The Condor 89:798–803

SEXUAL DIMORPHISM IN EGG SIZE AND IMPLICATIONS REGARDING FACULTATIVE MANIPULATION OF SEX IN MOUNTAIN WHITE-CROWNED SPARROWS[1]

PAUL S. MEAD,[2] MARTIN L. MORTON,[3] AND BRIAN E. FISH
Department of Biology, Occidental College, Los Angeles, CA 90041

Abstract. The volume of male eggs in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) was slightly larger than that of female eggs in every year of a 5-year study. The volume difference was highly significant ($P < 0.01$) when data for all years were combined. Male nestlings also grew faster than female siblings. Natural history observations on adults suggest that reproductive success is more variable in male than in female White-crowned Sparrows. Taken together, these data are consistent with facultative manipulation of offspring sex as proposed under the Trivers and Willard hypothesis (1973). In avian species it may be necessary when testing this hypothesis to consider the relationship between sex and parental investment for individual offspring rather than focusing solely on differences between broods.

Key words: White-crowned Sparrow; Zonotrichia leucophrys; *egg size; facultative manipulation; parental investment; sex control; sexual dimorphism.*

INTRODUCTION

Charles Darwin (1871) was openly perplexed by the tendency of some species to produce broods of almost exclusively one sex. Since his time it has been discovered that a number of animals not only control the sex of their offspring but do so in a manner likely to increase their overall reproductive fitness (Clutton-Brock 1982). This ability for "facultative manipulation"of offspring sex is best known among invertebrates where it is selected for by intense local mate competition as well as other factors (Hamilton 1967, Werren 1980, Charnov et al. 1981, Herre 1985). Trivers and Willard (1973) have proposed conditions under which selection will favor facultative manipulation among vertebrates, yet support for their hypothesis has remained elusive (Myers 1978, Williams 1979, Clutton-Brock 1982, Harmsen and Cooke 1983).

The Trivers-Willard hypothesis is based on the assumption that parental investment influences offspring quality and ultimate reproductive success. It further assumes that reproductive success varies more for offspring of one sex than the other. When these conditions are met, parents may increase their reproductive fitness by altering the sex of their offspring according to their ability to invest. For example, in a species where a single dominant male will inseminate several females, mothers able to produce particularly robust offspring will have more of their genes present in the subsequent generation if they produce sons. Conversely, those producing less robust offspring will benefit most by producing females since daughters need not compete to the same degree for mates.

Because of the way it was originally stated, previous tests of the Trivers-Willard hypothesis have generally focused on sex ratios in broods produced by females under varying environmental circumstances (Trivers and Willard 1973, Clutton-Brock 1982). Unfortunately, such an approach is likely to be insensitive. Female "condition" may be difficult to define and enormous sample sizes are required before valid conclusions can be derived from sex ratio data (Williams 1979, Harmsen and Cooke 1983). More importantly, this approach minimizes the differences in quality which may exist between siblings from the same brood. In avian species offspring quality can vary widely within clutches as a function of both egg size and hatching times (Kendeigh 1941; Gibb 1950; Lack 1954; Kendeigh et al. 1956; Ricklefs 1965; Klomp 1970; Parsons 1970, 1975; O'Connor 1975; Pinkowski 1975; Howe 1976; Ryden 1978; Ojanen et al. 1981; Zach 1982). Thus, while Trivers and Willard stated their hypothesis in terms of sex ratios of

---

[1] Received 9 November 1986. Final acceptance 15 April 1987.

[2] Present address: Dartmouth-Hitchcock Medical Center, Hanover, NH 03756.

[3] To whom reprint requests should be sent.

entire broods, in avian species their argument may be more appropriately evaluated by relating sex to parental investment for individual offspring.

Of the many forms of avian parental investment, egg size is one that is both easily quantified and well known to influence offspring quality. Egg size has been correlated with hatchling size, nestling growth rates, and nestling survival in a variety of species (Parsons 1970, 1975; Nisbett 1973; Schifferli 1973; O'Connor 1975; Howe 1976; Nolan and Thompson 1978; Pinkowski 1979; Bancroft 1984). In turn, egg size is influenced by a number of genetic and environmental factors and commonly varies both within and between clutches (Kendeigh 1941; Klomp 1970; Howe 1976; Ryden 1978; Ojanen et al. 1979, 1981; Zach 1982).

