

---

*The Auk* 119(3):840–845, 2002

### Maternal Condition, Reproductive Investment, and Offspring Sex Ratio in Captive Red Junglefowl (*Gallus gallus*)

TIMOTHY H. PARKER<sup>1</sup>

*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA*

**ABSTRACT.**—Maternal condition can affect reproductive investment in one or more ways. Captive female Red Junglefowl (*Gallus gallus*) that were heavier, controlling for tarsus length, produced larger eggs and initiated laying earlier, but did not produce more eggs per clutch. Maternal mass was also a positive predictor of offspring mass. That appears to re-

sult from the strong positive relationships between egg size and offspring mass. When the relationship between egg size and offspring mass was statistically controlled, maternal mass no longer predicted offspring mass. Mothers in better condition produced male-biased broods, as predicted when offspring condition depends on maternal condition and when male reproductive success is more dependent than female reproductive success on condition.

---

<sup>1</sup> Present address: Kansas Cooperative Fish and Wildlife Research Unit, 205 Leasure Hall, Kansas State University, Manhattan, Kansas 66506-3501, USA. E-mail: tparker@ksu.edu

**RESUMEN.**—La condición materna puede afectar la inversión reproductiva de una o más maneras. Las hembras cautivas de *Gallus gallus* que fueron más pe-

sadas, controlando por el largo del tarso, produjeron huevos más grandes y comenzaron a ponerlos antes, pero no produjeron más huevos por nidada. La masa materna también predijo positivamente la masa de la cría. Esto parece ser consecuencia de la fuerte asociación positiva entre el tamaño del huevo y la masa de la cría. Cuando la asociación entre el tamaño del huevo y la masa de la cría fue controlada estadísticamente, la masa materna dejó de predecir la masa de la cría. Las madres en mejor condición produjeron nidadas sesgadas hacia los machos, como se predice cuando la condición de la cría depende de la condición materna y cuando el éxito reproductivo del macho depende más que el éxito reproductivo de la hembra de la condición.

Relationship between parental condition and reproduction has been studied extensively (e.g. Sibly and Calow 1986, Meathrel 1991, Robb et al. 1992, Nilsson and Svensson 1993, Potti 1993, Smith et al. 1993, Williams 1996, Wiehn and Korpimaki 1997, Anderson and Alisauskas 2001). Parents with more resources might increase reproductive investment in several ways (Sibly and Calow 1986). In birds, initiation of egg laying, clutch size, egg size, and chick size can be affected by maternal condition (e.g. Robb et al. 1992, Potti 1993, Smith et al. 1993, Williams 1996).

In species where a male's reproductive success is limited by access to females, and a female's reproductive success is limited by the number of chicks she can rear, males in the best condition often experience greater reproductive success than females in the best condition. In such species, a mother capable of producing offspring of high quality could increase her fitness (her number of grand-offspring) by producing more sons (Trivers and Willard 1973, Bradbury and Blakey 1998). Mounting evidence suggests that adaptive alteration of the sex ratio occurs in some (e.g. Ligon and Ligon 1990, Ellegren et al. 1996, Nager et al. 1999, Albrecht 2000) but not all (Sheldon 1998, Saino et al. 1999) bird species.

I studied reproductive investment and sex ratio as functions of maternal condition in Red Junglefowl (*Gallus gallus*). I predicted a positive relationship between maternal mass (adjusted for body size) and initiation of egg laying, clutch size, egg size, and offspring mass. To further understand the reproductive correlates of maternal condition in this species, I investigated the relationship between egg size and offspring mass. Finally, I predicted that if chick mass was positively affected by maternal mass, heavier females would produce broods biased towards males, the sex with the higher reproductive variance (Collias and Collias 1996). By investigating those issues in a controlled laboratory setting, I was able to eliminate confounding factors such as posthatching maternal effects, differential exposure to predators, and varying access to food.

TABLE 1. Mean (SE) for number of male and female chicks per family before and after culling chicks from large families at age 11 weeks (see text).

