Crowing in relation to status in roosters

MARTY L. LEONARD* & ANDREW G. HORN
*Centre for Food and Animal Research, Central Experimental Farm, Ottawa, Ontario K1A 0C6,
Canada*

Abstract. The purpose of this study was to examine the relationship between crowing and dominance using domestic roosters, *Gallus gallus domesticus*. Dominant males crowed significantly more often than subordinate males and often attacked subordinates that crowed. Dominants also produced crows that were higher in frequency than subordinates. In addition, dominant males spent more time near the speaker when crows of dominant males were played than they did when crows of subordinate males were played. Neither subordinate males nor females responded to tapes from males of either status. These results suggest that both crow rate and quality vary with male status and that dominants can and do discriminate between males using crow quality as a cue. Crowing by roosters could thus potentially function as a signal of status.

In many species, individuals occupy a social position based on their fighting ability. Aggressive interactions can be costly in terms of energy and risk of injury, so signals that convey status in the absence of these interactions would be beneficial to both dominant and subordinate individuals. To function as indicators of status these signals should be variable and correlate with social rank and/or physical characteristics that relate to fighting ability, for example size (Rohwer 1975). In addition, they should also be used by other individuals to assess dominance prior to aggressive interactions (Geist 1966).

Vertebrates use a variety of signals to communicate status, for example plumage patterns in birds (e.g. Rohwer 1975; Jarvi & Bakken 1984; Watt 1986; Moller 1987; Wilson 1992; but see Jackson et al. 1988), and scent marking in mammals (e.g. Hurst 1987; Gosling & McKay 1990). Acoustic signals can also provide information on status, especially over long distances. In some cases these signals may be energetically expensive to produce (Ryan 1988), potentially making them reliable signals of quality or condition.

Male–male contests in some anurans (e.g. Davies & Halliday 1978) and red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979), are preceded by bouts of calling, in which rate and/or quality of the calls produced are related to the

*Present address: Department of Biology, Dalhousie University, Halifax, Novia Scotia B3H 4J1, Canada.

likelihood that the caller will win the interaction. Listeners respond differentially when these parameters are varied in playback experiments, providing more evidence that these vocalizations convey information on status or fighting ability.

Despite extensive work on the function of bird song in mate attraction and territory defence, relatively little is known of the direct relationship between acoustic signals and social status in birds (but see West et al. 1981). In a sense, singing by songbirds is a status signal, as usually only territory holders sing, and indeed various song parameters have been correlated with various measures of male quality (Lambrechts 1992). However, the overriding importance of prior occupancy and position effects (i.e. absolute dominance except near territory edges) make it hard to study how status information is conveyed in such systems (Lambrechts 1992).

Domestic chickens, *Gallus gallus domesticus*, are ideal for testing the role of acoustic signals as indicators of dominance. Males establish stable, linear, dominance hierarchies based on their fighting ability (e.g. Guhl 1962). Dominant males copulate more than subordinates, have a higher proportion of successful matings and interfere with the copulation attempts of subordinates (e.g. Guhl et al. 1945; Guhl & Warren 1946). Male chickens also produce loud, distinctive, highly stereotyped vocalizations called crows (Miller 1978). Although the function of crowing has not been systematically studied, earlier observations

suggest that it is related to dominance (e.g. Guhl 1962; McBride et al. 1969; Mench & Ottinger 1991).

If crows convey information about status then the crow rate and/or crow quality of dominant males should differ from that of subordinate males. In addition, males and, possibly females, should discriminate between the crows of males of differing status. Because only dominant males are territorial in the wild (McBride et al. 1969), they may respond more strongly than subordinate males to playback in general and to dominant males in particular. In addition, because dominant males may be of higher quality, females may discriminate between the crows of dominant and subordinate individuals. We used observations, acoustic analyses and a playback experiment to test these predictions.

METHODS

Housing and Experimental Conditions

The housing and experimental conditions described below were designed for other studies on chicken behaviour. However, these conditions allowed us to easily determine male status, record crows and play crows back to males and females separately.

At 9 weeks of age, we individually marked five male and 23 female white leghorn chickens with numbered wing tags and randomly assigned the group to one of 24 pens. Each pen was 3.65×5.10 m with a littered floor area at the front and a raised roosting area at the rear. Males and females in each pen could hear, but not see or interact with birds other than their penmates. Food and water were provided ad libitum throughout the entire study period.

