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The effects of age and previous experience on social rank in female red junglefowl, *Gallus gallus spadiceus*

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Social rank can influence lifetime reproductive success and therefore fitness. We examined the effects of morphology, age, previous social experience and aggressiveness on social rank in all-female flocks of red junglefowl. None of the morphological characters measured (mass, tarsus length, comb height or comb length) appeared to play a role in determining rank. Older females were not more likely to be dominant, while previous social experience and aggression levels were both important in dominance determination. Flock-experienced hens were more likely to be dominant as were more aggressive individuals. Red junglefowl females most likely use a combination of characters to establish social order in a newly formed flock.

Social dominance is one of the most important elements of life in animal groups. Higher social status confers numerous advantages on higher-ranked individuals, such as access to better food or territories (Collias 1970; Huntingford & Turner 1987; Archer 1988; Newton 1989; Hall & Fedigan 1997; Lahti et al. 1998). In addition to access to resources, dominant individuals are often able to obtain more matings, and/or produce and successfully rear more offspring (Lill 1966; Cheng & Burns 1988; Newton 1989; Jones & Mench 1991). In red junglefowl, the ancestor of domestic chickens, dominant hens produce more offspring over their lifetime than subordinate females (Collias et al. 1994).

Social rank and the outcome of dominance interactions have been particularly well-studied in domestic chickens, *G. g. domesticus*, and their ancestors, the junglefowl (Masure & Allee 1934; Banks 1956; Guhl 1958; Rushen 1982). Larger individuals of both sexes tend to be dominant, although body size is rarely the sole determining factor in social hierarchies (Zuk et al. 1990, 1998). In most birds including chickens, males are dominant over females (Masure & Allee 1934). Male junglefowl with larger combs are more likely to win aggressive encounters, but comb size appears to be less important in female junglefowl (Ligon et al. 1990; Zuk et al. 1998). Larger combined comb and wattle area have been linked to higher social status in domestic hens, but are probably correlated with winning, rather than used as cues to determine the outcome of an interaction (Martin et al. 1997a, b).

Prior experience, both with the site of an encounter and with the other interacting individuals, is also a key factor in social interactions. In domestic hens, when two prior winners interact, subsequent wins are shared and do not depend upon familiarity with a site, whereas when two losers are paired, the bird familiar with the site of its defeat is more likely to lose again (Cloutier et al. 1995, 1996). A theoretical model for establishment and maintenance of dominance hierarchies among hens suggested that a simple 'loser effect', in which previous experience dictates current strategy, is not viable (Pagel & Dawkins 1997); instead, individuals must recognize particular opponents or the social status category that they hold (Pagel & Dawkins 1997).

The present study examines factors that influence social rank determination in red junglefowl all-female flocks. These same factors that affect social rank may influence the hens' fitness. In addition, factors found to be correlated with high social rank, if heritable, would presumably be subject to selection. Specifically, we address the following questions.

What Are the Effects of Morphology on Social Rank?

Morphological characters such as mass, size or colour are important in determining dominance (Wilson 1975) in a variety of species, including white-crowned sparrows, *Zonotrichia leucophrys* (Parsons & Baptista 1980) and Harris' sparrows, *Z. guerula* (Rohwer 1985), as well as

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domestic chickens and junglefowl. Domestic hens with smaller combs, lesser degree of moult and lower mass are more likely to be subordinate (Collias 1943). In a study of red junglefowl hens, mass played a significant role in social rank determination, with heavier birds more likely to be dominant (Zuk et al. 1998). To determine whether large birds are more likely to be dominant regardless of their age or previous experience, we re-examined the relationship between rank and morphology in red junglefowl hens in the context of variation in the age or the social experience of some of the flock members.

Does the Age of the Bird Influence Its Rank in the Hierarchy?

Older individuals tend to be the dominant member of their social groups in various species (Wilson 1975; Clutton-Brock et al. 1976) including the domestic chicken (Masure & Allee 1934). Age may also be important in social rank determination of red junglefowl in birds with equal social experience.

