in 60% of the aggressive acts received by bright males (146 out of 243), while he was in only 33% of those received by dull males (73 out of 220, chi-square test: $\chi^2_1 = 32.44$, $P < 0.01$).

The readiness and strength of the aggressive response by males in the aviary towards novel males did not allow us to observe differences in the response by novel males to such aggression. All experimental males showed submissive signals, concealing the wattle display (Mateos & Carranza 1997) regardless of the frequency of wattle display they used to maintain before, when in the isolated cages.

We made a further statistical control for potential differences between males apart from the experimental manipulation. This consisted of pair-wise comparisons of aggressive acts received by each male in the two conditions by pairing the dull and bright scores for each male with each other. Because the two conditions for a given male occurred in different trials and days, and the total number of aggressive acts received by experimental males in 30 min varied between trials, we cannot compare the dull and bright conditions of the same male by using the absolute number of acts received, as we did within trials, and we have to use proportions. The results support previous findings. When an individual male had dull plumage, he received aggressive acts from a higher proportion of males than when he had bright plumage ($\bar{X} \pm SE = 0.57 \pm 0.02$ for dull condition, 0.41 ± 0.02 for bright condition; two-tailed Wilcoxon test: $Z = 2.220$, $N_1 = N_2 = 6$, $P < 0.05$). Similarly, bright males, compared with when they were dull, received a higher proportion of aggressive acts from dominant males ($\bar{X} \pm SE = 0.60 \pm 0.03$ when bright, 0.39 ± 0.03 when dull; two-tailed Wilcoxon test: $Z = 2.210$, $N_1 = N_2 = 6$, $P < 0.05$), while dull males received a higher proportion of aggressive acts from subordinates ($\bar{X} \pm SE = 0.64 \pm 0.06$ when dull,

0.34 ± 0.06 when bright; two-tailed Wilcoxon test: $Z = 2.210$, $N_1 = N_2 = 6$, $P < 0.05$).

Finally, a last statistical control showed that the results did not depend on the order in which each male was manipulated and introduced into the aviary (i.e. being bright or dull first, rather than second; chi-square test: χ^2_1 , NS).

DISCUSSION

The results of experiment 1 showed that pheasant males are more aggressive towards dull males. Since the six pairs of experimental males were of similar characteristics and rank (see Table I) and belonged to the same group where the trials took place, this difference can be explained only as an effect of the treatment. In this experiment there were no significant differences in status between males interacting with bright or dull males, although dominant males threatened and attacked dull males more often than bright males. One possibility here is that the treatment affected individual recognition, making the dull male, and not the bright one, an unknown male, and that he was attacked because he was perceived as an intruder.

Experiment 2 was designed to control this effect of individual recognition. The introduction of unknown males into the aviary elicited more aggression, and both members of the pair, bright and dull, received more aggression than the average for any member of the group. However, together with this effect, the results from this experiment showed clear differences between dull and bright males (see also statistical controls for male identity and order). The dull males received aggression from more males, mainly the subordinates, while the bright males received aggression from fewer males, mainly the dominants.

These results indicate the importance of individual recognition in the agonistic interactions in a group of male pheasants: any unknown individual was immediately tested and received a much higher rate of aggression than the average of the group. Second, changes in plumage brightness had a significant effect in male–male interactions: it may affect individual recognition (experiment 1), and it is used by males to assess the quality of competitors (experiment 2).

Recent studies on Galliformes do not suggest that plumage is important in male–male competition (Ligon et al. 1990) or in female mate choice

(Ligon & Zwartjes 1995; Mateos & Carranza 1995). As these authors indicate, (1) the male-type plumage in pheasants is not testosterone dependent because it develops fully in castrated males and appears in ovariectomized females (Lofts & Murton 1973), and (2) the moult takes place in the post-breeding period and hence plumage quality may reflect post-moult condition but does not convey accurate information about the physical condition of its bearer during the mating season (Ligon et al. 1990; Mateos & Carranza 1995). In short, plumage brightness and coloration do not appear to be related to the mating season, as would be expected for a sexually selected trait; they are maintained all year and are at their best after the post-breeding moult (September–October).