At 19 weeks, we moved the top- and bottom-ranked males from each group and assigned each pair of males to a randomly chosen pen. We then randomly selected 16 females from each original group and placed each new group in a pen adjacent to the pair of males with which they had been housed previously. We moved the remaining males and females to another building to be used in other studies. This arrangement resulted in 24 pairs of male/female pens (a total of 48 pens). These pens were evenly divided between two wings of a poultry building (12 pairs/wing). Individuals in separate wings could not hear each other. Within each pen, males and females were separated by a chicken wire partition that extended through the back half of the pen and a solid partition that extended throughout the front half. Thus they could see each other in the back of the pen, but they could not interact directly.

Observations and Measurements

To determine the dominance relationship among males, we conducted weekly 50-min observations on the birds in each pen between the ages of 9 and 19 weeks. Observations were made 5 days/week between 0800 and 1630 hours. We balanced observations on each pen for time of day and sequence through the 5-day period. Observers sat in the aisle outside the pen and allowed 2 min for the birds to become accustomed to their presence. They then recorded all interactions between males. Male dominance hierarchies were determined based on the outcome of agonistic interactions between pairs of birds. An individual lost an interaction if it fled when another pecked, chased or threatened it. A male was considered dominant to another if it won more interactions than it lost with that individual. The hierarchy was determined by ranking birds according to how many individuals they dominated. Males given a rank of 1 were dominant to all other males in the group and males given a rank of 5 were subordinate to all other males.

To examine the relationship between crowing and dominance we also recorded the identity of the crowing male, the number of crows given, whether the crowing male was attacked by other males and the attacking male's identity. This information was collected during weeks 18 and 19 when crowing rates were high and stable. Crowing rate did not differ significantly between these weeks, so we used their mean value as an overall measure of crow rate. Because features of the crow could be correlated with morphological features of dominance, we weighed males at 19 weeks and at 30 weeks. In addition, at 30 weeks we also measured the length and width of the comb and wattle. Because comb area (length × width) and wattle area were correlated ($r=0.66$, $N=48$, $P<0.01$) we report values for comb area only.

Crow Measurements

We made recordings of dominant ($N=24$) and subordinate ($N=24$) males from all male pens in

each wing at 1–5 m with a Beyer MCE86N(C)S Dynamic microphone and a Sony TCD/D3 DAT recorder. We digitized each recording using SoundEdit Pro software (MacroMind Paracomp, San Francisco, 1990) at a sampling rate of 22 kHz. We analysed the physical features of crows using the real-time spectrograph produced by Signal software for the IBM (Engineering Design, Belmont, Massachusetts, 1991). The display range was set at 11 kHz, sampling rate at 25 kHz, and frequency and time cursors measured to a resolution of 18 Hz and 1 ms, respectively (see Stoddard 1990 for a general explanation of sampling rate and resolution). Each crow contained four syllables. We measured the length and fundamental frequency of each syllable and the length of the entire crow.

Figure 1. Mean ($\pm$ SE) number of crows per 50-min period for males of different dominance rank. 1: Top-ranked, 5: lowest-ranked. Lines that overlap bars indicate no significant difference using the least-significance difference test. Each rank contains 24 males.

Playback Experiment

Between 28 and 30 weeks of age, we performed a playback experiment to test whether males and females discriminate between the crows of dominant and subordinate roosters. We made playback tapes from the four dominant–subordinate pairs (i.e. penmates) in each wing for which we had recordings with the highest signal/noise ratio. Playback tapes were edited so that they would play the same crow every 20 s for 2 min (six repetitions), then re-recorded onto a DAT tape. The tapes were played back from a Sony TCD/D3 DAT recorder through a Sony SRS/170 or Fostex 6301B speaker-amplifier at 100 dB at the source (C weighting). One tape from each pair of males was played back to each of three randomly selected pens of males and females in the opposite wing (i.e. three playbacks from each of four tapes/wing). This resulted in 12 playbacks/wing for a total of 24 trials.

The playback speaker was placed outside the pen, at a height of 15 cm and a distance of 5 cm, so that half of the speaker faced the male pen and half faced the female pen. In this way males and females could hear the playback equally well, but could not influence each other's response. Before beginning the trial we allowed 2 min for the birds to settle after the disturbance of setting up the playback apparatus.

