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DOMINANT RED JUNGLEFOWL (*GALLUS GALLUS*) HENS IN AN UNCONFINED FLOCK REAR THE MOST YOUNG OVER THEIR LIFETIME

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ABSTRACT.—The evolutionary success of individuals must ultimately be evaluated in terms of their lifetime contribution of mature young to the breeding population. The greater lifetime breeding success of the more dominant hens in an unconfined flock of Red Junglefowl (*Gallus gallus*) gave crucial evidence why female dominance hierarchies have evolved in this species. The number of chicks reared to independence by 28 hens of one flock from 1982 to 1988 was significantly associated with a hen's dominance, life-span, and year of hatching. Of these, dominance was by far the most important factor. It, by itself, could explain differences in the number of chicks reared as shown by log-linear analysis. This suggests that the associations with life-span and year of hatching may result from the fact that these are correlated with dominance. The top 3 hens in the peck order added more offspring of breeding age to the population than did the remaining 25 adult hens of the flock. Eleven of the 28 hens reared no young successfully. *Received 8 March 1993, accepted 2 July 1993.*

THE DIFFERENT INDIVIDUALS in a natural population vary greatly in the numbers of young that they manage to rear successfully, with profound implications for population dynamics and evolution. The purpose of this report is to identify and evaluate some of the important factors that account for this difference among individuals in an unconfined population of Red Junglefowl (*Gallus gallus*), taking into account differences in life-span, age class (year of hatching), and lifetime dominance status of adult hens.

Darwin (1887, vol. 1:258) concluded that the Red Junglefowl was the ancestor of the domestic fowl, and much recent evidence accumulated since then has tended to confirm his view (Delacour 1977, Crawford 1990, Stevens 1991). Not all breeds of domestic fowl have been thoroughly investigated from this viewpoint, and it is still considered possible that genes from other species of junglefowl might have been introduced by hybridization in some breeds (Crawford 1990, Stevens 1991). The Red Junglefowl has the special advantage that one may be able to relate behavioral observations to the vast amount of work that has been done on the behavior, physiology, and genetics of domestic fowl.

A field study of the behavior of Red Junglefowl in India (Collias and Collias 1967) and a parallel study of an unconfined population at the San Diego Zoo (Collias et al. 1966) showed that the behavior of the birds and the social structure of the population, aside from greater dispersion in nature, were basically and qualitatively similar in the two places. The Red Junglefowl is much hunted by humans and is one of the most wary of game birds (Bump and Bohl 1961). We returned to the zoo population for information on details of behavior of individuals over the adult life-span. This information would have been exceedingly difficult to obtain in the wild, and we feel that the observations on the zoo population generally will be found to apply in the field. We hope that the zoo studies will stimulate and provide some guidance for future studies under the more difficult field conditions.

The evolutionary significance of individuals ultimately must be evaluated in terms of their lifetime reproductive success in the population. In recent years there has been an increasing emphasis on the study of lifetime reproductive success in birds. A recent review volume (Newton 1989) summarized long-term studies on 23 species of birds. Despite great differences in body size and life history, in all of these species breeding life-span emerged as the major demographic determinant of lifetime reproductive success when measured as fledgling production. However, where lifetime reproductive success was measured by the number of recruits to local breeding populations rather than by the number of fledglings, life-span contributed much less to variance in lifetime reproductive