Although White-crowned Sparrows (*Zonotrichia leucophrys*) are principally monogamous (DeWolfe 1968), there are several lines of evidence to suggest that reproductive success varies more for males than for females. We have documented several cases of polygyny as indicated by adult males that were feeding nestlings at two nests simultaneously, and we have often identified "floater" (unmated) males but not females in our study population (Morton, unpubl. data). Males also have a lower recruitment rate to the breeding population and longer maximum life spans, suggesting that on average breeding males may outlive their mates to breed with another female (Baptista and Morton 1982; Morton, unpubl. data). Finally, cuckoldry appears to be common in this population (Sherman and Morton, unpubl. data) and should selectively increase the variance in male reproductive success (Trivers 1978). Under these circumstances, the Trivers-Willard hypothesis predicts that females producing better than average offspring will skew the sex ratio of their brood toward males (Trivers and Willard 1973). Extending this reasoning to individual eggs, we predict that larger eggs should become males and smaller eggs females.

METHODS

This study was conducted over a 5-year period in meadows near Tioga Pass, Mono County, California. Adult Mountain White-crowned Sparrows (*Z. l. oriantha*) were routinely trapped and banded with both U.S. Fish and Wildlife Service bands and color bands. During the egg-laying period, nests were visited daily and the eggs marked with indelible ink according to laying order. Measurements of egg length and breadth were made to the nearest 0.01 mm with calipers at various times during the incubation period and their volumes calculated according to Hoyt's (1979) formula. Egg weight was not measured because of its tendency to vary over the course of incubation (Ar and Rahn 1980, Carey 1986). To determine the relative size of eggs within the clutch, egg volumes were standardized by subtracting the mean volume of the clutch from the volume of each egg and dividing the sum by the standard error in volume for that clutch. Nests were visited frequently during hatching, allowing chicks to be identified according to the specific egg from which they hatched. The yield in terms of determining which chick emerged from which egg was increased during the last 2 years of the study by applying a longitudinally-oriented piece of thread around each egg with small amounts of glue. This helped restrain chicks within their respective eggs during the interval between visits (see Mayoh and Zach 1985). Hatchlings were toenail-clipped and later banded to assure identity. Data on chicks for whom egg identity could not be absolutely determined were not used.

Nestlings were weighed to the nearest 0.1 g at 1 and 8 days of age using a triple beam balance. The sex of each nestling was determined just prior to fledging by laparotomy and direct visualization of the gonads.

Because *Z. l. oriantha* chicks are often fed within a few minutes of hatching, it is difficult to evaluate the relationship between egg volume and hatchling size in the field. For this reason, eggs were collected from a conspecific population (*Z. l. nuttalli*) breeding near Lompoc, California, measured as above, and hatched in the laboratory. Chicks from these eggs were weighed to the nearest 0.01 g on a Mettler balance within 30 min of hatching.

RESULTS AND DISCUSSION

A comparison of egg volumes shows that male eggs were significantly larger than female eggs both between (one-tailed $t = 2.44$, $P < 0.01$) and within clutches (one-tailed $t = 2.08$, $P < 0.02$; Fig. 1). Mean egg volume was larger for males in each of the 5 years of our study. This difference was statistically significant when data for all years were combined but not when comparisons were limited to individual years (Table 1). There were no significant year-to-year differences in overall

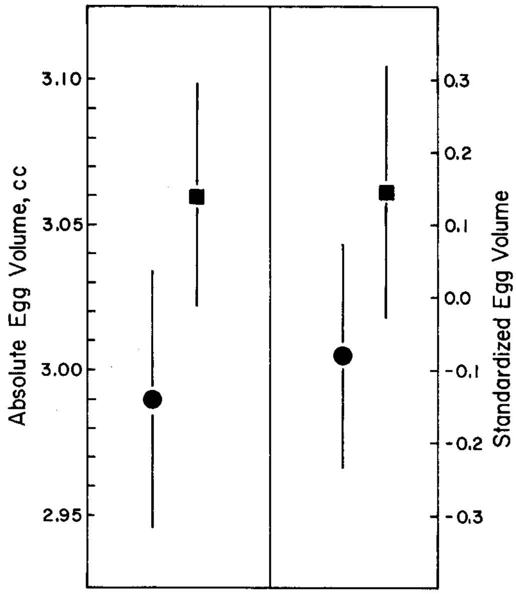

FIGURE 1. Mean absolute (between clutches) and standardized volumes (within clutches) of male (squares) and female (circles) Mountain White-crowned Sparrow eggs. Lines indicate ±2 SE. Sample sizes are males = 147, females = 147.

egg volume and sex ratio which might serve to bias the between-clutch data.