Each trial consisted of three 2-min periods: before, during and after playback. The position of subjects was noted by dividing each male and 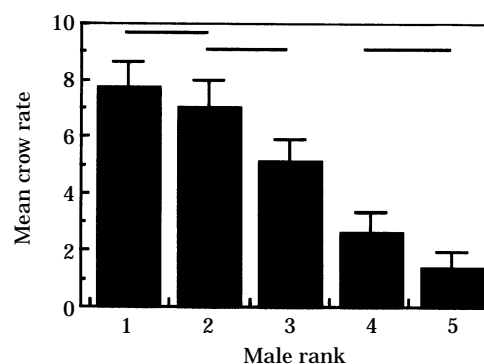female pen by length and width into four equal quadrants. Every 20 s throughout the trial we noted the number of females and the identity of the males that were in the quadrant of their respective pens nearest to the playback speaker, as well as the number of times each male crowed.

Our measures of response were therefore the median number of females near the speaker during scans (i.e. in the quadrant nearest the speaker), the number of 20-s scans in which each male was near the speaker, and the total number of times each crowed. We analysed the responses using pens as blocks in repeated-measures ANOVAs and paired t-tests. All means are reported ± 1 SE. We determined crowing rate, dominance status and body weight of males housed in groups of five during weeks 9–19.

RESULTS

Crow Rate and Male Rank

When males were housed in groups of five, higher-ranking males crowed more than lower-ranking males ($F_{4,115}=11\cdot1$, $P=0\cdot0001$; Fig. 1). The greatest differences were between the two highest-ranking males and the two lowest-ranking males (Fig. 1). We observed 12 interactions in separate pens in which a male was attacked immediately after it crowed. In nine of these 12 interactions a subordinate was attacked by the male one above it in the hierarchy. In one case the reverse was true, in another the top-ranked male

Table I. Comparisons of the mean ($\pm$ SE) crow characteristics (frequency (Hz) and length (ms) of syllables) for dominant and subordinate males using paired *t*-tests

Crow characteristic	Status		*t*	*P*
	Dominant	Subordinate		
Frequency				
Syllable 1	870 ± 17	810 ± 22	3·32	0·003
Syllable 2	1010 ± 16	960 ± 12	1·80	0·09
Syllable 3	980 ± 10	940 ± 10	2·47	0·02
Syllable 4	930 ± 11	890 ± 16	1·76	0·09
Length				
Syllable 1	28 ± 0·9	28 ± 0·8	− 0·73	0·47
Syllable 2	17 ± 1·3	18 ± 0·4	− 0·52	0·61
Syllable 3	34 ± 1·3	35 ± 1·4	− 1·16	0·26
Syllable 4	90 ± 4·0	95 ± 3·7	− 1·03	0·31

N=24 pairs of dominants and subordinates.

attacked the lowest-ranking male, and in the remaining case the two males were tied for the top rank at the time of the interaction.

Crow Quality and Male Rank

Syllables 1 and 3 in the crows of dominant males were significantly higher in frequency than in the crows of subordinate males (Table I). Syllables 2 and 4 showed a similar trend (Table I). In addition, the average frequency (mean of syllables 1–4) of the crows of dominant males was significantly higher than subordinates (dominant: 950 ± 11 Hz; subordinate: 900 ± 12 Hz; paired *t*-test: *t*=2·78, *df*=20, *P*=0·01). However, neither the length of each syllable (Table I) nor the total length of the crow differed significantly between males (total length: dominant: 168 ± 4·4; subordinate 176 ± 4·3; paired *t*-test: *t*=1·51, *df*=20, *P*=0·15).

Male Morphology, Rank and Features of the Crow

Morphology and rank

Body weight at 19 weeks tended to decrease with rank among the five males in each group ($F_{4,88}$=2·33, *P*=0·06). In particular, the top-ranked males were significantly heavier than the bottom-ranked males (top-ranked: 1·82 ± 0·01 kg; bottom-ranked: 1·74 ± 0·02 kg; paired *t*-test: *t*=2·55, *df*=23, *P*=0·009). At 30 weeks, when

males were in groups of two, dominant males again tended to be heavier than subordinate males (dominant: 1·97 ± 0·02 kg; subordinate: 1·91 ± 0·02 kg; paired *t*-test: *t*= − 1·77, *df*=23, *P*=0·06) and they also had significantly larger combs (dominant: 137 ± 3·4 mm²; subordinate: 125 ± 2·9 mm²; paired *t*-test: *t*= − 2·79, *df*=23, *P*=0·008).

