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Anna Papeschi

Universita di Firenze, dessi@unifi.it


John P. Carroll

University of Georgia, jcarroll2@unl.edu

Francesco Dessi-Fulgheri

Universita di Firenze

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WATTLE SIZE IS CORRELATED WITH MALE TERRITORIAL RANK IN JUVENILE RING-NECKED PHEASANTS

ANNA PAPESCHI^{1,4}, JOHN P. CARROLL^{2,5} AND FRANCESCO DESSI-FULGHERI^{1,3,4}

¹*Dipartimento di Biologia Animale e Genetica, Università di Firenze, Via Romana 17, 50125 Firenze, Italy*

²*The Game Conservancy Trust, Fordingbridge, Hampshire SP6 1EF, UK*

³*Centro di Studio per la Faunistica ed Ecologia Tropicali, C.N.R., Firenze, Italy*

Abstract. We used morphological measurements and behavioral observations to investigate the relationship between male ornaments and male social rank during the breeding season in a free-ranging population of one-year-old Ring-necked Pheasants (*Phasianus colchicus*). The sample was of birds of the same age class to avoid the confounding effect of age differences. Tail length, used by females in mate choice, and tarsal spur length, used by males as a weapon in fights, were not correlated with male rank, whereas the size of the wattle was the most important trait. This combined with recent studies showing that wattle size reliably indicates male testosterone levels at the beginning of the breeding season suggest that, among males, wattle size may be used as a signal of aggression level, and body condition.

Key words: *intrasexual selection, male ornaments, male rank, Phasianus colchicus, Ring-necked Pheasant, territoriality.*

El Tamaño de las Carúnculas Está Correlacionado con el Rango Territorial de los Machos en Faisanes *Phasianus colchicus* Juveniles

Resumen. Utilizamos medidas morfológicas y observaciones de comportamiento para investigar la relación entre los ornamentos de los machos y el rango social de éstos durante la época reproductiva en una población silvestre de faisanes *Phasianus colchicus* de un año de edad. La muestra consistió de aves de la misma clase de edad para evitar el efecto de diferencias entre edades. La longitud de la cola (utilizada por las hembras en la selección de pareja) y la longitud de la espuela tarsal (utilizada por los machos como un arma en enfrentamientos) no se correlacionaron con el rango de los machos, mientras que el tamaño de la carúncula fue el carácter más importante. En combinación con estudios recientes que muestran que el tamaño de la carúncula indica confiablemente los niveles de testosterona en los ma-

chos al inicio de la época reproductiva, esto sugiere que el tamaño de la carúncula podría ser usado como una señal de niveles de agresión y condición corporal entre los machos.

Several studies of the Ring-necked Pheasant (*Phasianus colchicus*; the Common Pheasant in Europe) have demonstrated that the tail, tarsal spur, and head ornaments play a role in intrasexual and intersexual interactions (von Schantz et al. 1989, Hillgarth 1990, Grahn et al. 1993, Mateos and Carranza 1995, 1996, 1997). However, the results of these studies are contradictory and they do not identify the information contained in the male signals, nor how they affect intraspecific interactions in natural conditions.

Von Schantz et al. (1989) showed that female Ring-necked Pheasants choose to mate with long-spurred males and that mating with long-spurred males increases female reproductive success. However, subsequent studies by the same authors demonstrated that tarsal spur length was not related to male success in attracting females, nor with female reproductive success measured as number of sired chicks and number of hatched young, respectively (Grahn et al. 1993). Surprisingly, tarsal spurs, which males use as weapons, did not show any relationship to a male's ability to gain a territory, or, among territorial males, with territory quality (Grahn et al. 1993). Other experimental studies have demonstrated that spur length does not affect female mate preference (Hillgarth 1990, Mateos and Carranza 1996), whereas some soft ornaments, such as the periocular wattle and tail, can influence both intersexual and intrasexual interactions (Mateos and Carranza 1995, 1997). These findings are the result of experimental studies conducted in controlled conditions, and little is known about the role of male traits as signals in nature. Indeed, male-male interactions and social hierarchy can be difficult to study in an aviary, considering the extent of the male territory in the wild and unknown effects of confinement on territorial behavior.

Our recent work on both wild and hand-reared populations of Ring-necked Pheasants documented a link between wattle size and testosterone plasma levels: wattle size increase is the first signal of seasonal gonadic recrudescence (Papeschi et al. 2000), and the wattle is the only male ornament positively affected by a testosterone administration (Briganti et al. 1999).