Does Previous Experience Affect Social Interactions and Hierarchy Determination?

Previous social experience can affect subsequent interactions with known or novel individuals; experienced individuals are more likely to win and winners are suggested to continue winning in later interactions (Collias 1943; Ratner 1961; Parsons & Baptista 1980; Jackson 1988). In some cases, simply having social experience, regardless of having previously 'won' or 'lost', is advantageous in subsequent social interactions or conflicts over space use (Stamps & Krishnan 1998). Hogue et al. (1996) allowed hens to observe dominance interactions before being placed in pairs with a previous winner or loser; their behaviour depended upon the status of the individual they had observed. Here, we examine whether previous social experience influences subsequent social rank attainment by red junglefowl hens.

Do Aggression Levels Predict Rank?

Aggression, as measured by the likelihood of initiating agonistic encounters, is often correlated with dominance, which can be defined by the likelihood of winning agonistic encounters (Jackson 1988; but see warnings by Francis 1988); this is the case with lizards (Molina-Borja et al. 1988), green anoles, *Anolis carolinensis* (Andrews & Summers 1996) and African wild dogs, *Lycaon pictus* (Creel et al. 1997) as well as male red junglefowl (Ligon et al. 1990). This trend may also hold true with the female red junglefowl.

MATERIALS AND METHODS

Origin and Maintenance of the Colony

Our study population is descended from 150 individuals obtained in 1985–1986 from a free-ranging population at the San Diego Zoo, which imported 30 red junglefowl from Asia in 1942. The chicks used in our experiments were incubated and hatched in the laboratory and kept in commercial brooders until they were 6 weeks old. They were then reared in mixed-sex groups of 60–130 individuals in outdoor pens. Chicks were given water and commercial poultry feed (18–21% protein) ad libitum, and supplemented with scratch, a mixture of seeds, after they were moved outside. When they were 3–4 months old, we separated the chicks into male–female pairs to minimize crowding but still allow the birds to have a normal social environment, placing two pairs per cage (1.5 × 1.8 m) (Zuk et al. 1995, 1998). When the birds were 6 months old, we housed the pairs singly in the smaller cages. In the age effects experiment (see below), we housed 30 hens from the previous year's study (referred to as the 2-year-old group) in flocks of three in the larger (2.5 × 1.1 m and 1.25 m high) wood and chicken wire cages. Each 2-year-old hen was part of one flock in the spring 1997 and part of another flock in late summer of 1997; each had been in two different social groups prior to this experiment.

Morphological Measurements

When females were sexually mature at 7 months of age, we measured tarsus length, comb length and height to the nearest 0.01 mm using digital callipers. Mass was recorded to the nearest 0.1 g using a digital scale (Zuk et al. 1995, 1998). In the age effects experiment, we measured the hens used in the 2-year-old group in the same manner when they were approximately 19 months old, shortly before behavioural observations were conducted.

Age Effects Experiment

In February 1998, when the females were 8 months old, we separated them into 10 flocks of three birds each. The flocks were housed in larger wood and chicken-wire cages as described above. Individuals within each flock had been visually isolated from each other for at least 1 month. To identify the females during observation, we marked each individual with yellow leg bands in addition to a metal identification band. In each flock each individual received a unique combination of bands (Zuk et al. 1998).

We observed the flocks from a distance of 4–6 m for 30 min, 15 min after the birds were introduced to the new cage, on the day of flock formation. On the second day we observed the birds during 15-min intervals until each pair had interacted at least 10 times and the ratio of dominant to subordinate interactions was large enough to allow testing for statistically significant differences in number of interactions in which one bird was dominant (Zuk et al. 1998). Sometimes we provided the birds scratch grain during the 15-min observations to instigate dominance interactions, but this did not qualitatively change the nature of the dominance behaviours (Zuk et al. 1998). On the third day we observed the flocks for

an additional 30 min to confirm that the recorded hierarchy was stable. All observations took place between 0700 and 1200 hours on fair-weather days (Zuk et al. 1998).