It is possible that the initial condition in the pheasant was plumage monomorphism, with the cryptic female-type plumage subsequently having evolved under natural selection from predators (Ligon & Zwartjes 1995). In fact, this hypothesis, formerly defended by Wallace (1889), is generally applicable to those birds, like pheasants, with a polygynous mating system without male parental care, that nest on the ground in open habitats, and are sexually dimorphic in plumage throughout the year (Andersson 1994). Also, it has not yet been proven that maintaining a colourful and bright plumage is costly, nor that it is a handicap for survival. Predation risk in pheasants is quite high. Up to 79% of all winter deaths in a pheasant population can be caused by predators, and detectability seems to be an important factor for predation pressure on this species because most predation occurs when the ground is covered with snow (Hill & Robertson 1988). However, aerial predators (sensitive to colours) selectively direct their attacks to females and juveniles with cryptic plumage, because males are too big for raptors (see review in Hill & Robertson 1988). A detailed study in Sweden showed that raptors (mainly goshawks, *Accipiter gentilis*) were responsible for 88% of total winter mortality of female pheasants and only 23% of male winter mortality (Kenward 1977; Kenward et al. 1981).

In general, studies on plumage coloration in birds and predation risk, although controversial (e.g. Götmark 1992; Slagsvold et al. 1995), point out that when predation risk is higher for females, selection will favour cryptic plumage in females (according to Wallace's hypothesis) and at the

same time colourful plumage may be selected for in males because conspicuous males may be signalling that they are a less easy prey to catch (the unprofitable prey hypothesis: Baker & Parker 1979), thus promoting sexual dimorphism in plumage coloration. Nevertheless, Wallace's hypothesis does not seem to explain adequately why the males of an initially monomorphic species acquire such extravagant plumage, while pressures such as sexual selection can lead to most conspicuous ornaments of polygynous males (Andersson 1994). The conspicuousness might not have been selected for a warning role, yet conspicuous males are often unprofitable to predators (Guilford & Dawkins 1993).

Some plumage ornaments of male pheasants (such as the tail and the head tufts), although maintained all year, are exhibited mainly (or only) during courtship behaviour and the related ritualized agonistic interactions; their size and the intensity of displaying are related to physical condition and rank, and affect per se mate choice and the outcome of male–male encounters (Mateos & Carranza 1995, 1997). In contrast to ornaments associated with the wattle display (wattle and ear-tufts, signals whose levels allow for strategic choice in signallers; Mateos & Carranza 1997), the plumage in male pheasants is a permanent trait and not related exclusively to the mating season. Although much of its variability in coloration is likely to be caused by cross-breeding between subspecies introduced in the Western Palearctic region (Biadi & Mayot 1990), its brightness, pigmentation, losses and breaks of feathers may reveal the existence of infectious diseases and parasite loads (even though it does not reflect condition during the mating season). In our study, two males highly affected by *Capillaria* sp. dramatically lost the pigmentation and brightness of the plumage, becoming quite similar to our experimentally dulled males; and Zuk et al. (1990a), in their work on parasites and mate choice in the red junglefowl, demonstrated that parasitized chicks not only grew more slowly but also had the feathers on the back significantly paler. Therefore, if the plumage contains information about health or parasite load, any pattern that enhances its perceptibility (e.g. brightness and pigmentation) may be regarded as an assessment signal (Guilford & Dawkins 1995). Our experiment manipulating healthy males suggests that plumage brightness is a signal that males use, independently of other

traits, probably to assess the health of the opponent. On the other hand, because the signal is broadcast all year, it can also be used in non-sexual contexts since male–male competition for access to resources occurs all year (Cramp & Simmons 1980; Hill & Robertson 1988; Biadi & Mayot 1990).