	Before	After
Male	3.0 (0.15)	2.4 (0.08)
Female	3.3 (0.15)	2.5 (0.07)

*Methods.*—Red Junglefowl, the ancestor of the domestic chicken (*Gallus gallus domesticus*), produce precocial young and only females provide parental care. Reproductive behavior in this population of Red Junglefowl has been studied extensively (e.g. Ligon et al. 1990; Zuk et al. 1990, 1995; Johnson et al. 1993; Ligon and Zwartjes 1995; Collias and Collias 1996). Zuk et al. (1990) describe the origin of the research flock.

As part of a study of inheritance of paternal ornamentation and maternal reproductive investment, female Red Junglefowl were bred under the following conditions: females were housed with vasectomized males and were artificially inseminated. This article does not consider effects of actual (sperm donor) or perceived (sterile male consort) paternity. Female condition was independent of these treatments, and accounting for them did not change the results of analyses presented here. Results of paternity treatments are presented elsewhere.

All females were first-year, naïve (never mated) individuals. Prior to the experiment, females were housed in all-female flocks. Females entered the experiment as soon as possible after laying their first egg, which in most cases was only a few days after initiation of laying. Each experimental female was housed in its own outdoor breeding pen (0.63 × 1.3 m) with a straw-filled nest bowl and *ad libitum* food (Purina Layena, 16% protein, Layena, Purina Mills, St. Louis, Missouri) and water. When incubation began, males were removed from the pens of females.

After hatching, chicks stayed in the breeding pen with their mother. Chicks were provided *ad libitum* with water and a moderate protein chicken feed (Pullet Start-n-Grow, 16% protein, unmedicated; Oñate Feed Mill, Albuquerque, New Mexico), thus it is unlikely that chick condition was affected by maternal provisioning behavior. When chicks were three weeks old, mothers were removed from breeding pens. At five weeks, chicks were removed from the breeding pens and placed in large outdoor aviaries in equal density same-age flocks of up to 60 individuals. Because of space constraints, chicks from large families were selected at random for culling at 11 weeks of age. Family size was reduced (Table 1) to no more than three male and three female chicks. Within a family, no chicks of a given sex were culled if there were three or fewer chicks of that sex in the brood.

TABLE 2. Results of linear regression analyses comparing hen mass and tarsus length to variables associated with reproductive allocation. Reported are partial  $r^2$  and  $P$ -values for effects of hen mass.

Dependent variable	Partial $r^2$	$P$	$n$
Clutch size	0.01	0.433	66
Female chick mass age 2 days	0.31	<0.0001 <sup>a</sup>	53
Female chick mass age 10 weeks	0.10	0.046	53
Female chick mass age 26 weeks	0.07	0.048	53
Male chick mass age 2 days	0.23	0.002 <sup>a</sup>	52
Male chick mass age 10 weeks	0.17	0.010	52
Male chick mass age 26 weeks	0.08	0.054	52
Male chick comb age 26 weeks	0.13	0.009	52

Critical  $P$ -value for other analyses is 0.05.

<sup>a</sup> Chick condition results significant after Bonferroni correction for multiple (6) comparisons.

Measurements were taken of hens, eggs, and chicks as follows: mass was measured to the nearest gram on an electronic balance. All lengths were measured to the nearest tenth of a millimeter by use of dial calipers. Mass and right tarsus length were measured for all hens prior to initiation of the breeding season. Number of eggs laid by each hen and length and width of each egg was recorded. Sex of each chick at six weeks of age was recorded, when sexual plumage dichromatism became unambiguous. Chick mortality from 0–6 weeks was low (6% [22 of 369] of all chicks hatched). Mass and length of the right tarsus of each chick was recorded at regular intervals through week 26, at which time comb length of male chicks was recorded (from the most anterior portion of the comb above the bill to the longest posterior tine of the comb).