We recorded the following three behaviours for dyads: fighting, pecking and displacements. In fighting, both hens in a dyad attacked each other and the one retreating was scored as subordinate in that interaction. Birds usually pecked each other on or near the head; the hen being pecked was considered subordinate upon retreating. In a displacement, one bird threatened another, as evidenced by elevation of the head and giving chase, sometimes raising her hackle feathers. In these situations, the target of the chase would retreat and the winner displaced the loser (Zuk et al. 1998). Based on at least 10 interactions per pair, we ranked the females on a scale of 1–3, 1 being the dominant and 3 the most subordinate. In this manner we determined the social hierarchies of all 10 flocks.

Approximately 10 days later, we assigned the birds to new flocks of three hens each, again consisting of birds that had been visually isolated from each other for at least a month. None of the birds were allowed to remain in the same cage they had been housed in to avoid territorial defence of a familiar area. We repeated behavioural observations as described above. This was done to standardize the amount of flock experience the 1998 (1-year-olds) and the 1997 (2-year-olds) groups had prior to forming flocks of mixed ages. Although the 1-year-olds' flock experience was more recent than the social interactions the 2-year-old birds experienced, all flock hierarchies and interactions were stable before testing for age effects. Therefore we feel any effect due to the difference in timing of social experience, given that it all took place after the birds had reached adulthood, is minimal.

In March 1998, once the females in the 1-year-old group had been in two different flocks, thereby equalizing the amount of previous social experience, we formed 12 flocks, each consisting of a 2-year-old hen and two 1-year-old hens and then we determined the social hierarchy within each flock. In addition to amount of previous social experience, we also controlled for the previous social rank of each hen; for example, if the 2-year-old female had attained rank 1 in the last flock she was in, then only 1-year-olds that had also attained rank 1 in their previous social environments were placed in that flock. All three ranks were used in the experiment. We formed four flocks using birds that had previously attained rank 1, another four consisted of rank 2 hens and the remaining flocks had females that had ranked 3. We determined and recorded the social structure as described above.

Previous Experience Effects

To test whether having previous flock experience affected present rank determination, we formed 12 flocks of three hens in April 1998. Each social unit consisted of one flock-experienced hen and two flock-naïve hens. Flock-experienced hens had been in at least two different flocks, while flock-naïve hens had been housed singly with a male their entire adult lives. Flock-naïve hens could see and hear but not interact with other females while they were housed in female–male pairs. All the birds used in any given flock had been visually isolated from each other for at least 2 months prior to the experiment. We formed four flocks each with experienced birds that had most recently attained ranks 1, 2 and 3. We determined the social hierarchies in the same manner as the previous experiments.

RESULTS

Effects of Morphology on Social Rank

We examined the relationship between morphology and social rank for both the age effects and the previous experience effects experiments. Comparison of the mean morphological characters in the 12 hens in the 2-year-old group and the 24 1-year-old female red junglefowl used in the age effects experiment showed that the 1-year-old birds had larger comb height measurements than the older birds (Student's t test: $t_{34}=3.96$, $P<0.001$). None of the other morphological characters measured including comb length ($t_{34}=1.40$, NS), tarsus length ($t_{34}=1.24$, NS) or mass ($t_{34}=-1.79$, NS) differed between the two age groups. To test for the effects of morphology on social rank after controlling for differences due to age, we conducted a multivariate analysis of covariance (ANCOVA) with comb height as the covariate and found that none of the characters taken into account explained variance in rank (type III SS mass=0.073, $F_{1,5}=0.1$, NS; type III SS comb length=0.134, $F_{1,5}=0.18$, NS; type III SS tarsus length=0.692, $F_{1,5}=0.92$, NS; $N=30$ hens). Additionally, we conducted a multivariate ANCOVA considering the effects of experience and morphology on social rank, holding experience as the covariate. Again, no significant associations were found (type III SS mass=0.037, $F_{1,5}=0.06$, NS; type III SS comb length=0.054, $F_{1,5}=0.09$, NS; type III SS tarsus length=0.075, $F_{1,5}=0.12$, NS; type III SS comb height=0.338, $F_{1,5}=0.56$, NS; type III SS experience=1.45, $F_{1,5}=0.13$, NS; $N=33$).