In terms of the Trivers-Willard (1973) hypothesis, differences in egg size have significance only to the extent that they reflect differences in offspring quality and ultimate reproductive success. Unfortunately such parameters are exceedingly difficult to test in the field. Instead we must make use of the indirect argument that greater egg size for males cannot be related to ultimate reproductive success if egg size does not correlate with hatchling size, or if female nestlings grow faster than their male siblings thereby countering the initial advantages of larger egg size.

TABLE 2. Mean body weights (g) of 17 matched pairs of male-female White-crowned Sparrow siblings at 2 and 8 days of age.

Age (days)	Males		Females		
	Mean	SD	Mean	SD	P
2	3.8	1.00	3.8	0.98	>0.05
8	21.5	1.35	20.4	1.10	<0.001

Egg volume has been correlated with hatchling size and subsequent growth in a number of altricial species (Parsons 1970, 1975; Nisbett 1973; Schifferli 1973; O'Connor 1975; Howe 1976; Nolan and Thompson 1978; Bancroft 1984). This was shown also in our data. There was a strong positive correlation between egg volume and hatchling weight in 10 laboratory-hatched *Z. l. nuttalli* ($r^2 = 0.90$, $P < 0.01$).

To assess relative growth rates of male and female nestlings at Tioga Pass, we selected 17 pairs of male and female siblings who, because of different hatching times and egg sizes, were of equal size on Day 2 of the nestling period. Six days later all 17 males were larger than their sisters and their mean weight was significantly greater (matched $t = 5.40$, $P < 0.001$; Table 2). Sexual differences in growth rates would thus be expected to enhance rather than reduce any size differences between male and female hatchlings.

Several factors could potentially bias our results. In White-crowned Sparrows, as in many birds, average egg size tends to increase with order of laying (Mead and Morton 1985). A tendency for later-laid eggs to be male could secondarily result in a larger average size for male eggs. When we compared egg sex with laying order for all eggs in which both were known, however, there was no tendency for eggs laid later in the clutch to be male ($\chi^2 = 2.64$, $P > 0.05$;

TABLE 1. Mean egg volume (cc) for male, female, and all White-crowned Sparrow eggs measured. *P* values refer to differences between mean volumes of male and female eggs.

Year	Egg volume, $\bar{x}$ ± SD (n)			
	All eggs	Males	Females	P
1981	2.990 ± 0.220 (118)	2.978 ± 0.190 (27)	2.896 ± 0.269 (20)	>0.05
1982	2.990 ± 0.240 (151)	3.084 ± 0.213 (29)	3.030 ± 0.220 (43)	>0.05
1983	2.935 ± 0.236 (176)	3.011 ± 0.237 (29)	2.965 ± 0.232 (29)	>0.05
1984	2.985 ± 0.270 (112)	3.124 ± 0.256 (41)	3.000 ± 0.299 (41)	>0.05
1985	3.040 ± 0.250 (67)	3.059 ± 0.221 (21)	3.019 ± 0.304 (14)	>0.05
All years		3.060 ± 0.232 (147)	2.990 ± 0.262 (147)	<0.01

Table 3). Indeed, there were more males than females among the first two eggs laid.

In some nests it was not possible to sex every chick. This too could bias our results if there was a tendency not to sex either females from large eggs or males from small eggs. Several factors argue against such bias. First, mean volume was nearly identical for sexed and unsexed eggs, 3.02 ± 0.20 cc and 3.01 ± 0.22 cc, respectively. Second, when considered as a group, the reasons for failing to sex eggs are unlikely to have selected for eggs that were at once both a particular size and sex. There were 58 unsexed eggs from clutches in which other chicks were sexed. The numbers and reasons for not sexing are as follows: failed to hatch (21), chicks disappeared from nest before age of possible fledging (11), nest subject to partial depredation (7), chick could not be associated with a specific egg (7), chicks fledged before laparotomy (5), laparotomy was inconclusive because of bleeding (5), egg was broken during handling (2).