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⁴ E-mail: dessi@unifi.it

⁵ Present address: Warnell School of Forest Resources, University of Georgia, Athens, GA 30602-2152.

Secondary male traits depending on testosterone levels are rare in birds, where plumage dimorphism involves an estrogen-based mechanism (Domm 1939, Witschi 1961, Owens and Short 1995): estrogen induces female plumage patterns, whereas the absence of estrogen results in male-like ornamentation (including tarsal spurs).

In birds, head traits are dynamic. They play the role of coverable badge (Hansen and Rohwer 1986, Rohwer 1982) in that they can change rapidly to notify an opponent (Maynard Smith 1991), rather than simply act as a static badge of status. Dynamic traits on the face or head are key signals involved in intrasexual contests of several galliforms (Buchholz 1997, Ligon et al. 1990, Mateos and Carranza 1997). Such ornaments may be favored because they provide more accurate and immediate information regarding male motivation and condition than a static badge.

The periocular wattle's sensitivity to testosterone, and its extremely dynamic nature, make this male ornament a potential key signal in male-male contests among Ring-necked Pheasants. It may function as honest advertisement (Kodric-Brown and Brown 1984, Folstad and Karter 1992) of male quality, condition, and motivation. We investigated the roles of three different male ornaments, the periocular wattle, tail, and tarsal spur, as signals in male-male interactions throughout the breeding season in natural conditions. We studied the correlation between these male ornaments measured at the end of winter and the ranks the males subsequently gained during the breeding season.

METHODS

STUDY AREA

We studied the behavior of 193 free-ranging male Ring-necked Pheasants on Clarendon Park Estate (50°56'N, 1°47'W), 5 km east of Salisbury, Wiltshire, UK, from 11 February until 30 April 1996. The estate covers approximately 20 km² and is dominated by intensive farming, with a large central area (360 ha) of mixed woodland. The farm releases pheasants each year to supplement the natural population, and it is possible that birds studied included surviving reared birds or their offspring.

MORPHOLOGICAL MEASUREMENTS

During February, we captured 193 male Ring-necked Pheasants with 10 pen traps scattered in the park. Each trap was baited with corn early in the morning, around 06:00 GMT, and checked between 08:00 and 09:00 GMT; the traps were then closed until the next morning. The handling time for each bird was limited to 10 min, necessary for the morphological measurements and tagging. Birds were then released into the wild at the trap site to avoid stress by translocation. Before its release, each male was individually marked with a rectangular neck poncho (21 × 6 cm). Ponchos were a medium green that is similar to neck and upper body plumage, with an individual code of 2 letters written on both sides of the poncho with black ink. We used green to avoid colors of male traits that have a role in

sexual interactions, such as red (wattle), dark blue (ear tufts) or blue and brown (tail).

For each male we measured body mass (to the nearest 10 g), flattened wing chord and tail lengths (length of the longest feather, to the nearest 1 mm), length of vertical wattle axis (to the nearest 0.1 mm), spur length (to the nearest 0.1 mm) and shaft diameter of the first (proximal) primary feather (to the nearest 0.1 mm).

AGE CLASSES

Males were divided into two age classes (juveniles = 1 year old; adults = 2 years or older) based on shaft diameter of the first proximal primary wing feather (Greenberg et al. 1972). The age ratio of trapped males was skewed due to management of the estate for hunting: of 193 measured males, we found 161 one-year-old males, 23 adults, and 9 indeterminate. In the Ring-necked Pheasant, older males may have more developed ornaments and are more likely to hold a territory (Ridley and Hill 1987; AP, unpubl. data). Thus to avoid confounding effects of age, we only considered one-year-old males.

BEHAVIORAL OBSERVATIONS

We carried out observations for 18 days in March and 18 days in April, 6 hr per day for a total of 216 hr of observation. Each day we drove in the park along three paths so as to cover the entire area every three days. When a tagged male was sighted we turned off the engine, waited about 1 min to allow the bird to recover from the alert, and then observed his behavior for 10 min. We recorded his position in the area, his main behavior (e.g., strutting, feeding, preening, sneaking, vigilance, chasing, etc.), his wattle score (1 = closed, 2 = half erected, 3 = erected), and the number of crowings (high-intensity vocalizations). If the tagged bird was interacting with another male, we waited to observe the result of the interaction.

