Anim. Behav., 1996, **51,** 725–731

Dominance rank and offspring sex ratios in domestic fowl

MARTY L. LEONARD* & PATRICK J. WEATHERHEAD†
**Centre for Food and Animal Research, Central Experimental Farm, Ottawa, Canada*
†Department of Biology, Carleton University, Ottawa, Canada

(Received 6 February 1995; initial acceptance 24 March 1995; final acceptance 21 July 1995; MS. number: A7252)

Abstract. Research on both mammals and birds suggests that parental features, such as body condition and dominance rank, could influence sex ratios. This study examined the effect of male and female dominance rank on hatching sex ratios in domestic chickens, *Gallus gallus domesticus*. Twenty-four dominant males and 24 subordinate males were each placed in a pen with eight females. Females that were mated to a dominant male in the first 3 weeks of the experiment were mated to a subordinate male in the second 3 weeks and vice versa. Sex ratios (number of females/male) at hatch were not directly affected by male and female dominance status. Females that were mated to a subordinate male in the first trial, however, produced more variable sex ratios in the second trial. This effect was not evident for females mated to dominant males first. In addition, both groups of females produced more daughters in the second trial than in the first, although this effect was only significant for females that mated with subordinate males first. The results did not support the hypothesis that females should alter the sex ratio of their offspring based on their own dominance status or that of their mates. They did provide evidence, however, that sex ratios in chickens may be indirectly influenced by the status of the male.

When parental investment influences the fitness of sons and daughters differently, parents are expected to bias the sex ratio to maximize their return per unit effort (Trivers & Willard 1973). Typically, in polygynous systems, male mating success is more variable than female mating success, and as a result, increased investment in sons may have a greater impact on parental reproductive success than increased investment in daughters (Trivers & Willard 1973). Therefore, parents capable of high levels of investment should produce sons, and parents capable of only limited investment should produce daughters.

In social hierarchies, dominant individuals usually have more access to resources than subordinate individuals. If these resources improve the fitness of sons more than daughters, then high-ranking parents should produce more sons than low-ranking parents (Trivers & Willard 1973). Adaptive biases in the sex ratio in response to maternal rank and/or condition have been documented for a number of mammals (e.g. Clutton-Brock et al. 1984; Meikle et al. 1993; Wiley & Clapham 1993) and a few birds (e.g. Meathrel & Ryder 1987; Weibe & Bortolotti 1992).

Correspondence: M. L. Leonard, Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4JI, Canada (email: MLEONARD@AC.DAL.CA). P. J. Weatherhead is at the Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada.

Similarly, paternal dominance rank and condition may also influence sex ratios. For instance, high male rank is often associated with increased mating success (e.g. Clutton-Brock et al. 1984; Graves et al. 1985). Therefore, inheritance of high rank (or features conferring rank) is more likely to benefit sons than daughters. Thus, females mated to dominant males should produce proportionally more sons than females mated to subordinate males (Burley 1981, 1986). Sex ratio bias in response to paternal features has been reported for zebra finches, *Poephila guttata* (Burley 1986) and yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Patterson & Emlen 1980).

The purpose of this study was to determine the effect of male and female dominance status on hatching sex ratios in white leghorn chickens. Domestic chickens, *Gallus gallus domesticus*, are

0003–3472/96/040725+07 $18.00/0

ideal for testing the relationship between male and female dominance rank and sex ratios. Feral chickens and red jungle fowl, *G. g. murghi*, form small social groups usually composed of a dominant male, several females and several subordinate males (Collias & Collias 1967; McBride et al. 1969). Male dominance hierarchies are based on fighting ability and are usually stable and linear (e.g. Guhl 1962). Dominant males copulate more than subordinate males, have a higher proportion of successful matings and interfere with the copulation attempts of subordinates (e.g. Guhl & Warren 1946; Graves et al. 1985). Thus, male mating success is likely to be variable, with dominant males having greater access to females than subordinate males. In addition, body size and aggressiveness are heritable (Siegel 1960) and are also positively correlated with male rank (e.g. Marks et al. 1960; Siegel & Hurst 1962; Graves et al. 1985; Leonard & Horn 1995). Thus, we predicted that females mated to dominant males would produce an excess of sons and those mated to subordinate males would produce an excess of daughters.