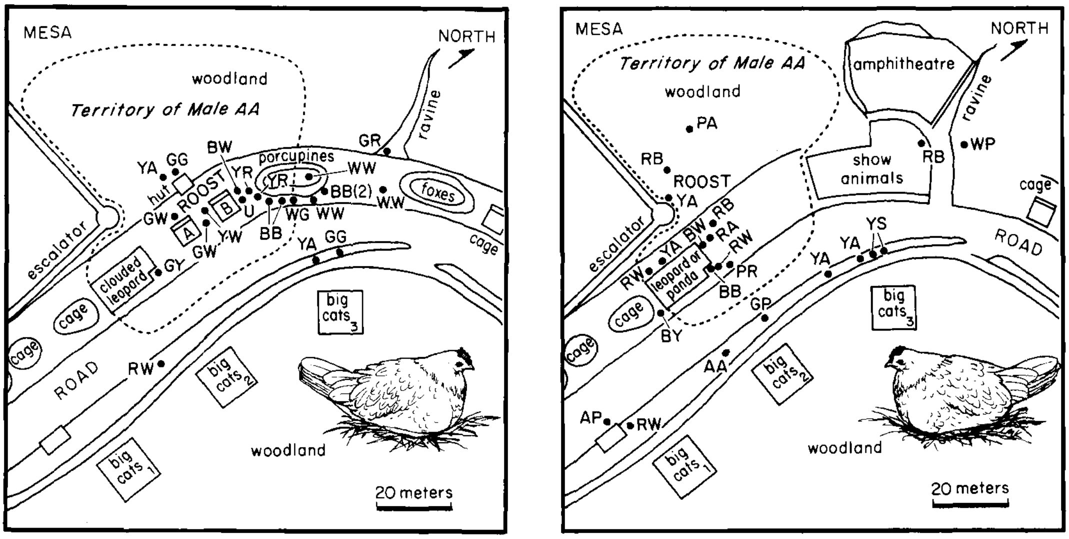

Fig. 1. Location of nest sites of hens from central flock. *Left map:* May 1982 to April 1984. *Right map:* May 1984 to August 1988. Note shift of most nest sites to south and near other roosting site after original roost trees and many favored nesting bushes were removed. Since maps cover a seven-year period, many of the nest sites shown close together are not contemporary.

success, and the survival of young between fledging and recruitment emerged as important. Furthermore, "wherever it could be studied social rank emerged as a correlate of breeding success in both sexes." Social rank influenced access to prime resources, such as territory, food or mates. However, none of these studies report evidence for social rank (i.e. dominance status) over the adult lifetime of the birds in quantitative terms.

We made a study of the number of young raised to independence (two months of age) and to maturity (yearlings) over their lifetime by color-banded hens in an unconfined flock of Red Junglefowl on the grounds of the San Diego Zoo in southern California. We attempt to relate the number of young reared to independence by individual hens to life-span, year of hatching or age class (cohort), and dominance status. We evaluate the relative importance of all three factors with appropriate statistical analysis.

The peck order of chickens is the classic example of dominance hierarchies (Schjelderup-Ebbe 1922, Collias 1944, Allee et al. 1949). In general, cocks and hens have separate peck orders. One hen has the "peck-right" over another hen, which consistently gives way when pecked or threatened by the former, whether competing for food or not. Each hen in the flock knows her place in relation to the others. Among Red Junglefowl, as in domestic chickens, the alpha hen dominates all the others, while the omega hen dominates none and yields to all (Banks 1956).

The first thing two strange hens will do on meeting is to settle their future dominance relations, either by active fighting, or by passive submission by one of the hens (Schjelderup-Ebbe 1922, Collias 1943). Once decided, such dominance relations often remain stable for months or even years, based on habitual deference by the subordinate hen reinforced by occasional pecks or threats from the dominant hen. Changes in the peck order are rare and result from active fighting and successful revolt by the subordinate bird.

The peck order in an undisturbed flock confers some stability to the flock organization. A flock may be kept in a state of perpetual disorganization by frequently removing one hen and replacing her with a new strange hen and, under these conditions, there is continual strife in the flock with the average hen being pecked more, getting less food, losing body mass, and laying fewer eggs (Guhl and Allee 1944). Guhl (1953, 1962) has summarized extensive studies of dominance hierarchies among chickens.

TABLE 1. Peck order among yearling and older hens of the central flock (November 1982 to February 1986) related to age classes (year of hatching). Number of pecks or threats by dominant birds in leftmost column over subordinates. Pecks or threats given subsequent to reversals of status are in boldface.

	Hatched before 1982			Hatched 1982									Hatched 1983								
	BB	GG	WW	WB	YR	GR	GB	GW	GY	YW	WA	YA	YB	RA	YS	RB	BY	YA_2	RW	BA	BW
BB	—	40	36	10	8	3	6	5	8	8	9	4	1	6	6	1	12	4	3	1	1
GG		—	45	9	4	1	5	7	4	9	15	1	1	6	7	6	4	1	3	2	2
WW			—	10	12	9	25	7	3	3	22	3	1	9	4	2	6	5	4	6	3
WB				—		7	9		7		3		2	3	7	2	9	5	3	5	1
YR					—	3	4	3	6	4	2		Last seen September 1983								
GR						—	1	6	11	7	7		Last seen August 1983								
GB							—	4	6	5	4		5	3	3		4	4	2	1	2
GW				11		**1**		—		1	9		2	26	13	9	2	10	13	7	10
GY							**1**		—	2			Last seen August 1983								
YW				**1**						—			Last seen August 1983								
WA				**5**							—			3	6	2	1	9	4	1	4
YA												—	Last seen April 1983								
YB													—		2		1		1	1	1
RA														—		13	3	4	1	3	8
YS															—	9		4	2	1	5
RB																—	1	5	6		4
BY																**3**	—				
YA_2																**5**		—	1	2	4
RW															**9**			**4**	—	4	4
BA																			**1**	—	7
BW																	**1**				—

Bradshaw (1992) critically reviewed methods that have been most commonly used to calculate dominance among domestic hens. Drickamer and Vessey (1992) provided a selected and balanced summary of the large and at times controversial recent literature on aggression and dominance among vertebrate animals.