Using Kruskal–Wallis chi-square approximations, we examined the relationships between social rank and morphology in the previous experience experiment. Comb height ($\chi^2_2=5.49$, NS), comb length ($\chi^2_2=0.78$, NS), tarsus length ($\chi^2_2=0.25$, NS) and mass ($\chi^2_2=0.08$, NS) had no significant associations with rank. In this analysis we used only 11 out of the 12 flocks because one flock contained a broody (incubating) female whose behaviour differed qualitatively from all other birds in the study.

Effects of Age on Rank

We analysed the dominance hierarchies of 12 flocks (36 hens) used in the age effects experiment using a Fisher's exact text because the sample size was insufficient to do a 3×2 chi-square analysis. Therefore, we had to collapse the three ranks into two categories. We chose to collapse rank 2 and rank 3 into the category 'not rank 1' because the difference between being dominant (rank 1) and

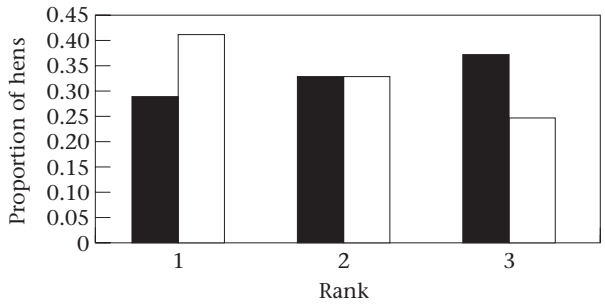

Figure 1. The distribution of the two age groups (■: 2-year-old hens, N=12; □: 1-year old hens, N=24) among the three social ranks, rank 1 being the highest. A Fisher's exact test combining ranks 2 and 3 into one category ('not rank 1') yielded nonsignificant results (N=36, P=0.2190).

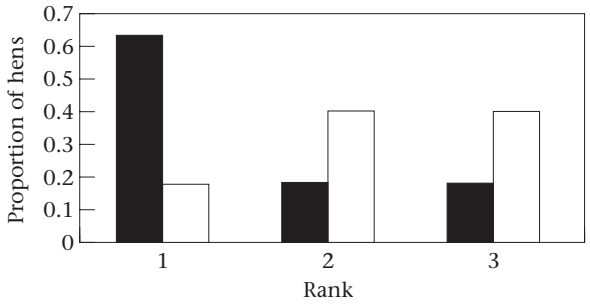

Figure 2. The distribution of flock-experienced (■; N=11) and flock-naïve (□; N=22) hens among the three social ranks; rank 1 being most dominant. Experienced hens were significantly more likely to be dominant in subsequent flocks (Fisher's exact test: N=33, P=0.0137; with categories 'rank 1' and 'not rank 1').

submissive seemed more meaningful than the difference between being the most submissive (rank 3) and the other ranks. The age of the bird did not seem to affect what social rank an individual attained (Fisher's exact test: N=36, P=0.219; Fig. 1). Although the difference between 'rank 1' and 'not rank 1' was not statistically significant, more 2-year-olds attained the dominant rank than 1-year-olds.

Effects of Previous Social Experience on Rank

In the social hierarchies of 11 flocks (33 hens), previous flock experience significantly affected subsequent social rank (Fisher's exact test: 'rank 1' versus 'not rank 1': N=33, P=0.0137; Fig. 2). Socially experienced hens were more likely to be rank 1, the most dominant of their new flock, regardless of what their rank had been in previous flocks. This trend was also apparent when all three ranks were considered, but the sample size did not allow for a reliable analysis in this case.