Female chickens also establish stable dominance hierarchies (e.g. Guhl 1962) and increased body size, which is associated with high female rank (e.g. Collias 1943; M. L. Leonard, unpublished data), is also heritable (Siegel 1960). In addition, larger females produce more eggs than smaller females and the mass of those eggs is also greater (R. W. Fairfull, personal communication). Thus, high-ranking (i.e. larger) females are capable of investing more than low-ranking (i.e. smaller) females. Therefore, the sons of larger, dominant females may be at an advantage relative to the sons of subordinate females. Thus both male and female status may be expected to influence offspring sex ratios.

Not only are domestic chickens appropriate for testing hypotheses about offspring sex ratios, but they also afford a potentially important applied aspect to our study. There would be a substantial economic benefit if one could manipulate sex ratios in chickens. For example, when producing chickens for egg laying, all but the very small percentage of males required for breeding stock are superfluous, making production only about 50% efficient up to the point that chicks are sexed. Identifying the circumstances under which sex ratios deviate from random may aid the development of techniques for biasing chicken sex ratios to enhance agricultural efficiency.

METHODS

Housing Conditions

Subjects were 24 groups of five male and 23 female white leghorn chickens. We individually marked them at 9 weeks of age with numbered wing tags and randomly assigned them to floor 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 remained in these rearing pens until they were 19 weeks old. Food and water were provided ad libitum throughout the study.

At 19 weeks we removed the top- and bottom-ranked males (see below) from each group and assigned each resulting pair of males to a randomly chosen pen. We then randomly selected 16 females from each original group of 23 females and placed each new group in a pen adjoining the pair of males with which they had been previously housed. This arrangement resulted in 24 pairs of male/female pens, with each pair consisting of a pen with two males adjacent to a pen with 16 females. Within each pair of pens, 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 through the front half. Thus, they could see each other in the back of the pen, but they could not directly interact, which gave females the opportunity to observe interactions between males.

Experimental Conditions

At 30 weeks we randomly divided the 16 females from each female pen into two groups of eight and placed one group on each side of the male/female pen. We then randomly assigned the dominant and subordinate males in each pen to one of the two groups of females, resulting in 24 pairs of pens. Each pair consisted of a pen with a dominant male and eight females and a pen with a subordinate male and eight females. Males remained with their assigned females for 21 days, after which males and females were again separated and returned to their original pens (i.e. a pen with two males adjacent to a pen with 16 females). We kept males and females separated for another 21 days to ensure that sperm stored by females from the first male had been depleted (R. W.

Fairfull, personal communication). Then we again divided the females into the same groups of eight and placed each group in the pen to which it had been assigned in the first trial. In the second trial, however, the opposite male was assigned to each group of females (i.e. we performed a cross-over, so if the dominant male was placed with group A in the first trial, the subordinate male was placed with this group in the second trial, and vice versa). Therefore, each group of females was ultimately exposed to both a dominant and a subordinate male, with half of the females pairing with a dominant male first and half pairing with a subordinate male first. Males and females again remained together for 21 days.

Behavioural Observations

To determine the dominance relationships within each original group of five 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 based on the outcome of agonistic interactions between pairs of birds. An individual lost an interaction if it fled when another bird 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 which individuals they dominated.

The day before males and females were placed together for each experimental trial, we reconfirmed dominance relationships between males that were originally ranked as top (dominant) or bottom (subordinate). We placed a handful of cracked corn in the centre of every male pen and recorded all interactions during a 15-min observation period. Because male rank could change after exposure to females, we also re-assessed dominance weekly during each trial. During these observations, we placed each pair of males in a holding area outside their pen in view of their females for a 15-min observation period. Observers blind to the previous rank of the males assigned dominance based on the criteria described above. Thus, we based our assignments of dominance ranks to the males used in the study on a total of 10 observation periods before the males were selected, one observation period immediately before each trial and two observation periods during each trial.

We determined female dominance hierarchies during weeks 37–39 by observing the eight females in each pen in a competitive situation. We removed feeders from the pens overnight and then replaced them, but with the access reduced to an area large enough for only two birds. We recorded interactions between females during 20-min observation periods that we conducted every day for 3 days. We randomized the order in which pens were observed each day. We determined female dominance hierarchies in the same manner as male hierarchies. In some instances females received the same dominance rank because, although they dominated the same females and were subordinate to the same females, they interacted with each other too infrequently to be ranked relative to one another. We could not rank several females because they interacted infrequently with other females, so we excluded them from the analysis.