METHODS

The Red Junglefowl in the San Diego Zoo are descended from 15 birds of the Indian race (*G. g. murghi*) and 12 birds of the Burmese race (*G. g. spadiceus*). These birds were released on the zoo grounds in 1942, and the current population is descended from them (Lint 1971). The zoo birds generally meet the criteria of Delacour (1977) for wild (versus domestic) Red Junglefowl, because the great majority of individuals have dark legs and the cocks molt their neck hackles in the summertime.

Gray foxes (*Urocyon cinereoargenteus*), domestic cats (*Felis cattus*), and Cooper's Hawks (*Accipiter cooperi*) roam the zoo grounds freely and capture junglefowl, especially chicks, but we made no quantitative study of predation.

We selected one flock, the central flock, for detailed study of social behavior and lifetime breeding success. Like other flocks in the zoo, this one occupied the same roosting trees each evening. Birds were captured for banding by driving them into mist nets and by baiting them into nooses on the ground, which were then drawn about their legs. Each bird was given two colored leg bands in an individually distinctive combination (the same on each leg for rapid identification).

As a rule, we visited the zoo every two months for three-day trips, observing the birds and recording broods from 1982 to 1989. Each individual, except the three oldest hens, was followed over its lifetime. We also made two visits in May 1981 for preliminary assessment of the situation. The three oldest hens when the study began all had broods when they were first observed (BB in 1981, GG and WW in 1982), so at that time they were at least of yearling age. The estimate of the life-span of these three hens is a minimum estimate, but over the whole study they were among the seven hens with the longest life-spans.

We judged the chicks to be able to care for themselves in feeding, roosting, and predator-avoidance behavior when they were about two months of age, and then we recorded them as having been reared to independence. Only one hen bred in the year in which she was hatched, and breeding by the hens generally began early in March of the following year. The birds were considered to be yearlings and adults at the start of the calendar year following the one in which they were hatched. Until the chicks reached independence at about two months, their survival was judged to be the primary responsibility of their mother. After this somewhat arbitrary period, the young were considered to be largely responsible for their own survival to maturity.

A mother hen and her small chicks form a very close family unit, and we routinely assigned chicks and a mother to each other simply by seeing them interacting close together time after time. Chick adoption and probably egg dumping are rare in this species. How frequently Red Junglefowl lay eggs in each other's nests is not known, but this possibility is minimized because individual hens often nest well apart from each other and away from the area most frequented by the flock, and because we usually found no more than one or two hens from the same flock incubating at the same visit.

We consistently sought and mapped nest sites (Fig. 1) by watching clucking hens return to their nests after being off the nest for 0.5 to 1.0 h, generally in the morning. We could then expect to see those hens with chicks at our next visit to the zoo. Domestic hens, like Red Junglefowl hens, resist or refuse copulation when incubating and broody (clucking). At this time the ovary is regressed, the hen ceases to lay, and the clutch can be assumed to be completed (Collias 1950). The average clutch size was 8.1 eggs for 18 hens for which we also knew the life-span, and only about 11% of 511 eggs laid in 64 clutches became chicks reared to independence. Not all nests were found, and since most small chicks are lost (Collias et al. 1966), the important criterion that we used for breeding success of hens was the number of chicks they reared to independence. Of 62 chicks reared to independence, 46 (74%) became yearlings (i.e. reached maturity).

During each visit we made opportunistic observations on the peck order and continued to do so over the lifetime of the birds. To ascertain dominance relations between any two birds, we tossed a bit of food, usually a peanut, sometimes a mealworm, between the birds and recorded which one pecked or threatened the other away from the food. We define the lifetime domination index for a hen as the proportion of hens she dominates among all she encounters agonistically. More precisely, let N_d be the number of hens she is seen to dominate at least once during her entire lifetime starting when she is classified as a yearling, and let N_s be the number of hens to which she is seen to be subordinate over the same period. The domination index for this hen is $N_d/(N_d + N_s)$. Most hens have no dominance reversals (i.e. there are no hens that she is seen to dominate on some occasions and to be subordinate to on later occasions). For such a hen, the domination index is simply the proportion of hens she is seen to dominate among all hens she is seen to encounter agonistically.