The behaviour of dominant and alpha males, in directing their threats and attacks mainly to novel males (experiment 1) or bright males (experiment 2), is consistent with the strategy of this group of males, observed during the 3 years of study. Dominant males were particularly aggressive to intruders, and they directed their threats and attacks mainly to other dominant males (Mateos & Illanes, in press; C. Mateos, personal observations). In experiment 2, it was the bright male (supposedly in a better condition) that threatened the status of dominant males. Dull males, in contrast, were attacked by more individuals, but especially the subordinate males in the group. Rowland et al. (1995) in their study on the effect on rivals of male sticklebacks', *Gasterosteus aculeatus*, nuptial coloration, found no differences in the overall percentage of aggressive acts received by bright and dull males, because fear and aggression interacted in agonistic encounters. Our results might be interpreted in the same way as bright males provoking more aggression and more fear, and therefore being attacked by dominant males, while dull males provoke less aggression but also less fear, and are attacked by subordinate males. Nevertheless, it is well documented in the literature on pheasant rearing (Manetti 1980), and we have observed in our aviaries, that when an individual falls ill he is systematically attacked by the other males, including the most subordinate males (on occasion, mainly by them), to the point that the only way to save his life is to remove him from the group. Such extremely high aggressiveness towards unhealthy males, with little competitive ability, is surprising. It is possible that aggressors benefit by learning about aggressive behaviour or social relationships, and raising their social rank if prior dominance experience increases the probability of winning future contests (e.g. Beacham & Newman 1987).

In conclusion, the brightness and pigmentation of male plumage can play a role in intra-sexual competition for resources which takes place all year in male–male groups, as well as during the establishment and defence of male mating

territories. The amount of empirical data on the evolution of epigamic traits, and their controversial nature, seem to point out that what determines the reproductive success of males is a complex suite of characters that produce differences between individuals, on which the effects of inter-sexual, intra-sexual and natural selection are difficult to delimit (Koenig & Albano 1986; Kodric-Brown 1993).