Effects of Aggression on Social Rank

To determine whether aggression level was correlated with social rank, we calculated the proportion of total aggressive interactions each bird initiated in the first half hour of behavioural observation. Social rank and the proportion of initiated aggressive interactions were strongly correlated (Spearman rank correlation: $r_S = -0.86$, P<0.0001) when data from 48 flocks, including all three behaviours, were used. Dominant individuals initiated a significantly higher proportion of the total aggressive interactions. Analysis using only the proportions of fights initiated within the first half hour of observation yielded similar results (Spearman rank correlation: $r_S = -0.59$, N=15 flocks, P<0.0001).

DISCUSSION

We were interested in determining what factors affect female dominance in red junglefowl. Unlike our previous study (Zuk et al. 1998), we found none of the morphological characters we measured to be significant factors in rank determination. The age of the hen also seemed unimportant in social interaction, although older individuals tended to be higher ranked. Previous social experience, regardless of previous rank, as well as high levels of aggression relative to other birds in the flock, were advantageous in dominance hierarchy determination.

Social Rank and Morphology

In our previous study (Zuk et al. 1998), larger females tended to have higher rank. In the present study, however, rank was unexplained by comb height, comb length, tarsus length or mass. Several factors may account for this discrepancy. For example, in our previous study, the only variable we controlled for was parasite status, and even then the results were examined separately for uninfected and parasitized hens (Zuk et al. 1998). In this study, the hens differed in age or social experience, depending on the experiment, introducing new factors that could detract from the apparent importance of mass in social rank determination.

Comb characters were not associated with social status in red junglefowl hens. In male red junglefowl, however, comb length and colour and body size have been found to be important in dominance determination (Ligon et al. 1990). Comb size is also correlated with dominance among domestic chickens (Collias 1943), although comb colour did not differ between winners and losers in another study of domestic chickens (Martin et al. 1997a). Most, although not all breeds of domestic chickens have much larger combs than junglefowl (Zuk et al. 1998), and artificial selection for increased fecundity or larger body size in domestic poultry may have caused inadvertent selection for an increase in comb size. If this is the case, comb size in female red junglefowl may be unimportant in a natural context.

Social Rank and Age

Age alone did not seem to influence dominance determination in red junglefowl hens. Unlike the studies conducted with Damaraland mole-rats, *Cryptomys damarensis* (Gaylard et al. 1998), Highland ponies and

cows (Clutton-Brock et al. 1976), boat-tailed grackles, *Quiscallus major* (Poston 1997) or even the domestic chicken, (Masure & Allee 1934), we did not find a correlation between the age of the individual and the social rank attained in red junglefowl females. Our results do agree with Collias (1943; domestic chicken) and Wallace & Bennett (1998; Zambian mole-rats, *C. mechowi*), who found that age did not influence dominance status. Older birds did attain dominant ranks more often than the 1-year-olds (Fig. 1), and a larger sample may have increased the power of our test and shown a stronger effect of age on dominance. While we controlled for social experience in our experiment, in nature it is likely that older birds are also the ones with more social experience, making the two factors difficult to tease apart and study separately.

Social Rank and Previous Flock Experience

Red junglefowl hens with previous social experience were significantly more likely to attain a higher rank than birds without flock experience of the same age. While many studies have reported that animals that win a dominance struggle are more likely to win subsequent confrontations or that losers keep losing (Collias 1943; Ratner 1961; Chase et al. 1994; Cloutier et al. 1995, 1996), we found that having any experience (past winner or loser) was advantageous in later social interactions. Females with social experience were more likely to be dominant in subsequent flocks than flock-naïve birds. The hens that had been in all-female flocks were likely to be dominant regardless of their previous rank. These results suggest that previous social experience is beneficial; that is, the hens first learn how to behave in a flock, and when placed with novel individuals, they react to the new situation. Socially naïve birds may not react as quickly to the new social environment, because they are not familiar with the situation and may not 'know' what to do. These results are similar to those of Martin et al. (1997a, b) on dominance in domestic hens, although in their studies prior winners initiated and won more often. Socially naïve hens may also be more likely to lose because they have been most recently housed with a male. In domestic chickens and red junglefowl, males, if larger than females, are dominant to them (Masure & Allee 1934; Collias et al. 1994 and references therein).