Since the hens on the average lived only two years, they interacted very largely with their own age class. Since the birds lived to widely different ages, the domination index, which can only refer to the interactions of a bird with living contemporaries, gives

TABLE 2. Peck order among yearling and older hens in central flock (February 1986 to December 1988). Pecks or threats given subsequent to reversals of status are in boldface.

	Hatched 1983					Hatched 1985				Hatched 1986			Hatched 1987	Age not known[a]	
	RW	YS	RB	YA_2	BW	WP	PR	GP	PA	GY_2	YR_2	AA	GR_3	GR_2	RA_2
RW	—	8		4	3	1	1	1						3	
YS		—	17	18	4	2	8	5	8	1		2		8	
RB	4	**1**	—	15	1	7	4	2	7		2	5	1	7	
YA_2		**3**		—	2	6	9	2	3	1				5	
BW					—		3	2							
WP						—	6	1	1						
PR	1						—	6	**10**	1	2			12	
GP								—	2						
PA							2		—						
GY_2										—	1				
YR_2											—				
AA			**2**									—	3		7
GR_3													—		
GR_2			**1**						1		2			—	
RA_2													8		—

[a] Adult when first observed.

the best estimate of the dominance status of a bird over its lifetime. The peck orders for all observed encounters are given in Tables 1 and 2, for early (1982–1986) and late (1986–1988) periods, respectively. The great majority of possible paired interactions between all the birds were observed.

Nicholas and Elsie Collias made the behavioral and population observations at the zoo. Robert Jennrich evaluated the relative importance and interrelations of the major factors in reproductive success of the hens using a log-linear model analysis. The analysis used the statistical program SAS PROC NLIN (SAS Institute 1985). Nonparametric statistical tests are from Siegel and Castellan (1988).

RESULTS

Tables 1 and 2 show the peck order in the flock from November 1982 to December 1988. Females BB, GG, and WW were the most dominant birds in the central flock and kept the same position in the peck order over their adult lifetime while in this flock. The peck order shown here is generally linear, but Table 1 illustrates a triangle involving GW who pecked WB who pecked GB who in turn pecked GW. The peck order among hens shows considerable stability over time, but there were occasional reversals of dominance and these persisted (Tables 1 and 2).

Only about 60% of the 28 hens in the flock with known life-spans managed to rear young to independence during a seven-year period, while the rest of the hens failed to raise any young to independence. The broods failed (eggs or chicks lost) for seven hens (25%), and four hens (14%) apparently never had eggs or chicks. Of the 28 hens of the central flock whose approximate life-spans were known, 17 hens that reared chicks to independence had average life-spans of about three years (35 months), and the 11 hens that failed to rear any young to independence had average life-spans of about two years (23 months; $t = 2.1126$, $P < 0.025$, one-tailed test). The average lifetime domination index of successful hens was 0.51 and that of unsuccessful hens was 0.30 ($t = 1.8359$, $P < 0.05$, one-tailed test).

The four most successful hens (BB, GG, WW, YS) in their lifetimes raised more chicks (30) to independence successfully than did the 24 remaining hens combined (29 chicks), and these four hens also averaged about twice the life-span and over twice the dominance status of the remaining 24 hens (Table 3).

We also considered the life-span and average dominance status of the different age classes (cohorts) of adult hens in the central flock that hatched from 1981 to 1987 in relation to their breeding success (Table 3). The age class refers to the year in which each class of hens was hatched. The most dominant and successful hens belonged to the oldest age class (Table 4). Hens in each age class usually dominated the birds

TABLE 3. Lifetime breeding success in relation to age class (year hatched), life-span, and dominance status of 28 hens in the central flock of Red Junglefowl, 1982–1989.

