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Are Rooster Crows Honest Signals of Fighting Ability?

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Rooster crows are loud, stereotyped vocalizations that appear to function as assertions of social dominance over conspecific males in wild Red Junglefowl (*Gallus gallus*) and their domestic counterparts (Miller 1978, Leonard and Horn 1995). Roosters establish linear dominance hierarchies that reflect individual fighting ability, and dominant males have preferential sexual access to females in a flock (Miller 1978, Leonard and Horn 1995).

Honest signaling theory (Grafen 1990, Zahavi 1991) predicts that assertions of status should entail costs that reveal phenotypic quality, rendering such signals accurate, condition-dependent advertisements of resource-holding potential (Maynard Smith 1982). Costly signals are sometimes referred to as "handicap" signals (Zahavi 1991, Folstad and Karter 1992). Natural selection should favor honest advertisements of resource-holding potential because both participants in such systems (i.e. signal sender and signal receiver) reduce their risk of unnecessarily engaging in dangerous fighting behaviors. By announcing high resource-holding potential, dominant individuals reduce the incidence of fights and the fitness effects that even victorious animals can face during combat, whereas receivers avoid challenging individuals that they are unlikely to overpower, thereby avoiding injury or death.

Parameters of agonistic acoustic displays produced among males in species as varied as tarbush grasshoppers (*Ligurotettix planum*), toads (*Bufo bufo*), and red deer (*Cervus elephus*) predict which contestants will prevail in combat (Davies and Halliday 1978, Clutton-Brock and Albon 1979, Greenfield and Minckley 1993; also see Arak 1983). It has long been suspected that the rooster's crow similarly advertises fighting ability (Fisher 1930). Rooster crows recently have been shown to entail no significant metabolic production costs, raising doubts about this signal's honesty (Chappell et al. 1995, Horn et al. 1995). However, other mechanisms may ensure a condition-dependent quality of crows, such as immunological handicapping by testosterone (Folstad and Karter 1992), social costs (attacks on crowing subordinates; Leonard and Horn 1995) or neurodevelopmental integrity (Furlow 1997). Hence, rooster crows may honestly advertise resource-holding potential to social competitors despite their low immediate production costs (Kodric-Brown and Brown 1984).

To make a preliminary assessment of whether crows signal resource-holding potential, we analyzed the crows of 20 adult male Red Junglefowl. We measured three condition-dependent markers of phenotypic quality known or presumed to be correlated with fighting success: (1) body size, (2) size and asymmetry of fighting spurs, and (3) length of fleshy head combs. We then compared the acoustic parameters of crows with these phenotypic measures.

Methods.—Twenty sexually mature, 1-year-old male Red Junglefowl were measured and recordings were made of their crows. Rearing conditions are described in Kimball et al. (1997). The roosters were free-ranging from about six weeks until seven months of age, at which time they were individually penned. At the time of recording, all roosters used in this study had been individually penned for approximately five months.

Each rooster's comb length and fighting spurs were measured to the nearest 0.1 mm using dial calipers. Standardized body size was obtained by summing the standardized lengths of the humerus, tarsus, tibia, and femur. The fluctuating asymmetry (FA) of spurs, a measure of developmental integrity and a possible correlate of fighting success in birds (Møller 1992), was calculated as the difference between right and left measures divided by mean spur length (Parsons 1990; see also Kimball et al. 1997). Spur asymmetry met the statistical definitions of FA (Palmer 1994, Kimball et al. 1997). Because spur length and FA were not correlated, we calculated absolute (vs. relative) FA values (Palmer 1994). Doing this rendered a half-normal distribution for FA values from our sample (see Palmer 1994).

Crows were recorded at a distance of 1 to 3 m with a Radio Shack VSC-2002 recorder and an Electret 33-3007 unidirectional microphone. Recordings were digitized on an Apple Macintosh computer using Cornell University's Canary 1.1 bioacoustical analysis software. Sampling rate was 22 kHz and display range 11 kHz. Sample size for Canary software is set at 8 bits (see Charif et al. 1993).

The software was used to generate spectrographs from which the crow's physical features were measured. Crow duration, mean fundamental frequency, and dominant frequency (Hz at peak amplitude) were measured. We did not measure amplitude because of the variation in recording distances (recording distance is unlikely to affect relative measures such as which frequency has the highest amplitude, but comparisons of absolute amplitudes of different individuals could be affected). Only one crow was analyzed for each rooster, because junglefowl crow acoustics exhibit high individual stability (Miller 1978).

Statistical analyses were performed using SAS 6.04 software. Dominant frequency was split into two categories because the crows of all roosters fell into a low (782 to 869 Hz) or high (1,740 to 2,170 Hz) dominant-frequency category. We compared phenotypic differences between the low and high dominant-frequency categories. Fundamental frequency and crow duration were continuously distributed; therefore, these data were analyzed with correlation analyses. We used parametric tests for comb length (t-test), standardized body size (Pearson correlation), and spur length (Pearson correlation), and nonparametric tests for spur asymmetry (Wilcoxon rank sum and Spearman correlations). Because we tested for possible relationships among multiple acoustic and physical variables, all P-values were subsequently adjusted with sequential Bonferroni corrections (Rice 1989). Means, ranges, and correlations between trait sizes, as well as calculations of fluctuating asymmetry error, are detailed in Kimball et al. (1997).