Previous reports in the avian literature have varied widely in their support of the Trivers-Willard hypothesis. Field studies have demonstrated seasonal variations in primary sex ratio of both Common Grackles, *Quiscalus quiscula* (Howe 1977), and Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus* (Patterson and Emlen 1980). In each case the observed trends were postulated to coincide with seasonal changes in food supply. Ryder (1983) has reported nonrandom distribution of the sexes according to laying order in clutches of Ring-billed Gulls (*Larus delawarensis*). Ankney (1982) has published similar findings for Lesser Snow Geese (*Chen caerulescens*), but these could not be confirmed by a larger study (Cooke and Harmsen 1983). On more theoretical grounds, Myers (1978) has criticized the Trivers-Willard hypothesis for failing to consider the costs of facultative manipulation. Although adjustment of postconception sex ratios through sex-specific mortality may indeed be costly (Burley 1982), adjustment of the primary sex ratio need not be. In birds the female is the heterogamete (Sturkie 1986), and sex is determined when the follicle undergoes meiosis. Because one-half of the ovum's genome is normally discarded in the polar body, nonrandom segregation of sex chromosomes during meiosis could allow for manipulation of offspring sex without significant cost. Finally, it has been argued that facultative manipulation should result in the production of unisex clutches (Williams 1979, Fiala 1981a). Clearly field data for birds have failed to confirm this prediction (Harmsen and Cooke 1983). It may be, however, that the assumption underlying this prediction is in error. Unisex clutches can be expected if offspring quality within a clutch will be consistently better or worse than the mean for the population. In fact, as already noted, offspring quality varies widely between siblings from the same clutch.

TABLE 3. Number of male and female eggs by laying order in four-egg clutches of Mountain White-crowned Sparrows.

	Laying order	
	Eggs 1 and 2	Eggs 3 and 4
Males	50	52
Females	32	54

Our data indicate that in White-crowned Sparrows male eggs are larger than female eggs. To our knowledge, this is the first demonstration of sexual dimorphism in avian egg size. We also report that larger eggs produce larger hatchlings and that male nestlings grow faster than females. These latter findings have been documented in a number of other species (Parsons 1970, 1975; Nisbett 1973; Schifferli 1973; Howe 1976; Nolan and Thompson 1978; Fiala 1981b; Bancroft 1984), and together they support the suggestion that larger egg size may be of some significance in determining adult quality. Our findings are not without contradiction. Weatherhead (1985) has similarly examined egg size and sex in Red-winged Blackbirds (*Agelaius phoeniceus*). Interestingly, he too found that male eggs were larger than female eggs in four-egg clutches in both years of his study. As in our study, the degree of difference was not statistically significant in any one year. Our analysis differs in that we combined data from several years.

While our results can be predicted on the basis of the Trivers-Willard hypothesis, they should not necessarily be taken as evidence for facultative manipulation of sex at this time. First, it is essential to measure the effect in nature, if any, that small differences in egg size have on adult quality. The task of relating parental investment to ultimate reproductive success of offspring remains a major challenge for all tests of this hypothesis. Second, there is much to be learned about the mechanisms of sex determination and egg provisioning. Specifically, it is necessary to determine whether the observed size difference reflects manipulation of egg sex according to provisioning or simply greater provisioning of male eggs in a species, such as White-crowned Sparrows, where adult males are larger. Data currently available indicate that in birds sex determination occurs when the follicle undergoes meiosis about 3 to 4 hr before ovulation (Olsen and Fraps 1950, Sturkie 1986). At this time the yolk of the egg has been deposited (Lehrman 1961; Gilbert 1970, 1971). In at least one altricial and several precocial species, yolk size is proportional to final egg size (Romanoff and Romanoff 1949, Parsons 1970, Howe 1978, Ricklefs et al. 1978), suggesting that final egg size is in effect determined prior to egg sex. If this is true in White-crowned Sparrows, our results would suggest manipulation of the sex-determining meiotic division (see Howe 1977 and Ankney 1982 for discussions of nonrandom sex determination). Alternately, there could be differential deposition of albumin in male eggs after ovulation. This deceptively simple explanation would require transcription and translation of a sex-specific gene, along with a differential response by the oviduct, all before the first cleavage of the zygote (Olsen 1942). If it occurs, such an early gene expression might prove of interest to those studying gene expression during development (Müller et al. 1984, Rubin et al. 1986).