Egg Collection, Storage and Sexing

During each 21-day trial, we trapped females in nestboxes when laying and individually marked their eggs and stored them in nitrogen gas. This storage technique will keep eggs viable for up to 21 days. We only saved eggs that we could assign to a specific female. We did not save eggs laid between the first and second trial while females were separated from males. At the end of each egg-save period we placed the eggs in the same Robbins incubators for 22 days. Incubators were set at 37.8°C. At 18 days, we checked eggs for fertility, and recorded the number of dead eggs at 18 and 22 days. The same commercial sexor vent-sexed all chicks that hatched for both trials. This sexor has an average error rate of 0.10% (R. W. Fairfull, personal communication). Chicks dead in the egg were sexed post-mortem.

Analyses

We only included pens in which male rank was stable over all observation periods. During some of the male dominance observations, males that were originally assigned subordinate status were dominant to the other male. In 10 of 24 pens this reversal in dominance occurred during at least one of the six observation periods. Although conservative, we excluded these pens, which resulted in a total of 28 males (14 pairs) being included in our analyses based on male rank. Similarly, only females in which dominance was reliably assigned were included in the female dominance analyses ($N=184$ females within the pens analysed). Because individuals within pens are not independent, we used pen means in analyses of the effect of male status on sex ratio. For analyses of female dominance, we classified females as either dominant (the top ranked individual(s) in each pen; $N=31$), subordinate (the bottom ranked individual(s) in each pen; $N=37$), or intermediate (the remainder of the females to which we could assign dominance status; $N=116$). Initially we separated analyses of sex ratios based on chicks that hatched from those based on chicks that were sexed by post-mortem. The results of these analyses did not differ, so we report results based on all chicks. Sex ratios are reported as the number of females/male and means are reported $\pm$ SD.

Table I. Mean ($\pm$ SD) sex ratios (number of females/male) of offspring produced by dominant, intermediate and subordinate females mated to dominant and subordinate males

		Male status	
Female status	N	Dominant	Subordinate
Dominant	31	1.11 ± 0.65	0.92 ± 0.45
Intermediate	116	1.14 ± 0.82	1.26 ± 0.91
Subordinate	37	1.17 ± 0.81	1.29 ± 1.10

Table II. Mean ($\pm$ SD) sex ratios (number of females/male) produced by females that mated with a dominant male first and females that mated with a subordinate male first when they were paired with both dominant and subordinate males

	Male status	
Mating order	Dominant	Subordinate
Dominant first	1.11 ± 0.16 (trial 1)	1.31 ± 0.37 (trial 2)
Subordinate first	1.18 ± 0.29 (trial 2)	1.07 ± 0.18 (trial 1)

RESULTS

To assess the effect of male and female dominance on offspring sex ratios, we performed an ANOVA using the pen in which the chickens were housed as the main effect. Sex ratios were not affected by male dominance status ($F_{1,335}=0.03$, $P=0.86$), female dominance status ($F_{2,335}=1.28$, $P=0.28$), or the interaction ($F_{2,335}=0.84$, $P=0.43$; Table I). There was also no main effect of pen ($F_{27,335}=0.77$, $P=0.80$). We used a power analysis to assess the likelihood that sample size limited our ability to detect a difference in the sex ratios between the treatment groups. At a type II error rate of 0.20, the minimum detectable difference in sex ratio (females/male) between treatment groups would be 0.33, which is above the differences we observed (Table I).

Although male and female dominance rank appeared not to influence the sex ratio, it is possible that the order in which females mated with dominant and subordinate males could have an effect; because half the female groups mated with a dominant male first and half mated with a subordinate male first. Because female dominance rank had no effect on sex ratios, we pooled the information on females in the following analyses. The results of a repeated-measures ANOVA indicated no effect of mating order ($F_{1,26}=1.14$, $P=0.29$) or male status ($F_{1,26}=0.48$, $P=0.49$) on sex ratio, but there was a significant interaction between order and status ($F_{1,26}=6.66$, $P=0.01$; Table II). This interaction appeared to be due to an overall increase in the number of females produced in trial 2 compared to trial 1 (Table II).

Indeed, the mean sex ratio per pen was significantly more female-biased in trial 2 compared to trial 1 (paired t-test: $t=-2.61$, $df=27$, $P=0.01$). The mean standard deviation per pen also increased in the second trial (paired t-test: $t=-2.35$, $df=27$, $P=0.03$). Separating the pens according to whether the females were first paired with the dominant or subordinate male indicated that the trial effect may be partially related to male dominance. In pens in which females mated with the subordinate male first, both the mean sex ratio and the mean variance in the sex ratio significantly increased in the second trial (paired t-test: $t=-2.19$, -2.23, $df=13$, $P=0.05$, 0.04, respectively). In pens in which females mated with the dominant male first, the mean sex ratio tended to become more female-biased in the second trial (paired *t*-test: $t = -1.81$, $df = 13$, $P = 0.09$), but there was no evidence of a change in mean standard deviation (paired *t*-test: $t = -1.26$, $P = 0.23$).