Morphology and features of the crow

Within ranks, crow rate was positively correlated with body weight for the top-ranked males only (*r*=0·51, *df*=23, *P*<0·01). The length and frequency of crow syllables, the average frequency and the length of the entire crow were not correlated with weight or comb area for dominants or subordinates (dominants: all *r*s<0·32, *P*s≥0·15); subordinates: all *r*s≤0·36, *P*s≥0·10). However, the length of the third syllable was negatively correlated with weight for dominants (*r*= − 0·49, *P*=0·03) and weakly associated with weight for subordinates (*r*= − 0·40, *P*=0·07). Comb area was also weakly associated with the length of the third syllable for subordinates (*r*= − 0·42, *P*=0·06), but not for dominants (*r*= − 0·09, *P*=0·70).

Response to Playbacks

The crows presented during the playback study were similar in quality to those in the general population. That is, the frequency of each syllable and the average frequency for the entire crow were significantly higher for dominant males (average frequency: dominants: 950 ± 10 Hz; subordinates: 890 ± 17 Hz; paired *t*-test: *t*=4·14, *df*=7, *P*=0·004). Similarly, the length of each syllable and the total length did not differ between dominants and subordinates (total length: dominants: 169 ± 8·0; subordinates: 169 ± 7·5; paired *t*-test: *t*=0·05, *df*=7, *P*=0·97).

Females

The number of females near the speaker during the playback of either dominant or subordinate males did not change significantly from the numbers present before or after the playback (dominant: $F_{2,46}$=1·01, *P*=0·37; subordinate: $F_{2,46}$=1·14, *P*=0·33). Their numbers also did not vary during the playback of dominant or subordinate males (dominant playback: 3·8 ± 0·36;
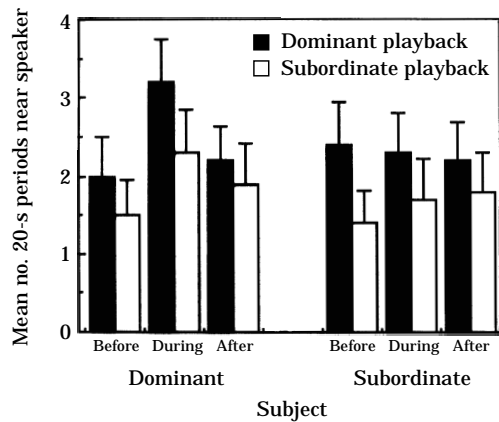
Figure 2. Mean (± SE) number of 20-s periods dominant and subordinate males were in the quadrant nearest the speaker before, during and after the playback of dominant and subordinate males. *N*=24 playbacks from males of each status.
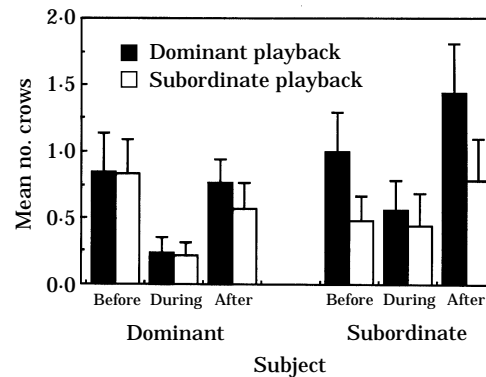

Figure 3. Mean (± SE) number of crows given by dominant (*N*=24) and subordinate (*N*=24) males before, during and after the playback of dominant and subordinate males. *N*=24 playbacks from males of each status.

subordinate playback: 4.2 ± 0.38; paired *t*-test: $t= -0.83$, *df*=23, *P*=0.42).

Dominant males

Dominant males spent significantly more time near the speaker during playback than before or after if the recording was of a dominant male ($F_{2,71}=4.42$, *P*=0.02; Fig. 2). Responses did not vary if the playback was of a subordinate male ($F_{2,71}=1.85$, *P*=0.17; Fig. 2). Dominant males also spent significantly more time near the speaker during the playback of a dominant male than during the playback of a subordinate male (dominant playback: 3.2 ± 0.54; subordinate playback: 2.3 ± 0.51; paired *t*-test: $t=2.57$, *df*=23, *P*=0.02). This was not simply a function of the position of the males before the playback because the number of 20-s intervals near the speaker during this period did not differ significantly between dominant and subordinate playback trials ($t=1.75$, *df*=23, *P*=0.10).