Results and Discussion.—Roosters that produced low dominant-frequency crows had longer combs ($\bar{x} = 82.7 \pm$ SD of 5.1 mm) than those that produced high dominant-frequency crows ($\bar{x} = 75.3 \pm 3.8$ mm; $t = 3.6$, $P < 0.05$ after Bonferroni adjustment). No other variables (i.e. body size, spur length, and spur asymmetry) varied significantly with acoustic parameters of rooster crows.

Comb length is a condition-dependent signal of plasma testosterone levels and immunological health (Zuk et al. 1990, 1995, Folstad and Karter 1992) and has been shown to correlate with fighting ability in the population of Red Junglefowl used in this study (Ligon et al. 1990). Junglefowl comb turgidity is maintained by connective tissue fibroblasts that produce viscous, capillary-dilating mucoid in response to testosterone (see Ligon et al. 1998). Males with larger combs have relatively high levels of circulating testosterone and relatively low levels of circulating lymphocyte (Zuk et al. 1995), as predicted by the immunological handicap hypothesis (Folstad and Karter 1992).

Another galliform species, the Gray Partridge (*Per-*

dix perdix), has a syringeal structure very similar to that of *Gallus* (Gaunt and Gaunt 1985). Testosterone administration in this species thickens tracheal and bronchial lumina membranes during development (Beani et al. 1995) and lowers the dominant frequency of vocalizations (Fusani et al. 1994, Beani et al. 1995). A similar mechanism may be responsible for the correlation between testosterone-dependent comb length and the dominant frequency of junglefowl crows. If so, then crows offer a "snapshot" of androgen levels during syringeal development, whereas comb quality conveys information about a rooster's current immunological and hormonal status (see Zuk et al. 1995). Hence, crow quality may reflect an ontogenetic, Zahavian "pay now, display later" strategy. Junglefowl crows may be crudely indicative of phenotypic quality, whereas comb quality is a more precise indicator of current condition.

Why multiple signals evolve has been the subject of considerable interest (e.g. Møller and Pomiankowski 1993, Omland 1996, Ligon et al. 1998). In agonistic signaling contexts, sequential assessment theory (e.g. Enquist et al. 1990) may help explain the evolution of multiple signals. Sequential assessment theory posits that contestants should escalate agonistic encounters from cheap, general signals to more costly and more accurate (i.e. difficult to falsify) signals of resource-holding potential. Well-matched contestants continue to escalate until the interaction becomes violent, whereas power asymmetries are detected during earlier assessment steps such that the individual less likely to win retreats from the encounter. Hence, multiple signals with overlapping information domains in some cases may be explained as components of sequential agonistic-assessment displays.

The evolved audience of crows in the wild may have included conspecific territory intruders. If distant males were of roughly equivalent quality as that indicated by a territorial male's crow, closer inspection of a more accurate signal—comb size—may have been the next step in assessing the territorial male's resource-holding potential. It is also possible that crowing attracts unaffiliated hens in the wild.

In a previous study, Leonard and Horn (1995) found no significant relationship between comb length and fundamental frequency of crows among healthy domestic roosters, but they did identify a significant correlation between status and fundamental frequency (dominants had higher-pitched crows than subordinates.) The authors did not analyze dominant frequency. Their roosters were interacting and had established dominance hierarchies enforced by subordinate-directed attacks. Roosters in our study had been individually penned for five months prior to recording (roosters were not in visual contact but could hear one another's crows, rendering their social isolation incomplete). It is possible that aspects of an individual rooster's crow acoustic structure (such as fundamental frequency) vary with social conditions and motivational states, as Leonard and Horn (1995) found to be the case with crow rate, whereas other acoustic characteristics constitute a relatively "fixed" marker of hormone levels and other aspects of phenotypic quality during development. A longitudinal study of crow acoustic quality of roosters whose social status is experimentally manipulated is needed. Unfortunately, we were unable to perform social manipulations. Future studies should compare the crows of socially isolated roosters (and phenotypic measures) with those of roosters in dominance hierarchies to differentiate between the effects of social dominance (status) per se versus intrinsic phenotypic quality.

The quality of rooster crows is related to comb length—a trait previously shown to be a testosterone-dependent signal of immunocompetence and a correlate of fighting success in the population of Red Junglefowl that we studied (Ligon et al. 1990, Zuk et al. 1990). Both immunological health and aggressiveness (another possible correlate of testosterone levels) are probable correlates of fighting success among roosters. The preliminary results that we report suggest that resource-holding potential is accurately indicated by the dominant frequency of rooster crow vocalizations, despite the low metabolic expense of crowing.

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