MALE RANK ASSESSMENT

We assessed male ranks on the basis of the behavioral observations carried out in March and April. Rank assessment was performed only for those males with at least five independent observations (made on different days); 80% of ranked males had 10 independent observations each. As a first criterion to assess rank we distinguished sexually active males (showing aggression toward other males and sexual interactions with females) from sexually inactive males (showing a prevalence of maintenance activities, i.e., feeding, resting, or preening).

Within the first group, we distinguished "sneakers" from territorial males. Territorial males were recognized by typical behaviors of this species (Taber 1949, Ridley and Hill 1987): permanent defense of a territory, strutting and crowing displays, and full wattle engorgement (head display). We ranked a male as territorial when we observed permanent defense of the same territory in each observation, together with the presence of at least one territorial display in each observation. "Sneaker" males did not defend their home ranges and were often clustered in male groups; their home ranges were larger than ranges of territorial males, and they did not

TABLE 1. Mean \pm SE morphological traits measured in February for male Ring-necked Pheasants categorized by one of three different ranks during the following breeding season. One-way ANOVAs tested each male trait; $df = 2,83$ for all comparisons except spur length, where $df = 2,82$.

Male trait	Peripheral males ($n = 42$)	Sneaker males ($n = 34$)	Territorial males ($n = 10$)	F	P	Observed power ^a
Body weight (g)	1638 \pm 20	1660 \pm 28	1708 \pm 42	1.0	0.39	0.20
Wing length (cm)	24.4 \pm 0.1	24.4 \pm 0.1	24.6 \pm 0.6	0.3	0.76	0.11
Tail length (cm)	45.4 \pm 1.1	47.5 \pm 1.1	48.9 \pm 2.2	1.6	0.21	0.29
Spur length (mm)	10.4 \pm 0.3	10.5 \pm 0.4	10.6 \pm 0.6	0.1	0.95	0.06

^a Computed using $\alpha = 0.05$.

show strutting and head displays, although they did occasionally crow. Sneakers waited at the border of a territory for an opportunity to force a female living with a resident male to copulate. Forced copulations and harassments toward females in this species are particularly aggressive and recognizable (Ridley and Hill 1987). We classified three male ranks: (a) sexually inactive males, or peripherals, (b) sexually active males without a territory or sneakers, and (c) territorial males.

STATISTICAL ANALYSIS

All data were analyzed using SPSS version 11 for Windows (SPSS Inc. 2002). We performed univariate ANOVAs for each morphological variable to test for differences among the three male ranks. For nonsignificant ANOVAs we used power analysis to evaluate the probability of type II errors. We used ANCOVA to test for wattle size differences among ranks controlling for body mass. We examined the data for departures from normality by means of preliminary

graphing and testing; the data did not depart from normality. Probability tests are two-tailed. Significance was accepted at $P < 0.05$.

RESULTS

During the study we resighted 114 of the 161 tagged young males and we were able to assess the ranks of 86 of them. There were 42 peripherals, 34 sneakers, and 10 territorial males.

Body weight, tail length, and wing length were not different among males of different ranks (Table 1), whereas we found that vertical wattle size was significantly longer in territorial males than in sneakers ($F_{2,83} = 4.1, P < 0.02$; Fisher *post-hoc* test = 1.8, $P < 0.05$) and peripheral males (Fisher *post-hoc* test = 1.8, $P < 0.05$; Fig. 1). ANOVA did not show any difference of spur length among males of different ranks; however the observed power for this analysis was particularly low (Table 1) indicating a high probability of type II error for this result.

Since larger males had larger wattles ($n = 86, r = 0.44, P < 0.001$) we performed an ANCOVA on vertical wattle size with body mass as the covariate. This analysis showed that territorial males had larger wattles than expected for their body size ($F_{1,2,82} = 3.3, P < 0.05$).

DISCUSSION

We found that the vertical dimension of the periocular wattle measured in February was related to the male rank, measured as the ability of the male to gain a territory later in the breeding season. Tail and spur lengths measured in February were not correlated with subsequent male rank during the breeding season. Our findings are in line with the results of Mateos and Carranza (1997) who found that taxidermic mounts of male pheasants with larger periocular wattles decreased aggressive behavior of opponent males. Our results are also consistent with the observation by Mateos and Carranza (1997) that a shorter tail tends to elicit more aggressive behavior by an opponent male, and with Grahn et al. (1993) that tarsal spur length is not related to territoriality. However our conclusion about spur length cannot be considered definitive since the power of our result on this trait was weak. A larger sample size may reveal new information on this intriguing male trait.