Hen	Year hatched	Life-span (months)	Domination index	No. chicks reared to: Independence	No. chicks reared to: Maturity
BB	Before 1982	57	1.000	7	7
GG	Before 1982	47	0.950	10	9
WW	Before 1982	41	0.900	11	10
GW	1982	37	0.684	3	3
WA	1982	36	0.529	3	3
WB	1982	30	0.684	0	0
GB	1982	24	0.632	0	0
YR	1982	18	0.667	5	2
GR	1982	17	0.454	2	0
GY	1982	17	0.222	1	0
YW	1982	17	0.110	1	0
YA	1982	13	0.000	0	0
YS	1983	71	0.522	5	4
RB	1983	57	0.520	0	0
YA_2	1983	47	0.500	3	1
RW	1983	41	0.364	2	2
BW	1983	33	0.176	2	1
BA	1983	21	0.143	0	0
RA	1983	20	0.461	1	0
YB_2	1983	12	0.454	0	0
GP	1985	34	0.125	1	1
WP	1985	26	0.429	1	1
PA	1985	25	0.125	0	0
PR	1985	18	0.461	0	0
AA	1986	33	0.600	4	2
GY_2	1986	17	0.250	0	0
YR_2	1986	15	0.000	0	0
GR_2	1987	23	0.000	0	0

of the next younger age class (Tables 1 and 2). More of the chicks that reached maturity (i.e. became yearlings [26]), were offspring of the three hens of the oldest year class than were produced (20) by the remaining 25 hens with known life-spans (Table 3). These three hens were also at the top of the peck order (Tables 1 and 4).

TABLE 4. Lifetime breeding success and dominance of different age classes of hens in an unconfined flock of Red Junglefowl.

Year hatched (n hens)	Mean life-span (months)	Mean domination index	Mean no. chicks reared per hen to: Independence	Mean no. chicks reared per hen to: Maturity
Before 1982[a] (3)	48	0.950	9.3	8.7
1982 (9)	23	0.442	1.7	0.9
1983 (8)	38	0.392	1.6	1.0
1984 Breeding largely failed				
1985 (4)	26	0.285	0.5	0.5
1986 (3)	22	0.283	1.3	0.7
1987 (1)	23	0	0	0

[a] Year of hatching unknown for three starting adult hens in 1981 and 1982.

A plot of the number of young reared to independence (number of young) against dominance of the hens (Fig. 2A) shows a relationship between these two variables. Similar plots of the number of young against life-span (Fig. 2B) and against age class (Fig. 2C) show weaker relations.

Log-linear-model significance and goodness-of-fit tests were carried out for each plot. For the plot of number of young y on dominance d, it was assumed the counts y have independent Poisson distributions with expectations:

$$f = e^{\alpha + \beta d}. \tag{1}$$

This defines a log-linear Poisson model (e.g. see Haberman 1974). The curve displayed in Figure 2A is the maximum-likelihood fit under this model to the data displayed. As can be seen from Table 5, dominance is a very significant

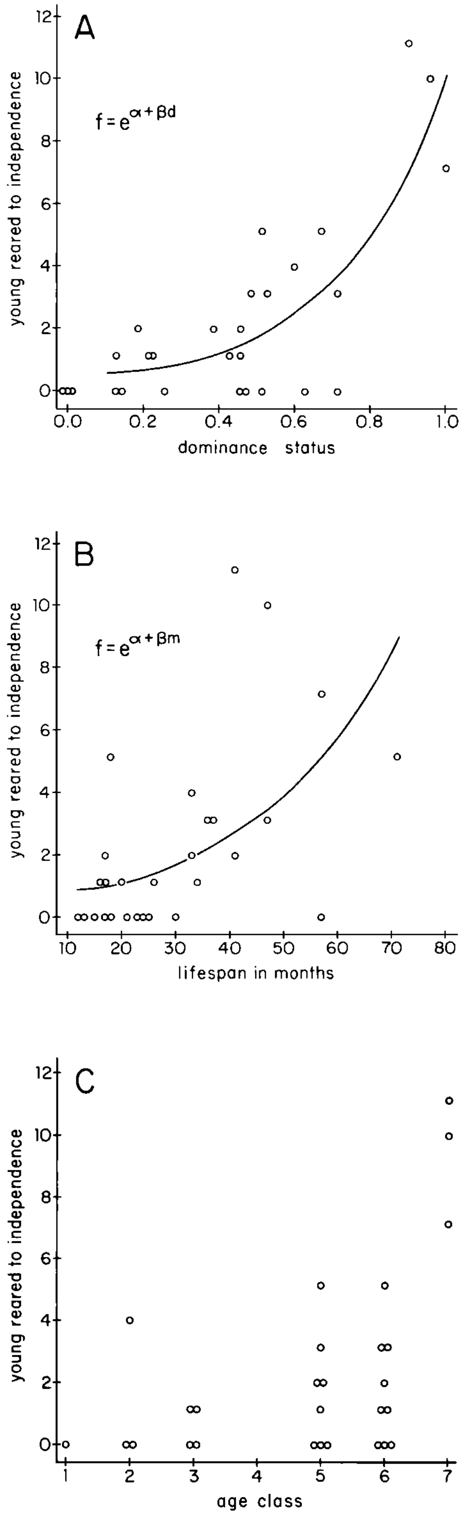

Fig. 2. Number of young reared to independence by 28 hens in their lifetime plotted against: (A) dominance status d of hens; (B) life-span m in months; and (C) age class c of the hens. On abcissa, 1 refers to youngest age class (1987) and 7 to oldest age class (hatched before 1982).