Finally, we suggest that discrepancies within and between studies of the Trivers-Willard hypothesis may be due in part to excessive emphasis on sex ratios and to the neglect of factors which operate within each brood to modify the reproductive potential of siblings. Emphasizing the latter, we have obtained results that are consistent with the hypothesis. Many factors, operating simultaneously and in complex ways, may influence the reproductive success of offspring (Burley 1982). It may be essential, therefore, to consider simultaneously such factors as egg size, hatching order, time of season, and parental attractiveness (Burley 1981, 1982; Immelmann et al. 1982, Thissen and Martin 1982) when testing for facultative manipulation.

ACKNOWLEDGMENTS

For assistance in the field and laboratory we thank M. Alego Gilsdorf, A. Lee, M. Pereyra, and S. Warschaw. We thank T. Clutton-Brock, R. Mead, K. Rassbach, and P. Sherman for their comments on an earlier draft of this manuscript. Funding was provided by a National Science Foundation Graduate Fellowship and Occidental College.

LITERATURE CITED

ANKNEY, C. D. 1982. Sex ratio varies with egg sequence in Lesser Snow Geese. Auk 99:662–666.

AR, A., AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. Am. Zool. 20:373–384.

BANCROFT, G. T. 1984. Patterns of variation in size of Boat-tailed Grackle *Quiscalus major* eggs. Ibis 126:496–509.

BAPTISTA, L. F., AND M. L. MORTON. 1982. Song dialects and mate selection in Montane White-crowned Sparrows. Auk 99:537–547.

BURLEY, N. 1981. Sex ratio manipulation and selection for attractiveness. Science 211:721–722.

BURLEY, N. 1982. Facultative sex-ratio manipulation. Am. Nat. 120:81–107.

CAREY, C. 1986. Tolerance of variation in eggshell conductance, water loss, and water content by red-winged blackbird embryos. Physiol. Zool. 59:109–122.

CHARNOV, E. L., R. L. LOS-DEN HARTOGH, W. T. JONES, AND J. VAN DEN ASSEM. 1981. Sex ratio evolution in a variable environment. Nature 289:27–33.

CLUTTON-BROCK, T. H. 1982. Sons and daughters. Nature 298:11–12.

COOKE, F., AND R. HARMSEN. 1983. Does sex ratio vary with egg sequence in Lesser Snow Geese. Auk 100:215–217.

DARWIN, C. 1871. The descent of man, and selection in relation to sex. John Murray, London.

DEWOLFE, B. B. 1968. *Zonotrichia leucophrys oriantha*: Mountain White-crowned Sparrow, p. 1338–1343. *In* O. L. Austin [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237

FIALA, K. L. 1981a. Sex ratio constancy in the red-winged blackbird. Evolution 35:898–910.

FIALA, K. L. 1981b. Reproductive cost and the sex ratio in red-winged blackbirds, p. 198–214. *In* R. D. Alexander and D. W. Tinkle [eds.], Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

GIBB, J. 1950. The breeding biology of the Great and Blue titmice. Ibis 92:507–539.

GILBERT, A. B. 1970. Yolk deposition in the chicken oocyte and its relationship with ovulation. J. Reprod. Fertil. 23:539–540.

GILBERT, A. B. 1971. The ovary, p. 1163–1708. *In* D. J. Bell and B. M. Freeman [eds.], Physiology and biochemistry of the domestic fowl. Vol. 3. Academic Press, New York.

HAMILTON, W. D. 1967. Extraordinary sex ratios. Science 156:477–488.

HARMSEN, R., AND F. COOKE. 1983. Binomial sex-ratio distribution in the Lesser Snow Goose: a theoretical enigma. Am. Nat. 121:1–8.

HERRE, E. A. 1985. Sex ratio adjustment in fig wasps. Science 228:896–898.

HOWE, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57:1195–1207.

Howe, H. F. 1977. Sex-ratio adjustment in the Common Grackle. Science 198:744–746.