To be able to distinguish between these two possibilities we would have to examine whether the nature of male–female aggressive interactions differs from that of female–female interactions. Repeating the experiment with the naïve group completely isolated from any other bird might shed light on whether male–female aggressive interactions differ from female–female dominance struggles, and if previous social experience in female flocks is more advantageous than no social experience at all.

Social Rank and Aggression

Like many other researchers, we found a strong correlation between aggression, as measured by the proportion of interactions initiated by an individual in this study, and social rank obtained (Jackson 1988; Molina-Borja et al. 1988; Ligon et al. 1990; Hogue et al. 1996; Creel et al. 1997). Individuals that initiated aggressive interactions usually attained the most dominant rank in their flocks. This result was significant for all interactions (fights, pecks and displacements) and for fight behaviour only. Aggressive red junglefowl are more likely to be dominant. Collias et al. (1994) found that dominant hens produce the most offspring for their flock, which should select for increased aggressiveness over time. It would be interesting to evaluate the relative costs and benefits of aggression over the long term to determine whether more aggressive hens are always more fit. For example, spending time on aggressive activity can be costly in terms of potential injury, time that could be spent foraging or on other activities, and the attraction of potential predators.

General Conclusions

Hens seem to use multiple factors, particularly previous social experience, as well as aggression, parasite status (Zuk et al. 1998), morphological characters (Zuk et al. 1998) and possibly age, in social rank determination. Some factors play a larger role in rank determination than others and in nature it is likely that some of the factors will be intercorrelated (i.e. age and experience). Indeed, teasing apart some of the factors analysed in this study would be very difficult in the field. Socially dominant females of this species have a higher fitness than subordinates (Collias et al. 1994). Therefore, factors that influence dominance will also affect fitness in red junglefowl. We expect hens with previous social experience (regardless of previous rank), higher levels of aggression and freedom from parasites to have higher fitness than parasitized, inexperienced birds or hens displaying low levels of aggression.

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References

Andrews, T. J. & Summers, C. H. 1996. Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. *Behaviour*, **13**, 1265–1279.

Archer, J. 1988. *The Behavioural Biology of Aggression*. Cambridge: Cambridge University Press.

Banks, E. M. 1956. Social organization in red jungle fowl hens (*Gallus gallus* subsp.). *Ecology*, **37**, 239–248.

Chase, I. D., Bartolomeo, C. & Dugatkin, L. A. 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning? *Animal Behaviour*, **48**, 393–400.

Cheng, K. M. & Burns, J. T. 1988. Dominance relationship and mating behavior of domestic cocks: a model to study mate-guarding and sperm competition in birds. *Condor*, **90**, 697–704.

Cloutier, S., Beaugrand, J. P. & Lague, P. C. 1995. The effect of prior victory or defeat in the same site as that of subsequent encounter on the determination of dyadic dominance in the domestic hen. *Behavioural Processes*, **34**, 293–298.

Cloutier, S., Beaugrand, J. P. & Lague, P. C. 1996. The role of individual differences and patterns of resolution in the formation of dominance orders in the domestic hen. *Behavioural Processes*, **38**, 227–239.

Clutton-Brock, T. H., Greenwood, P. J. & Powell, R. P. 1976. Ranks and relationships in Highland ponies and Highland cows. *Zeitschrift für Tierpsychologie*, **41**, 202–216.

Collias, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. *American Naturalist*, **77**, 519–538.

Collias, N. E. 1970. Aggressive behavior among vertebrate animals. In: *Animal Aggression: Selected Readings* (Ed. by C. H. Southwick), pp. 14–39. New York: Van Nostrand Reinhold.

Collias, N., Collias, E. & Jennrich, R. I. 1994. Dominant red junglefowl (*Gallus gallus*) hens in an unconfined flock rear the most young over their lifetime. *Auk*, **111**, 863–872.

Creel, S., Marusha Creel, N., Mills, M. G. L. & Monfort, S. L. 1997. Rank and reproduction in co-operatively breeding African wild dogs: behavioral and endocrine correlates. *Behavioral Ecology*, **8**, 298–306.