Dominant males crowed less often during playback than before or after, although this difference was only significant if the playback was of a subordinate male (dominant playback: $F_{2,71}=2.81$, *P*=0.07; subordinate playback: $F_{2,71}=4.10$, *P*=0.02; Fig. 3). The number of crows given during the playback period did not vary with the status of the playback male (dominant playback: 0.24 ± 0.11; subordinate playback: 0.22 ± 0.09; $t= -0.70$, *df*=23, *P*=0.49).

Subordinate males

The time subordinate males spent near the speaker during playback of either dominants or subordinates did not vary significantly from that spent before or after playback (dominant: $F_{2,71}=0.11$, *P*=0.90; subordinate: $F_{2,71}=0.51$, *P*=0.51; Fig. 2) nor did it vary with the status of the playback male (dominant playback: 2.3 ± 0.55; subordinate playback: 1.7 ± 0.52; paired *t*-test: $t=1.24$, *df*=23, *P*=0.23).

Subordinates tended to give fewer crows during playback than before or after, but only if the playback was of a dominant male (dominant playback: $F_{2,71}=3.47$, *P*=0.04; subordinate playback: $F_{2,71}=0.90$, *P*=0.41; Fig. 3). Like dominant males, subordinate males did not vary their crow rate during the playback period (dominant playback: 0.56 ± 0.22; subordinate playback: 0.44 ± 0.25; $t=0.75$, *df*=23, *P*=0.46).

DISCUSSION

Dominant males crowed more than subordinates and produced crows that were higher in frequency. Receivers could therefore use either crow rate or quality to assess status. In addition, dominant males responded more strongly to crows of other dominant males suggesting that they can and do discriminate. Although additional experiments would be needed to confirm that crowing maintains a rooster's status, the results do

demonstrate that it conveys the status of the signaller to other roosters.

Observations of natural behaviour offer further evidence that crowing is used to signal status. Feral chickens and junglefowl form small social groups usually composed of a dominant rooster, several females and several subordinate males (feral chickens: McBride et al. 1969; junglefowl: Collias & Collias 1967; Collias 1987). Male roosters usually crow after winning aggressive interactions and dominant males also crow on the boundaries of their territories and during territorial intrusions. Subordinate males also crow, but usually at lower rates (Collias & Collias 1967; McBride et al. 1969). Thus potential intruders, even at long distances, could use crow rate/quality to determine whether there was a dominant male present on the territory and thereby avoid costly interactions.

Cues Used to Assess Status

Our study confirms early observations (Guhl et al. 1945: chickens; Collias & Collias 1967: red junglefowl, *Gallus gallus murghi*) that dominant males crow more than subordinates and that they also attack subordinates that crow (Guhl et al. 1945). Measurements of oxygen consumption during crowing suggest that it is not energetically expensive (Horn et al., in press), so differences in crowing rate are probably not related to differences in energy budgets. However, variation in rate could be maintained by the aggressive behaviour of dominants towards subordinates that crow. This form of social control could also reduce cheating by subordinates and function to keep the signal 'honest' (Whitfield 1987).

Dominant males produced crows that were higher in frequency than those of subordinate males and they also responded more strongly to playbacks of other dominants. The frequency difference between high- and low-status males held for the crows used in the playback tapes as well. Because crow rate was constant in the playback experiments individuals must have discriminated on the basis of crow quality. Our measurements suggest that frequency might be the main cue, although other cues might be available.

Differences in the structure of the vocalizations of dominant and subordinate males have been reported for two other species of bird (West et al. 1981; Lambrechts & Dhondt 1986). In cowbirds, *Molothorus ater*, dominants sing at a higher rate and produce songs that evoke more intense copulatory responses (are more 'potent') than the songs of subordinates. As in roosters, the honesty of this signal might be maintained by dominant attacks on subordinates that sing potent songs (West et al. 1981). In great tit, *Parus major*, song, strophe length (phrases repeated in a burst of song) and drift (time between phrases) during the breeding season are correlated with dominance in winter flocks. However, unlike roosters and cowbirds, great tits do not use their songs during dominance interactions in flocks (Lambrechts & Dhondt 1986).