Howe, H. F. 1978. Initial investment, clutch size, and brood reduction in the Common Grackle (*Quiscalus quiscula* L.). Ecology 59:1109–1122.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

Immelmann, K., J. P. Hailman, and J. R. Baylis. 1982. Reputed band attractiveness and sex manipulation in Zebra Finches. Science 215:422.

Kendeigh, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. Ecology 22:237–248.

Kendeigh, S. C., T. C. Kramer, and F. Hamerstrom. 1956. Variations in egg characteristics of the House Wren. Auk 73:42–65.

Klomp, H. 1970. The determination of clutch size in birds. A review. Ardea 58:1–124.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ., London.

Lehrman, D. S. 1961. Hormonal regulation of parental behavior in birds and infrahuman mammals, p. 1268–1382. *In* W. C. Young [ed.], Sex and internal secretions. Williams and Wilkins, Baltimore.

Mayoh, K. R., and R. Zach. 1985. A new method for matching hatchlings with their eggs. Condor 87:300–301.

Mead, P. S., and M. L. Morton. 1985. Hatching asynchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? Auk 102:781–792.

Müller, M. M., A. E. Carrasco, and E. M. DeRobertis. 1984. A homeo-box-containing gene expressed during oogenesis in *Xenopus*. Cell 39: 157–162.

Myers, J. H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? Am. Nat. 112:381–388.

Nisbett, I.C.T. 1973. Courtship-feeding, egg-size and breeding success in common terns. Nature 241: 141–142.

Nolan, V., Jr., and C. F. Thompson. 1978. Egg volume as a predictor of hatchling weight in the Brown-headed Cowbird. Wilson Bull. 90:353–358.

O'Connor, R. J. 1975. Initial size and subsequent growth in passerine nestlings. Bird-Banding 46: 329–340.

Ojanen, M., M. Orell, and R. A. Vaisanen. 1979. Role of heredity in egg size variation in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scand. 10:22–28.

Ojanen, M., M. Orell, and R. A. Vaisanen. 1981. Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. Ornis Fenn. 58:93–108.

Olsen, M. W. 1942. Maturation, fertilization and early cleavage in the hen's egg. J. Morphol. 70: 513–528.

Olsen, M. W., and R. M. Fraps. 1950. Maturation changes in the hen's ovum. J. Exp. Zool. 114:475–489.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228:1221–1222.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117:517–520.

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

Pinkowski, B. C. 1975. Growth and development of Eastern Bluebirds. Bird-Banding 46:272–289.

Pinkowski, B. C. 1979. Effect of nesting history on egg size in Eastern Bluebirds. Condor 81:210.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67:505–510.

Ricklefs, R. E., D. C. Han, and W. A. Montevecchi. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. Auk 95:135–144.

Romanoff, A. L., and A. J. Romanoff. 1949. The avian egg. John Wiley and Sons, New York.

Rubin, M. R., L. E. Toth, M. D. Patel, P. D'Eustachio, and M. C. Nguyen-Huu. 1986. A mouse homeo box gene is expressed in spermatocytes and embryos. Science 233:663–667.

Ryden, O. 1978. Egg weight in relation to laying sequence in a south Swedish urban population of the Blackbird *Turdus merula*. Ornis Scand. 9:172–177.

Ryder, J. P. 1983. Sex ratio and egg sequence in Ring-billed Gulls. Auk 100:726–730.

Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. Ibis 115:549–558.

Sturkie, P. D. 1986. Avian physiology. Springer-Verlag, New York.

Thissen, D., and E. Martin. 1982. Reputed band attractiveness and sex manipulation in Zebra Finches. Science 215:423.

Trivers, R. L. 1978. The evolution of reciprocal altruism, p. 189–226. *In* T. H. Clutton-Brock and P. H. Harvey [eds.], Readings in sociobiology. W. H. Freeman and Co., San Francisco.

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

Weatherhead, P. J. 1985. Sex ratios of Red-winged Blackbirds by egg size and laying sequence. Auk 102:298–304.

Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. Science 209: 1157–1159.

Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc. R. Soc. London B Biol. Sci. 205:567–580.

Zach, R. 1982. Hatching asynchrony, egg size, growth, and fledging in Tree Swallows. Auk 99:695–700.