To determine relationship between hen condition prior to reproduction and reproductive allocation, separate linear regression analyses were conducted with hen mass as the independent variable, hen tarsus length as a covariate, and the following dependent variables: clutch size, mean egg volume (volume =  $0.519 \times \text{length} \times \text{width}^2$ ; Romanoff and Romanoff 1949) per hen, approximate date of first egg laid, and proportion of male chicks in a brood. The date of first egg laid is approximate because hens housed in groups were cycled through individual pens to detect laying, and therefore over a week could pass before detection of laying by a particular hen. Sample size was lower for the sex-ratio test because eight nests failed to hatch any chicks and in one nest all chicks died prior to development of sexual dichromatism.

I also used hen mass adjusted for body size (by including hen tarsus length as a covariate) prior to reproduction in linear regression to predict mean chick mass at age 2 days, 10 weeks, and 26 weeks, and mean comb length of male chicks at 26 weeks. Because they exhibited different growth trajectories,

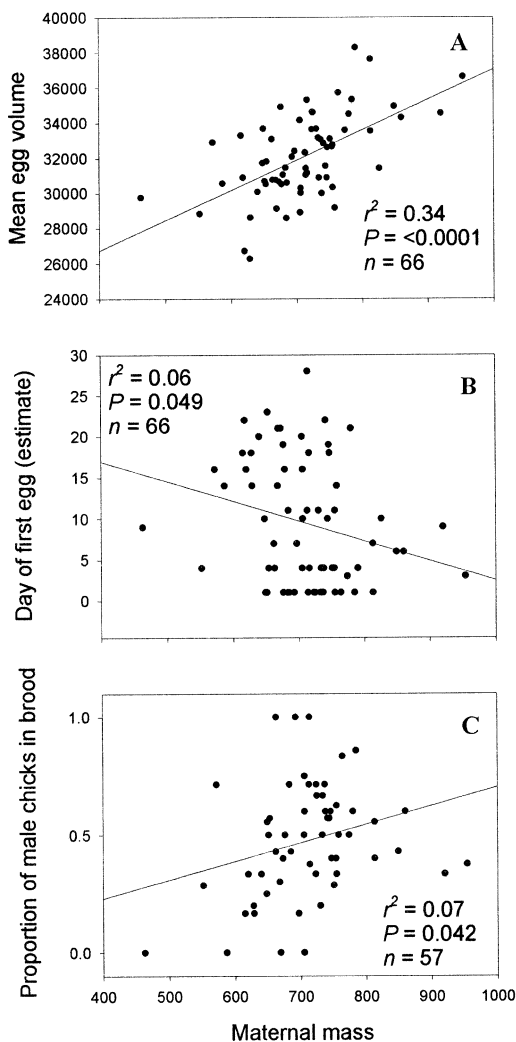


FIG. 1. Relationships (including partial  $r^2$  and  $P$ -value) between maternal mass (grams) and (A) mean egg volume per mother, (B) estimated date of first egg production, and (C) proportion of male chicks in a brood.

male and female chicks were analyzed separately. Mean egg volume per clutch was added to that model as another predictor of mean chick mass and comb length per brood. That allowed me to determine the relative extents to which egg volume and hen mass and tarsus explained variation in chick mass. Sample sizes differ between male and female chick mass analyses because several broods contained only male or only female chicks.

**Results.**—Maternal mass did not influence clutch size (Table 2), but was a significant predictor of egg size, chick sex ratio, and onset of laying (Fig. 1). Maternal mass was also significantly positively related

TABLE 3. Results of linear regression analyses comparing egg volume, hen mass, and hen tarsus length to chick mass and comb length. Reported are partial  $r^2$  and  $P$ -values for the effects of egg volume and hen mass.