In summary, male and female dominance rank did not appear to affect offspring sex ratios. The overall sex ratio increased between trials; however, this effect was only significant for females that mated with subordinate males first. In addition, females mated to subordinate males first produced more variable sex ratios in the second trial. Females paired to a dominant male first did not have a significant change in the variation between trials.

DISCUSSION

Several studies on birds have reported a relationship between sex ratios and parental features, such as the attractiveness of mating partners and condition (e.g. Burley 1986; Meathrel & Ryder 1987; Wiebe & Bortolotti 1992). Similarly, numerous studies on mammals have reported a relationship between maternal dominance/condition and sex ratio (e.g. Clutton-Brock et al. 1984; Meikle et al. 1993; Wiley & Clapham 1993). In chickens, sex ratios generally tend to be close to unity (e.g. Landauer 1957; Champion 1960), although earlier studies have reported sex ratios that were slightly biased towards either males (Mussehl 1924) or females (e.g. Landauer & Landauer 1931). Studies examining heterogeneity in sex ratios between strains and parents have also produced equivocal results. Duber (1974) found no differences between parents in the sex of offspring produced, yet other studies have shown significant effects of strain (Champion 1960; Hartmann & Steinke 1974), family (Champion 1960) and sire (Merat 1970; Foster & McSherry 1980) on sex ratio. In our study, we found some evidence that sex ratios were non-random, but the prediction that dominant individuals should produce more sons was not supported.

Significantly more females were produced in the second of our two trials. Maternal age has been associated with an increasing number of male offspring in the red-winged blackbird, *Agelaius phoeniceus* (Blank & Nolan 1983), but this occurs over years, not weeks as in our study. Seasonal differences in sex ratios have been reported for several avian species (e.g. Eurasian kestrels, *Falco tinnunculus*: Dijkstra et al. 1990; common grackles, *Quiscala quiscala*: Howe 1977; red-winged blackbirds: Weatherhead 1983). These differences are usually associated with fluctuating food supplies, however, and are unlikely to apply in the present situation. Differences in the proportion of eggs hatching might also explain the change in the sex ratio, because embryonic mortality in chickens tends to be biased towards males (e.g. Landauer & Landauer 1931; MacArthur & Ballie 1932; Hartmann & Steinke 1974). We found no significant difference in the proportion of eggs hatching between the two trials (trial 1: 0.75 ± 0.06; trial 2: 0.76 ± 0.07; paired *t*-test: $t = -0.70$, $P = 0.49$). Finally, decreased temperature during incubation in chickens has also been associated with an increase in the proportion of males (Shubina et al. 1972, cited in Deeming & Ferguson 1991). Our eggs were incubated under identical conditions during each of the trials, however. It is not clear why the number of females increased between trials.

Another interesting result of this study was that females exposed to a subordinate male first produced sex ratios that were significantly more variable when they paired with a dominant male, which was not the case for females that mated with dominant males first. We do not have a simple explanation for our results. One possibility may have come from a constraint in our experimental design. For us to have subordinate males sire offspring, we had to house those males with females. Under natural circumstances, a subordinate male would not gain exclusive access to females. Thus, the behaviour of subordinate males, in particular, may have changed as they gained experience with females. If females mating for the first time varied in their perception of the status of these males, this may have influenced the variance, although not until the second trial.

In conclusion, our results did not support the hypothesis that females should adjust the sex ratio of their offspring in response to either their own dominance status or that of their mate. Our results did provide evidence, however, that sex ratios in domestic chickens are not just a function of random assortment of sex chromosomes (Charnov 1982; Clutton-Brock 1986). Given the scope for experimentation offered by domestic chickens and the potential economic value of being able to manipulate sex ratios in this species, further exploration of these results seems worthwhile.