Francis, R. C. 1988. On the relationships between aggression and social dominance. *Ethology*, **78**, 223–237.

Gaylard, A., Harrison, Y. & Bennett, N. C. 1998. Temporal changes in the social structure of a captive colony of the Damaraland mole-rat, *Cryptomys damarensis*: the relationship of sex and age to dominance and burrow-maintenance activity. *Journal of Zoology*, **244**, 313–321.

Guhl, A. M. 1958. The development of social organisation in the domestic chick. *Animal Behaviour*, **6**, 92–111.

Hall, C. L. & Fedigan, L. M. 1997. Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, **53**, 1069–1082.

Hogue, M-E., Beaugrand, J. P. & Lague, P. C. 1996. Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger. *Behavioural Processes*, **38**, 241–252.

Huntingford, F. A. & Turner, A. K. 1987. *Animal Conflict*. New York: Chapman & Hall.

Jackson, W. M. 1988. Can individual differences in history of dominance explain the development of linear dominance hierarchies? *Ethology*, **79**, 71–77.

Jones, M. E. J. & Mench, J. A. 1991. Behavioral correlates of male mating success in a multisire flock as determined by DNA fingerprinting. *Poultry Science*, **70**, 1493–1498.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M. 1998. Social influences on food caching in willow tits: a field experiment. *Behavioral Ecology*, **9**, 122–129.

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. *Animal Behaviour*, **40**, 367–373.

Lill, A. 1966. Some observations on social organisation and non-random mating in captive Burmese red junglefowl (*Gallus gallus spadiceus*). *Behaviour*, **26**, 228–242.

Martin, F., Beaugrand, J. P. & Lague, P. C. 1997a. The role of hen's weight and recent experience on dyadic conflict outcome. *Behavioural Processes*, **41**, 139–150.

Martin, F., Beaugrand, J. P. & Lague, P. C. 1997b. The role of recent experience and weight on hen's agonistic behaviour dyadic conflict resolution. *Behavioural Processes*, **41**, 159–170.

Masure, R. H. & Allee, W. C. 1934. The social order in flocks of the common chicken and the pigeon. *Auk*, **51**, 306–327.

Molina-Borja, M., Padron-Fumero, M. & Alfonso-Martin, T. 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). *Ethology*, **104**, 314–322.

Newton, I. (Ed.) 1989. *Lifetime Reproduction in Birds*. London: Academic Press.

Pagel, M. & Dawkins, M. S. 1997. Peck orders and group size in laying hens: 'futures contracts' for non-aggression. *Behavioural Processes*, **40**, 13–25.

Parsons, J. & Baptista, L. F. 1980. Crown color and dominance in the white-crowned sparrow. *Auk*, **97**, 807–815.

Poston, J. P. 1997. Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles. *Behavioral Ecology and Sociobiology*, **41**, 89–98.

Ratner, S. C. 1961. Effect of learning to be submissive on status in the peck order of domestic fowl. *Animal Behaviour*, **9**, 34–37.

Rohwer, S. 1985. Dyed birds achieve higher social status than controls in Harris' sparrows. *Animal Behaviour*, **33**, 1325–1331.

Stamps, J. A. & Krishnan, V. V. 1998. Territory acquisition in Lizards. IV. Obtaining high status and exclusive home ranges. *Animal Behaviour*, **55**, 461–472.

Wallace, E. D. & Bennett, N. C. 1998. The colony and social organisation of the giant Zambian mole-rat, *Cryptomys mechowi*. *Journal of Zoology*, **244**, 51–61.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge, Massachusetts: Harvard University Press.

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

Zuk, M., Popma, S. T. & Johnsen, T. S. 1995. Male courtship displays, ornaments and female mate choice in captive red jungle fowl. *Behaviour*, **132**, 821–836.

Zuk, M., Kim, T., Robinson, S. I. & Johnsen, T. S. 1998. Parasites influence social rank and morphology, but not mate choice, in female red junglefowl (*Gallus gallus*). *Animal Behaviour*, **56**, 493–499.