Dependent variable	Egg volume		Hen mass		$n$
	Partial $r^2$	$P$	Partial $r^2$	$P$	
Female chick mass age 2 days	0.66	<0.0001 <sup>a</sup>	0.01	0.429	53
Female chick mass age 10 weeks	0.27	0.001 <sup>a</sup>	0.00	0.863	53
Female chick mass age 26 weeks	0.18	0.016	0.00	0.798	53
Male chick mass age 2 days	0.53	<0.0001 <sup>a</sup>	0.00	0.950	52
Male chick mass age 10 weeks	0.22	0.028	0.03	0.373	52
Male chick mass age 26 weeks	0.15	0.051	0.00	0.654	52
Male chick comb age 26 weeks	0.14	0.124	0.02	0.197	52

Critical  $P$ -value for comb analysis is 0.05.

<sup>a</sup> Chick condition results significant after Bonferroni correction for multiple (6) comparisons.

to chick mass (Table 2). Relationship between maternal mass and chick mass appears have been mediated via the strong relationship between egg size and chick mass, because when the relationship between egg size and chick mass was controlled by including egg size as a predictor variable, maternal condition no longer predicted chick mass (Table 3). Maternal mass was a significant predictor of comb length of male offspring (Table 2), though as with chick mass, maternal mass no longer predicted comb length after controlling for egg size (Table 3).

*Discussion.*—These data are from captive birds that always had ready access to food and water. Nevertheless, condition varied among individual mothers, thus it is reasonable to ask whether that condition affected their reproductive tactics. Variation in condition could be due to environmental challenges, or more likely, interactions between genotype and environmental challenges. Those challenges could have been (1) stress induced by dominance interaction in flocks (Parker et al. 2002) prior to the experiment, (2) pathogens, or (3) some other factors.

Heavier female junglefowl produced larger eggs and began laying earlier, but did not lay more eggs per clutch. In nature, timing of reproduction is often affected by parental condition or food availability (e.g. Pietiainen and Kolunen 1993, Winkler and Allen 1995). In some species, condition or food availability affects egg number (e.g. Haywood and Perrins 1992, Bolton et al. 1993, Erikstad et al. 1993, Pietiainen and Kolunen 1993, Selman and Houston 1996) or egg volume (e.g. Smith et al. 1993, Selman and Houston 1996, Williams 1996, Ramsay and Houston 1997), though it is not unusual to find one or more of those variables unaffected by condition or food availability (e.g. Williams 1996, Ramsay and Houston 1997).

The positive relationship between maternal mass and chick mass could be due to maternal egg investment, inheritance of maternal condition, or both. Junglefowl chicks fed themselves on *ad libitum* food within a day of hatching, thus the role wild mothers play in locating food for their chicks was minimal

here; that is, under these conditions, maternal provisioning behavior was unlikely to have significantly affected chick condition. Egg size is typically a good predictor of chick condition in precocial birds (Williams 1994), and was probably the principle factor relating maternal mass to chick mass because after statistically controlling for egg size, maternal mass no longer showed a relationship to chick mass. However, I cannot rule out the possibility of maternal genetic effects, because controlling for egg size would mask a genetic effect if there were a strong relationship between maternal genetic quality and egg size.

The biased sex ratios in this study are predicted by both evolutionary theory and empirical evidence. Maternal mass was correlated with male offspring mass and comb length. Male condition has a strong positive effect on attractiveness (comb length; T. H. Parker unpubl. data), which in turn predicts dominance rank (Parker et al. 2002) and thus probably male reproductive success. Male Red Junglefowl exhibit higher variance in reproductive success than do females (Collias and Collias 1996), and thus a top-condition male can produce more offspring than a top-condition female. Therefore, female junglefowl in better condition should be able to maximize their number of grandchildren by producing a greater proportion of sons, because those high-quality sons will be better able to translate their good condition into reproductive success. Because I did not sex dead embryos or chicks that died at a young age, I cannot conclusively demonstrate that the observed trend was due to a sex bias at laying or hatching. However, mounting evidence supports adaptive sex bias at laying and hatching in birds (e.g. Sheldon 1998, Nager et al. 1999, Sheldon et al. 1999), as predicted by Trivers and Willard (1973). Another factor that could influence chick condition—and thus chick sex ratio—might be clutch size. However, clutch size did not predict offspring mass at any age, nor did it predict sex ratio (data not shown).