Both weight and comb size have been positively correlated with dominance for chickens and junglefowl (chickens: Marks et al. 1960; Siegel & Hurst 1962; Graves et al. 1985; this study; junglefowl: Ligon et al. 1990). There are reasons for expecting a relationship between acoustic features and body size (e.g. Ryan & Brenowitz 1985). However, in this study the relationship between weight and status was weak, suggesting that weight may not be a reliable cue of dominance. Indeed, the length of the third syllable which was the only crow feature that correlated with weight did not differ between dominants and subordinates. Frequency, which did differ with status, did not correlate with weight. Thus conspecifics may actually assess weight and status independently. It is unclear why comb size, which was strongly correlated with status, was not correlated with differences in crow frequency.

Response to Playback

The response of dominant roosters to the playbacks of dominant males is consistent with the behaviour of feral chickens and male junglefowl in the wild. Dominant males are reported to respond to the crows of other dominants and to ignore the crows of subordinate males, perhaps because subordinates pose less of a threat (feral chickens: McBride et al. 1969; junglefowl: Collias & Collias 1967; Collias 1987).

Females showed no significant response to the crows of either dominant or subordinate males. Previous work suggests that visual, rather than acoustic, signals may be important to females. Female junglefowl prefer males with longer, brighter combs, redder irises and lighter saddle feathers (Zuk et al. 1990). Similarly, neither crow

rate nor quality appears to be important in female choice in chickens (M. Leonard & L. Zanette, unpublished data). This may explain why females in the present study did not attend to the crows of either type of male. In general, our results suggest that crowing functions as an intra-sexual rather than an inter-sexual signal.

Crows as Coverable Badges

Unlike most plumage badges, acoustic signals can be turned on and off. This behavioural control is also possible in certain coverable badges of conspicuous coloration, such as the crown and shoulder patches of many birds (Hansen & Rohwer 1986). Coverable badges are useful in situations where status changes frequently and unpredictably, or when concealing one's status is useful (Hansen & Rohwer 1986). This is true of acoustic signals, too. In the case of roosters, beta males quickly assume dominance if the alpha male is removed, and there is some weak experimental evidence that they assume the alpha male's former crowing rate as well (Salomon et al. 1966; Mench & Ottinger 1991). In feral chickens, subordinates may wander through the territories of several different flocks (McBride et al. 1969), and at such times it might be useful to pass through unnoticed. Junglefowl cease crowing when disturbed by humans (Collias & Collias 1967). Thus facultative avoidance of predators might be another advantage to both coverable badges and acoustic status signals.

The lack of contextual cues in acoustic signals as opposed to plumage badges would seem to make acoustic signals especially open to cheating. The distance over which acoustic signals can travel increases the cost to receivers of uncovering cheaters by fighting or visual assessment of the signaller's body size (Dawkins & Guilford 1991). In roosters, this cost is reduced within social groups on a territory, so some social enforcement of honesty is possible. However, over longer distances, the more important costs maintaining honesty in acoustic signals are likely to be those that affect the production and transmission of the signal itself, that is energetic costs, predation costs and habitat acoustics. The latter two costs have not been assessed in the case of crowing.

In conclusion, we have shown that crows can communicate the signaller's status to other males. Crow rate and quality differ according to status, and dominant males respond differentially to the crows of dominant and subordinate males. Direct tests of how crowing maintains dominance relationships still need to be conducted.

REFERENCES

Clutton-Brock, T. C. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69,** 145–169.

Collias, N. E. 1987. The vocal repertoire of the red jungle fowl: a spectrographic classification and the code of communication. *Condor*, **89,** 510–524.

Collias, N. E. & Collias, E. C. 1967. A field study of the red jungle fowl in North central India. *Condor*, **69,** 360–386.

Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads, *Bufo bufo. Nature, Lond.*, **274,** 683–685.

Dawkins, M. S. & Guilford, T. 1991. The corruption of honest signalling. *Anim. Behav.*, **41,** 865–873.

Geist, V. 1966. The evolutionary significance of mountain sheep horns. *Evolution*, **20,** 558–566.

Gosling, L. M. & McKay, H. V. 1990. Competitor assessment by scent-matching: an experimental test. *Behav. Ecol. Sociobiol.*, **26,** 415–420.

Graves, H. B., Hable, C. P. & Jenkins, T. H. 1985. Sexual selection in *Gallus*: effects of morphology and dominance on female spatial behavior. *Behav. Proc.*, **11,** 189–197.