TABLE 5. Pearson chi-square statistics for six log-linear Poisson models. The X_g^2 is goodness-of-fit statistic for indicated model and X_s^2 is difference chi-square statistic for significance of indicated variable in indicated model.

Model (log f)	X_g^2	Variable[a]	X_s^2	df	P-value
α	109.61			27	0.0000
$\alpha + \beta d$	31.85			26	0.1981
		d	77.76	1	0.0000
$\alpha + \beta m$	74.23			26	0.0000
		m	35.38	1	0.0000
$\alpha + \gamma_c$	38.79			22	0.0149
		c	70.82	5	0.0000
$\alpha + \beta_1 d + \beta_2 m$	28.86			25	0.2698
		d	45.37	1	0.0000
		m	2.99	1	0.0838
$\alpha + \beta d + \gamma_c$	27.92			21	0.1424
		d	10.87	1	0.0010
		c	3.93	5	0.5595

[a] d = dominance, m = months of life-span, c = age class.

predictor of number of young ($X_s^2 = 77.76$, $P = 0.0000$). The chi-square statistic for the significance of a particular term is obtained by subtracting the goodness-of-fit chi-square for the model from the goodness-of-fit chi-square statistic for the model with the term omitted. Here the two models are $\alpha + \beta d$ and α and the subtraction gives $X^2 = 109.61 - 31.85 = 77.76$. Moreover, the Pearson chi-square goodness-of-fit test for model 1 is not rejected ($X_g^2 = 31.85$, $P = 0.1981$). This says that dominance alone provides a reasonably adequate fit. A similar analysis using life-span shows that it also is a highly significant predictor ($P = 0.0000$), but that it alone does not provide an adequate fit ($P = 0.0000$). Because age class is not expected to be ordinally related to the number of young, an exponential relation similar to that in model 1 is not expected. One can, however, use an exponential relation that treats age class as a categorical variable; when this is done, age class is a highly significant predictor of number of young ($P = 0.0000$), but it alone is not an adequate predictor ($P = 0.0149$). These results say that dominance, life-span, and age class are each highly significant predictors of the number of young, but that only dominance is, by itself,

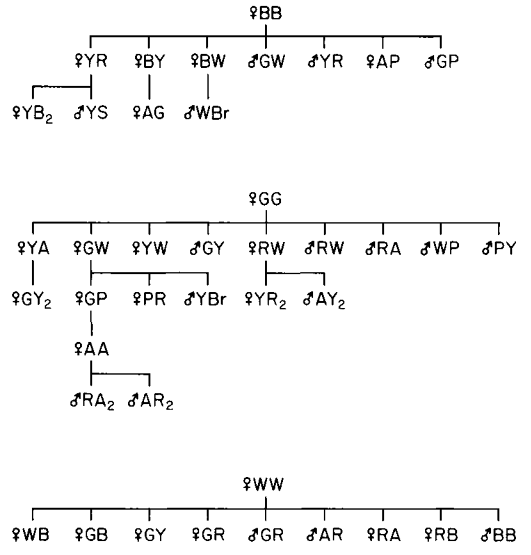

Fig. 3. Matrilines, showing descendants that reached at least yearling age, of three top hens (BB, GG, WW) in peck order of central flock.

sufficient to explain the variation in the number of young, at least to the degree expected under our log-linear model. Life-span alone and age class alone fail by significant margins to explain this variation.

Since life-span is correlated with dominance ($r = 0.523$), it is possible that the relation between number of young and life-span may result only from this correlation. To investigate this we considered a log-linear model of the form

$$f = e^{\alpha+\beta_1 d+\beta_2 m},$$

using both dominance d and life-span m. The chi-square significance tests given in Table 5 indicate that dominance is very significant in this model ($P = 0.0000$), but life-span is not ($P = 0.0838$). This says that after accounting for dominance, life-span does not have a significant effect. A similar analysis using dominance and age class with the latter treated as a categorical variable indicates again that dominance is quite significant ($P = 0.0010$), but age class is not ($P = 0.5595$).