*Acknowledgments.*—I thank J. D. Ligon, the chair of my Ph.D. committee, along with committee members

A. Kodric-Brown and R. Thornhill, for advice and cooperation throughout the project. J. Rosenfield and anonymous reviewers provided helpful comments on an earlier version of this manuscript. J. Abbott, M. Edgar, J. Mayfield, S. Mercen, E. O'Keefe, N. Parker, G. Quintana, and Y. Romero assisted with animal care, husbandry, and data collection. R. Ricci and F. Gurule were consistently helpful in facilitating animal care. Funding for this project came from a National Science Foundation Grant (IBN-0072995), a Sigma Xi Grant-in-Aid of Research, the American Ornithologists' Union, and University of New Mexico sources including the Department of Biology's Graduate Research Allocation Committee and Grove Scholarship Committee, the Graduate and Professional Student Association's Student Research Allocation Committee, and the Office of Graduate Studies' Research, Planning, and Travel fund. The research presented here was described in Animal Research Protocol no. 9817-B approved on 25 September 1998 by the Institutional Animal Care and Use Committee of the Main Campus of the University of New Mexico.

## LITERATURE CITED

- ALBRECHT, D. J. 2000. Sex ratio manipulation within broods of House Wrens, *Troglodytes aedon*. *Animal Behaviour* 59:1227-1234.
- ANDERSON, V. R., AND R. T. ALISAUSKAS. 2001. Egg size, body size, locomotion, and feeding performance in captive King Eider ducklings. *Condor* 103:195-199.
- BOLTON, M., P. MONAGHAN, AND D. C. HOUSTON. 1993. Proximate determination of clutch size in Lesser Black-backed Gulls: The roles of food-supply and body condition. *Canadian Journal of Zoology* 71:273-279.
- BRADBURY, R. R., AND J. K. BLAKEY. 1998. Diet, maternal condition, and offspring sex ratio the Zebra Finch *Poephila guttata*. *Proceedings of the Royal Society of London, Series B* 265:895-899.
- COLLIAS, N. E., AND E. C. COLLIAS. 1996. Social organization of a Red Junglefowl *Gallus gallus* population related to evolution theory. *Animal Behaviour* 51:1337-1354.
- ELLEGREN, H., L. GUSTAFSSON, AND B. C. SHELDON. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proceedings of the National Academy of Sciences USA* 93:11723-11728.
- ERIKSTAD, K. E., J. O. BUSTNES, AND T. MOUM. 1993. Clutch-size determination in precocial birds: A study of the Common Eider. *Auk* 110:623-628.
- HAYWOOD, S., AND C. M. PERRINS. 1992. Is clutch size in birds affected by environmental-conditions during growth? *Proceedings of the Royal Society of London, Series B* 249:195-197.
- JOHNSON, K., R. THORNHILL, J. D. LIGON, AND M. ZUK. 1993. The direction of mothers' and daughters' preferences and the heritability of male ornaments in Red Junglefowl (*Gallus gallus*). *Behavioral Ecology* 4:254-259.
- LIGON, J. D., AND S. H. LIGON. 1990. Female-biased sex-ratio at hatching in the Green Woodhoopoe. *Auk* 107:765-771.
- LIGON, J. D., R. THORNHILL, M. ZUK, AND K. JOHNSON. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in Red Junglefowl. *Animal Behaviour* 40:367-373.
- LIGON, J. D., AND P. W. ZWARTJES. 1995. Female Red Junglefowl choose to mate with multiple males. *Animal Behaviour* 49:127-135.
- MEATHREL, C. E. 1991. Variation in eggs and the period of rapid yolk deposition of the Silver Gull *Larus novaehollandiae* during a protracted laying season. *Journal of Zoology (London)* 223:501-508.
- NAGER, R. G., P. MONAGHAN, R. GRIFFITHS, D. C. HOUSTON, AND R. DAWSON. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Sciences USA* 96:570-573.
- NILSSON, J. A., AND E. SVENSSON. 1993. Causes and consequences of egg mass variation between and within Blue Tit clutches. *Journal of Zoology (London)* 230:469-481.
- PARKER, T. H., R. KNAPP, AND J. A. ROSENFELD. 2002. Social mediation of sexually selected ornamentation and steroid hormone levels in male junglefowl. *Animal Behaviour* 64:in press.
- PIETIAINEN, H., AND H. KOLONEN. 1993. Female body condition and breeding of the Ural Owl *Strix uralensis*. *Functional Ecology* 7:726-735.
- POTTI, J. 1993. Environmental, ontogenic, and genetic variation in egg size of Pied Flycatchers. *Canadian Journal of Zoology* 71:1534-1542.
- RAMSAY, S. L., AND D. C. HOUSTON. 1997. Nutritional constraints on egg production in the Blue Tit: A supplementary feeding study. *Journal of Animal Ecology* 66:649-657.
- ROBB, L. A., K. MARTIN, AND S. J. HANNON. 1992. Spring body condition, fecundity and survival in female Willow Ptarmigan. *Journal of Animal Ecology* 61:215-223.
- ROMANOFF, A. L., AND A. J. ROMANOFF. 1949. *The Avian Egg*. John Wiley and Sons, New York.
- SAINO, N., H. ELLEGREN, AND A. P. MØLLER. 1999. No evidence for adjustment of sex allocation in relation to paternal ornamentation and paternity in Barn Swallows. *Molecular Ecology* 8:399-406.
- SELMAN, R. G., AND D. C. HOUSTON. 1996. The effect of prebreeding diet on reproductive output in Zebra Finches. *Proceedings of the Royal Society of London, Series B* 263:1585-1588.
- SHELDON, B. C. 1998. Recent studies of avian sex ratios. *Heredity* 80:397-402.