Guhl, A. M. 1962. The behaviour of chickens. In: *The Behaviour of Domestic Animals* (Ed. by E. S. E. Hafez), pp. 491–530. London: Bailliere, Tindall & Cox.

Guhl, A. M., Collias, N. E. & Allee, W. C. 1945. Mating behavior and the social hierarchy in small flocks of white leghorns. *Physiol. Zool.*, **18,** 365–390.

Guhl, A. M. & Warren, D. C. 1946. Number of offspring sired by cockerels related to social dominance in chickens. *Poult. Sci.*, **25,** 460–472.

Hansen, A. J. & Rohwer, S. 1986. Coverable badges and resource defence in birds. *Anim. Behav.*, **34,** 69–76.

Horn, A. G., Leonard, M. L. & Weary, D. M. In press. Oxygen consumption during crowing by roosters: talk is cheap. *Anim. Behav.*

Hurst, J. L. 1987. The functions of urine marking in a free-living population of house mice, *Mus domesticus* Rutty. *Anim. Behav.*, **35,** 1433–1442.

Jackson, W. M., Rohwer, S. & Winnegrad, R. L. 1988. Social status signalling is absent within age and sex classes of Harris' sparrows. *Auk*, **105,** 424–427.

Jarvi, T. & Bakken, M. 1984. The function of the variation in the breast-stripe of the great tit, *Parus major. Anim. Behav.*, **32,** 590–596.

Lambrechts, M. M. 1992. Male quality and playback in the great tit. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 135–152. New York: Plenum Press.

Lambrechts, M. M. & Dhondt, A. A. 1986. Male quality, reproduction and survival in the great tit (*Parus major*). *Behav. Ecol. Sociobiol.*, **19,** 57–63.

Ligon, J. D., Thornhill, R., Zuk, M. & Johnson, K. 1990. Male–male competition, ornamentation and the role of testosterone in sexual selection in red junglefowl. *Anim. Behav.*, **40,** 367–373.

McBride, G., Parer, I. P. & Foenander, F. 1969. The social organization and behaviour of the feral domestic fowl. *Anim. Behav. Monogr.*, **2,** 125–181.

Marks, H. L., Siegel, P. B. & Kramer, C. Y. 1960. Effect of comb and wattle removal on the social organization of mixed flocks of chickens. *Anim. Behav.*, **8,** 192–196.

Mench, J. A. & Ottinger, M. A. 1991. Behavioral and hormonal correlates of social dominance in stable and disrupted groups of male domestic fowl. *Horm. Behav.*, **25,** 112–122.

Miller, D. B. 1978. Species-typical and individually distinctive acoustic features of crow calls for red junglefowl. *Z. Tierpsychol.*, **47,** 182–183.

Moller, A. P. 1987. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Anim. Behav.*, **35,** 1637–1644.

Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution*, **29,** 593–610.

Ryan, M. J. 1988. Energy, calling and selection. *Am. Zool.*, **28,** 885–898.

Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.*, **119,** 87–100.

Salomon, A. L., Lazorcheck, M. J. & Scien, M. W. 1966. Effects of social dominance on individual crowing rates of cockerels. *J. comp. physiol. Psychol.*, **61,** 144–146.

Siegel, P. B. & Hurst, D. C. 1962. Social interactions among females in dubbed and undubbed flocks. *Poult. Sci.*, **41,** 141–145.

Stoddard, P. K. 1990. Audio computers: theory of operation and guidelines for selection of systems and components. *Bioacoustics*, **2,** 217–239.

Watt, D. J. 1986. A comparative study of status signalling in sparrows (genus *Zonotrichia*). *Anim. Behav.*, **34,** 1–15.

West, M. J., King, A. P. & Eastzer, D. H. 1981. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. *Anim. Behav.*, **29,** 490–501.

Whitfield, D. P. 1987. Plumage variability, status signalling and individual recognition in avian flocks. *Trends Ecol. Evol.*, **2,** 13–18.

Wilson, J. D. 1992. A re-assessment of the significance of status signalling in populations of wild great tits, *Parus major. Anim. Behav.*, **43,** 999–1009.

Zuk, M., Thornhill, R., Ligon, J. D., Johnson, K., Austad, S., Ligon, S. H., Thornhill, N. W. & Costin, C. 1990. The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. *Am. Nat.*, **136,** 459–473.