In conclusion, among the adult hens of this flock, all three of the factors—dominance, life-span, and age class—are strongly related to the number of young reared to independence. However, in our study, lifetime dominance status of the adult hen was by far the most important factor.

Yearling hens often fail to raise chicks to independence in their first year after the one in which they hatched, but may breed successfully in later years. When success in the first year and the average success in later years for each hen was compared, a Wilcoxon matched-pairs, signed-ranks test (Siegel and Castellan 1988) for eight hens for which we had more than one year's breeding record gave a P-value of 0.005 (one-tailed test).

We compared the dominance status of 20 Red Junglefowl hens in the central flock with the dominance status of their mothers. There was no significant correlation ($r = 0.09$). However, the different generations were intermingled as they occurred naturally. Most hens were daughters or granddaughters of the three top hens in the flock. The more senior hens of the older age classes tended to dominate hens of younger generations regardless of relationship. Figure 3 shows the yearling descendants of the three top hens. These three hens and some of their yearling offspring comprised two-thirds (6 males and 6 females) of the 18 emigrants from the central flock roost to other flock roosts from 1982 to 1988.

DISCUSSION

The results of our study are consistent with the principle that relatively few individuals often produce most of the young added to the breeding population in the next generation (Newton 1989). Statistical analysis showed that an important reason for this result was the high dominance status of the more productive hens. This result was based on the lifetime dominance status and breeding success of 28 hens in one large flock over a seven-year period. It would of course be desirable to study other flocks in this fashion. However, such data are difficult to obtain and, as yet, there seem to be no comparable data in the literature. That the results have general significance is strongly implied by the many studies that have been done on peck orders of domestic hens using aggressive precedence to food as the primary criterion for dominance. Dominant mother hens, therefore, should generally be able to nourish their chicks more adequately than do subordinate hens.

While the degree of egg dumping is apparently still unknown for Red Junglefowl, such conspecific egg parasitism is likely to be infrequent. Any egg dumping that occurred would not seriously affect the validity of the conclusion that by far most of the apparent reproduction was by the more dominant hens. If a subordinate hen laid an egg in the nest of a dominant hen, the latter might be credited with an extra young one. Conversely, if a dominant hen laid in the nest of a subordinate hen, this would reduce the number of chicks credited to the dominant bird. Nevertheless, despite such hypothetical qualifications, or any genetic advantage from effective egg dumping, the facts are that the more dominant hens still succeeded in rearing by far the greatest number of young to independence. In nature, the lower population densities that generally prevail (Collias and Collias 1967) would make egg dumping even less likely.

The dominance factor can be analyzed further into terms of genetics. Siegel and Dunnington (1990) recently have reviewed the behavioral genetics of poultry. For example, Guhl et al. (1960) effectively selected for high and low levels of aggressiveness in two different strains of White Leghorns carried to the F_4 generation. Beginning with the F_2 generation, the two lines showed significant differences in the percentage of initial paired encounters won or lost, as well as in high or low ranks in the peck orders when hens from the two lines were put in the same flock. However, there was no significant correlation in our study between the dominance status of hens and of their daughters, indicating considerable importance of nongenetic and environmental factors helping to decide dominance status.

Senescence in domestic hens was reviewed by Hutt (1949:333–339). Production of eggs tends to decline in successive years after the first year of laying. Maternal motivation may also decline with age. In the Japanese Nagoya breed of domestic fowl, Saeki (1957) found a steady decrease after the first laying year in the percentage of hens that became broody and in the average number of broody periods per hen each year. However, we do not believe senescence was an important factor influencing the number of chicks reared in the central flock of Red Junglefowl, since the three oldest hens were also the hens which raised most young in their lifetime (Table 5).

The identification of significant causes of differences in lifetime breeding success depends in part on what we choose to measure. There may be other correlations between reproductive success of the hens and factors as yet unmeasured. Thus, the dominance status of mother hens has not been separated from differences in certain other correlates of motherhood, including such things as effectiveness in protecting the young from predators, skill in guiding chicks to food or shelter, or diligence in brooding the chicks.