Our results are also consistent with those of several studies investigating the function of pigment-

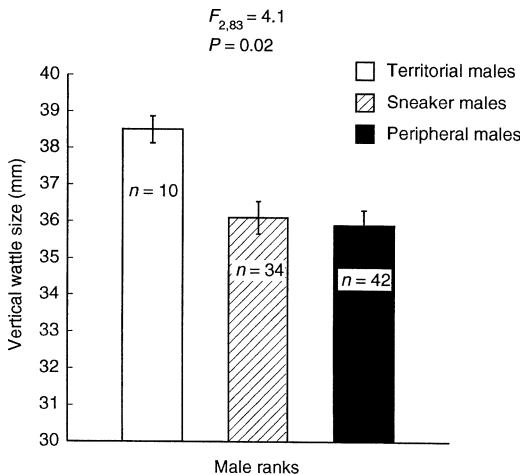


FIGURE 1. Mean \pm SE vertical wattle sizes, measured in February 1996 in Ring-necked Pheasant males that gained different social ranks in April of the same year. Males becoming territorial in April had bigger wattles in February than males that gained lower ranks.

based plumage ornaments, where researchers found positive correlations between these male traits and territory acquisition or social dominance (Hill 1988, Veiga 1993, Wolfenbarger 1999). Although classic studies view melanin-based ornaments as indicators of social rank, recent findings suggest that ornaments containing melanin pigments are poorer signals of phenotypic quality than those containing carotenoid pigments (Hill 1996, Hill and Brawnner 1998, Badyaev and Hill 2000). Field and captive studies of Gambel's Quail (*Callipepla gambelii*) have found no relationship between the size of male ornaments containing melanin and other aspects of male condition (Hagelin and Ligon 2001). Periocular wattles of the Ring-necked Pheasant are red ornaments, and although little is known about their chemical composition a recent study by Ohlsson et al. (2001) has shown that the color of the wattle reflects protein availability in the diet, early in life.

Traditionally ornament evolution is viewed as occurring through intersexual selection; however, biologists have long recognized that conspicuous ornaments may function both in male-male competition and in female choice (Hingston 1933, Noble 1938). The evolution of male ornaments through intrasexual selection was renewed by several authors in the 1970s (Peck 1972, Borgia 1979); in that period others stressed how ornaments may signal status in other contexts such as in competition for food and other resources (Rohwer 1975, West-Eberhard 1979). Berglund et al. (1996) re-proposed the evolution of male ornaments through male contest: females could use male ornaments as honest signals since they have evolved as status signals among males. In this light, it is not surprising that a soft, extremely dynamic ornament like the periocular wattle may be related to male rank while the tarsal spur, a main weapon in pheasants, is not. In the Ring-necked Pheasant, male-male competitions begin at the end of winter and last until the end of spring; male fights are intense and the loser can be severely wounded (Hill and Robertson 1988). Males avoiding higher quality individuals reduce their risk of severe injuries and defeat. Thus, status signals may be more adaptive than selection for a mere weapon. Experimental studies on the Ring-necked Pheasant and the Red Junglefowl (*Gallus gallus*) support this idea: Ligon et al. (1990) showed that comb size and comb chroma were significantly related to winning in controlled fights whereas spur length was not, and Mateos and Carranza (1997) showed that larger wattles reduced the aggressiveness of male opponents.

Testosterone levels have a positive influence on both the development of the wattle during fall and winter in yearling males and the variation of wattle size at the end of the winter in adult males (Briganti et al. 1999, Papeschi et al. 2000). Moreover, wattle size is positively correlated with male physical condition (Papeschi et al. 2000) and with male survival (Papeschi and Dessì-Fulgheri 2003). Since the development and size of the wattle depend on testosterone levels and physical condition of a male during the winter (Papeschi et al. 2000), conspecifics assessing

male ornamentation in the spring receive information about the physical condition and hormonal status of the bearer. Wattles can be fully engorged in a few seconds (AP, pers. obs.), making this ornament a direct signal of a male's immediate hormonal status, readiness to fight, fighting ability, and perhaps to other testosterone-related traits, such as immunocompetence (Folstad and Karter 1992).

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