ACKNOWLEDGMENTS

We thank Andrew Horn, Susan Leech, Barry Milligan, Kevin Teather, Sandy Walde, Dan Weary and Hal Whitehead for reading the manuscript and providing many helpful comments. We also thank Brian Thompson for advice on experimental design, Wayne Fairfull for information on chicken biology, Drew Hoysak and Greg Brown for help with data analyses and Saskia Koning, Sue Leffler, Perry Comm and the staff of the CFAR poultry unit for assistance in the field. Special thanks to Maryanne Reid, Kevin Schock and Brian McCleery for their help in organizing and carrying out this logistical nightmare. This study was supported in part by a NSERC grant to P.J.W. This is CFAR contribution number 2297.

REFERENCES

Blank, J. L. & Nolan, V. 1983. Offspring sex ratios in red-winged blackbirds is dependent on maternal age. *Proc. natn. Acad. Sci. U.S.A.*, **80,** 6141–6145.

Burley, N. 1981. Sex-ratio manipulation and selection for attractiveness. *Science*, **215,** 721–722.

Burley, N. 1986. Sex-ratio manipulation in color-banded populations of zebra finches. *Evolution*, **40,** 1191–1206.

Champion, L. R. 1960. Sex ratio in two strains of leghorns and their reciprocal crosses. *Poult. Sci.*, **39,** 876–881.

Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T. H. 1986. Sex ratio variation in birds. *Ibis*, **128,** 317–329.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature, Lond.*, **308,** 358–360.

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

Deeming, D. C. & Ferguson, M. W. J. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (Ed. by D. C. Deeming & M. W. J. Ferguson), pp. 147–172. Cambridge: Cambridge University Press.

Dijkstra, C., Daan, S. & Buker, J. B. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. *Funct. Ecol.*, **4,** 143–147.

Duber, M. M. 1974. Chromosome abnormalities, sex ratio and fertility in *Gallus domesticus*. *Diss. Abstr. int.*, **34B,** 545.

Foster, W. H. & McSherry, D. M. G. 1980. A search for genetic variation in the sex ratio at hatching. *Br. Poult. Sci.*, **21,** 131–134.

Graves, H. B., Hable, C. P. & Jenkins, T. H. 1985. 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. & Warren, D. C. 1946. Number of offspring sired by cockerels related to social dominance in chickens. *Poult. Sci.*, **25,** 460–472.

Hartmann, W. & Steinke, L. 1974. Effect of mating combination on fertility, hatchability and sex ratio in crossbred leghorn lines. *Anim. Breed. Abstr.*, **44,** 156.

Howe, H. F. 1977. Sex ratio adjustment in the common grackle. *Science*, **198,** 744–746.

Landauer, W. 1957. Primary sex ratio of fowl. *Nature, Lond.*, **180,** 1139–1140.

Landauer, W. & Landauer, A. B. 1931. Chick mortality and sex ratio in the domestic fowl. *Am. Nat.*, **45,** 492–501.

Leonard, M. L. & Horn, A. G. 1995. Crowing in relation to status in roosters. *Anim. Behav.*, **49,** 1283–1290.

MacArthur, J. W. & Ballie, W. H. T. 1932. Sex differences in mortality in abraxas-type species. *Q. Rev. Biol.*, **7,** 313–325.

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.

Meathrel, C. E. & Ryder, J. P. 1987. Sex ratios of ring-billed gulls in relation to egg size, egg sequence and female body condition. *Colon. Waterbirds*, **10,** 72–77.

Meikle, D. B., Drickamer, L. C., Vessey, S. H., Rosenthal, T. L. & Fitzgerald, K. S. 1993. Maternal dominance rank and secondary sex ratio in domestic swine. *Anim. Behav.*, **46,** 79–85.

Merat, P. 1970. Proportion des sexes chez les volailles: variation dans la descendance du meme pere suivant la date d'eclosion. *Annls. Génét. Sel. Anim.*, **2,** 269–272.

Mussehl, F. E. 1924. Sex ratios in poultry. *Poult. Sci.*, **3,** 72–73.

Patterson, C. B. & Emlen, J. M. 1980. Variation in nestling sex ratios in the yellow-headed blackbird. *Am. Nat.*, **115,** 743–747.

Siegel, P. B. 1960. A method for evaluating aggressiveness in chickens. *Poult. Sci.*, **53,** 1597–1603.

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

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179,** 90–92.

Weatherhead, P. J. 1983. Secondary sex ratio adjustment in red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.*, **12,** 57–61.

Wiebe, K. L. & Bortolotti, G. R. 1992. Facultative sex ratio manipulation in American kestrels. *Behav. Ecol. Sociobiol.*, **30,** 379–386.

Wiley, D. N. & Clapham, P. J. 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? *Anim. Behav.*, **46,** 321–324.