In conclusion, we have managed statistically to evaluate the relative importance of life-span, age class, and dominance for number of chicks reared successfully by the hens in one unconfined flock of Red Junglefowl over a seven-year period, but even these factors are highly correlated and often work together. Dominance status of the hen gives priority to food and other resources, and was the most important factor in our study. Many of the factors accounting for variation in numbers of chicks reared are unknown. However, the large contribution to the next generation coming from the most dominant hens, and most probably also from the most dominant cock, suggests that some genetic basis for aggressiveness will be maintained in the population.

Acknowledgments

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Literature Cited

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia.

Banks, E. M. 1956. Social organization in Red Jungle Fowl hens (*Gallus gallus* subsp.). Ecology 37:240–248.

Bradshaw, R. H. 1992. Describing social order in laying hens (*Gallus domesticus*). J. World Pheasant Assoc. Vols. 15 and 16:81–92.

Bump, G., and W. H. Bohl. 1961. Red Junglefowl and Kalij Pheasants. U.S. Fish and Wildlife Service, Washington, D.C., Spec. Sci. Rep., Wildlife no. 62.

COLLIAS, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. Am. Nat. 77:519-538.

COLLIAS, N. E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool. 17:83-123.

COLLIAS, N. E. 1950. Hormones and behavior with special reference to birds and to the mechanisms of hormone action. Pages 277-329 *in* Steroid hormones (E. S. Gordon, Ed.). Univ. Wisconsin Press, Madison.

COLLIAS, N. E., AND E. C. COLLIAS. 1967. A field study of the Red Jungle Fowl in north-central India. Condor 69:360-386.

COLLIAS, N. E., E. C. COLLIAS, D. HUNSAKER, AND L. MINNING. 1966. Locality fixation, mobility, and social organization within an unconfined population of Red Jungle Fowl. Anim. Behav. 14:396-411.

CRAWFORD, R. D. 1990. Origin and history of poultry species. Pages 1-41 *in* Poultry breeding and genetics (R. D. Crawford, Ed.). Elsevier, Amsterdam.

DARWIN, C. 1887. The variation of animals and plants under domestication, 2nd ed. 2 vols. D. Appleton and Co., New York.

DELACOUR, J. 1977. The pheasants of the world, 2nd ed. Spur Publications, Hindhead, England.

DRICKAMER, L. C., AND S. H. VESSEY. 1992. Animal behavior: Mechanisms, ecology and evolution, 3rd ed. Wm. C. Brown, Dubuque, Iowa.

GUHL, A. M. 1953. Social behavior of the domestic fowl. Tech. Bull. 73, Kansas Agric. Exp. Station, Manhattan, Kansas.

GUHL, A. M. 1962. The behaviour of chickens. Pages 491-530 *in* The behaviour of domestic animals (E. S. E. Hafez, Ed.). Balliere, Tindall and Cox, London.

GUHL, A. M., AND W. C. ALLEE. 1944. Some measurable effects of social organization in flocks of hens. Physiol. Zool. 17:320-347.

GUHL, A. M., J. V. CRAIG, AND C. D. MUELLER. 1960. Selective breeding for aggressiveness in chickens. Poult. Sci. 39:970-980.

HABERMAN, S. J. 1974. The analysis of frequency data. Univ. Chicago Press, Chicago.

HUTT, F. B. 1949. Genetics of the fowl. McGraw-Hill Book Co., New York.

LINT, K. C. 1971. Jungle fowl and their importance to man. Zoonooz 44(8):6-11.

NEWTON, I. (Ed.). 1989. Lifetime reproduction in birds. Academic Press, London.

SAEKI, Y. 1957. Inheritance of broodiness in Japanese Nagoya fowl, with special reference to sex-linkage and notice in breeding practice. Poult. Sci. 36:378-383.

SAS INSTITUTE INC. 1985. SAS user's guide: Statistics, version 5th ed. SAS Institute, Inc., Cary, North Carolina.

SCHJELDERUP-EBBE, T. 1922. Beiträge zur Sozialpsychologie des Haushuhns. Z. Psychol. 88:225-252. Reprinted 1975, plus English translation, pages 35-49 *in* Social hierarchy and dominance (M. W. Schein, Ed.). Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

SIEGEL, P. B., AND E. A. DUNNINGTON. 1990. Behavioral genetics. Pages 877-895 *in* Poultry breeding and genetics (R. D. Crawford, Ed.). Elsevier, Amsterdam.

SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. Nonparametric statistics for the behavioral sciences, 2nd ed. McGraw-Hill Book Co., New York.

STEVENS, L. 1991. Genetics and evolution of the domestic fowl. Cambridge Univ. Press, Cambridge.