- SHELDON, B. C., S. ANDERSSON, S. C. GRIFFITH, J. ORNBORG, AND J. SENDECKA. 1999. Ultraviolet colour variation influences Blue Tit sex ratios. *Nature* 402:874–877.
- SIBLY, R. M., AND P. CALOW. 1986. *Physiological Ecology of Animals: An Evolutionary Approach*. Blackwell Scientific, Oxford.
- SMITH, H. G., U. OTTOSSON, AND T. OHLSSON. 1993. Interclutch variation in egg mass among starlings *Sturnus vulgaris* reflects female condition. *Ornis Scandinavica* 24:311–316.
- TRIVERS, R. L., AND D. E. WILLARD. 1973. Natural selection of parent ability to vary the sex ratio of offspring. *Science* 179:90–92.
- WIEHN, J., AND E. KORPIMAKI. 1997. Food limitation on brood size: Experimental evidence in the Eurasian Kestrel. *Ecology* 78:2043–2050.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews of the Cambridge Philosophical Society* 69:35–59.
- WILLIAMS, T. D. 1996. Intra- and inter-individual variation in reproductive effort in captive breeding Zebra Finches (*Taeniopygia guttata*). *Canadian Journal of Zoology* 74:85–91.
- WINKLER, D. W., AND P. E. ALLEN. 1995. Effects of handicapping on female condition and reproduction in Tree Swallows (*Tachycineta bicolor*). *Auk* 112:737–747.
- ZUK, M., T. S. JOHNSEN, AND T. MACLARTY. 1995. Endocrine-immune interactions, ornaments and mate choice in Red Junglefowl. *Proceedings of the Royal Society of London, Series B* 260:205–210.
- ZUK, M., R. THORNHILL, J. D. LIGON, K. JOHNSON, S. AUSTAD, S. H. LIGON, N. W. THORNHILL, AND C. COSTIN. 1990. The role of male ornaments and courtship behavior in female mate choice of Red Junglefowl. *American Naturalist* 136:459–473.

Received 9 July 2001, accepted 26 March 2002.

Associate Editor: B. Loiselle

---