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REFERENCES

- Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature, Lond.*, **299**, 818–820.
- Andersson, M. 1994. *Sexual Selection*. Princeton: University Press.
- Baker, R. R. & Parker, A. 1979. The evolution of bird colouration. *Phil. Trans. R. Soc. Ser. B*, **287**, 63–130.
- Beacham, J. L. & Newman, J. A. 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish, *Lepomis gibbosus*. *Anim. Behav.*, **35**, 1560–1563.
- Biadi, F. & Mayot, P. 1990. *Les Faisans*. Paris: Hatier.
- Boyd, R. & Silk, J. B. 1983. A method for assigning cardinal dominance ranks. *Anim. Behav.*, **31**, 45–58.
- Buchholz, R. 1995. Female choice, parasite load and male ornamentation in wild turkeys. *Anim. Behav.*, **50**, 929–943.
- Butcher, G. S. & Rohwer, S. 1989. The evolution of conspicuous and distinctive colouration for communication in birds. *Curr. Ornithol.*, **6**, 51–108.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.*, **27**, 211–225.
- Cramp, S. & Simmons, K. E. L. (Eds) 1980. *The Birds of the Western Palearctic, Vol. II*. Oxford: Oxford University Press.
- Evans, M. R. & Hatchwell, B. J. 1992. An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. The role of pectoral tufts in territorial defence. *Behav. Ecol. Sociobiol.*, **29**, 413–419.
- Götmark, F. 1992. Anti-predator effect of conspicuous plumage in a male bird. *Anim. Behav.*, **44**, 51–55.
- Grafen, A. 1990. Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.*, **144**, 473–516.
- Guilford, T. & Dawkins, M. S. 1993. Are warning colors handicaps? *Evolution*, **47**, 400–416.
- Guilford, T. & Dawkins, M. S. 1995. What are conventional signals? *Anim. Behav.*, **49**, 1689–1695.
- Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–387.
- Hill, D. A. & Robertson, P. 1988. *The Pheasant. Ecology, Management and Conservation*. Oxford: BSP Professional Books.
- Hill, G. E. 1991. Plumage colouration is a sexually selected indicator of male quality. *Nature, Lond.*, **350**, 337–339.
- Hillgarth, N. 1990. Parasites and female choice in the ring-necked pheasant, *Phasianus colchicus*. *Am. Zool.*, **30**, 227–233.
- Kenward, R. E. 1977. Predation on released pheasants (*Phasianus colchicus*) by goshawks (*Accipiter gentilis*) in Central Sweden. *Viltrevy*, **10**, 79–109.
- Kenward, R. E., Marcström, V. & Karlbom, M. 1981. Goshawk winter ecology in Swedish pheasant habitats. *J. Wildl. Mgmt*, **45**, 397–408.
- Kodric-Brown, A. 1993. Female choice of multiple criteria in guppies: interacting effects of dominance, colouration and courtship. *Behav. Ecol. Sociobiol.*, **32**, 415–420.
- Koenig, W. D. & Albano, S. S. 1986. On the measurement of sexual selection. *Am. Nat.*, **127**, 403–409.
- Lofts, B. & Murton, R. K. 1973. Reproduction in birds. In: *Avian Biology, Vol. III* (Ed. by D. A. Farner & J. R. King), pp. 1–107. New York: Academic Press.
- Ligon, J. D. & Zwartjes, P. W. 1995. Ornate plumage of male red junglefowl does not influence mate choice by females. *Anim. Behav.*, **49**, 117–125.
- Ligon, J. D., Thornhill, R., Zuk, M. & Johnson, K. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Anim. Behav.*, **40**, 367–373.
- Manetti, O. 1980. *Allevamento del Fagiano*. Bologna: Edagricole.
- Mateos, C. & Carranza, J. 1995. Female choice for morphological features of male ring-necked pheasants. *Anim. Behav.*, **49**, 737–748.
- Mateos, C. & Carranza, J. 1996. On the inter-sexual selection for spurs in the ring-necked pheasant. *Behav. Ecol.*, **7**, 362–369.
- Mateos, C. & Carranza, J. 1997. Signals in intra-sexual competition between ring-necked pheasant males. *Anim. Behav.*, **53**, 471–485.
- Mateos, C. & Illanes, M. C. In press. Dominancia social en machos de faisán común: posible origen metodológico de las discrepancias entre estudios. *Etología*.
- Rohwer, S. 1977. Status signaling in Harris sparrows: some experiments in deception. *Behaviour*, **61**, 107–121.
- Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. *Am. Zool.*, **22**, 531–546.

- Rohwer, S. & Ewald, P. W. 1981. The cost of dominance and advantage of subordination in badge signaling system. *Evolution*, **35**, 441–454.
- Rowland, W. J., Bolyard, K. J. & Halpern, A. D. 1995. The dual effect of stickleback nuptial coloration on rivals: manipulation of a graded signal using video playback. *Anim. Behav.*, **50**, 267–272.
- Slagsvold, T., Dale, S. & Kruszewicz, A. 1995. Predation favours cryptic coloration in breeding male pied flycatchers. *Anim. Behav.*, **50**, 1109–1121.
- Studd, M. V. & Robertson, R. J. 1985. Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). *Anim. Behav.*, **33**, 1102–1113.
- Wallace, A. R. 1889. *Darwinism*. 2nd edn. London: Macmillan.
- Zuk, M., Thornhill, R. & Ligon, J. D. 1990a. Parasites and mate choice in red jungle fowl. *Am. Zool.*, **30**, 235–244.
- Zuk, M., Thornhill, R., Ligon, J. D., Johnson, K., Austad, S., Ligon, S. H., Thornhill, N. W. & Costin, C. 1990b. The role of male ornaments and courtship behaviour in female mate choice of red jungle fowl. *Am. Nat.*, **136**, 459–473.