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SEX AND EGG SIZE IN GREAT-TAILED GRACKLES¹

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Trivers and Willard (1973) suggested that when the variance in reproductive success of one sex is greater than that of the other, females in good condition should produce more offspring of the sex that exhibits the higher variance. This assumes that the condition of the female is reflected in the condition of the offspring and that the survival and breeding success of an individual is at least partially dependent on the condition of the individual at the end of parental care. Although Trivers and Willard's model predicts different strategies for different females, it is clear that nestling quality within individual broods may vary greatly and that females may potentially influence this variability in an adaptive way. For example, sequence-related hatching trends found in Lesser Snow Geese (*Chen caerulescens*, Ankney 1982) and Bald Eagles (*Haliaeetus leucocephalus*, Bortolotti 1984) may function to provide a competitive advantage for the larger sex in both species.

Mead et al. (1987) recently found that eggs from which male White-crowned Sparrows (*Zonotrichia leucophrys*) hatched were larger than those from which females were hatched. Since the variance in reproductive success of males in this species is probably greater than that of females and since egg size has been shown in many studies to be correlated with nestling growth and survival, they interpreted these results as being an

adaptive response in accordance with the predictions generated by the Trivers and Willard model. Because their study is one of few among altricial birds that provides evidence that parents might adaptively apportion their investment into sons and daughters, I decided to examine similar data for a species in which much greater difference in variance in breeding success for males and female would lead to the prediction of even greater size differences between eggs from which sons and daughters hatch.

Great-tailed Grackles (*Quiscalus mexicanus*) exhibit extreme sexual size dimorphism which becomes apparent shortly after hatching (Teather and Weather-

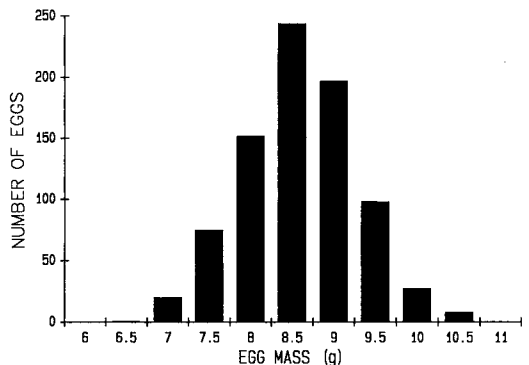


FIGURE 1. Distribution in the sizes of eggs laid by Great-tailed Grackles.

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TABLE 1. Mass (± 1 SD) of eggs from which nestlings of known sex hatched. Sample sizes are given in parentheses. Probabilities based on *t*-tests.

Year	Males $\bar{x} \pm \text{SD} (n)$	Females $\bar{x} \pm \text{SD} (n)$	<i>P</i>
1985	8.58 \pm 0.66 (145)	8.52 \pm 0.63 (122)	0.445
1986	8.33 \pm 0.60 (147)	8.30 \pm 0.68 (142)	0.753
1987	8.19 \pm 0.70 (127)	8.12 \pm 0.67 (139)	0.411
Total	8.37 \pm 0.67 (419)	8.30 \pm 0.68 (403)	0.150

head 1988). Although detailed studies of their mating system have not been carried out, they are generally thought to be polygynous (Kok 1972) or promiscuous (Selander and Giller 1961). My own observations of unmarked birds suggest that harem sizes of males range from one to at least five females. Between 1985 and 1987 I investigated the growth and development of this species at the Wedler Wildlife Refuge in southern Texas. Nesting areas were checked daily (see Teather et al. 1988) and eggs were marked sequentially with a felt-tipped pen. For a subset of nests in each year I recorded the length and width of each egg to the nearest 0.05 mm. The mass of eggs was estimated from the equation: $\text{mass} = 0.7144(\text{width}) + 0.0036(\text{length})^2 - 11.1211$ ($r^2 = 0.962$) that was derived from 100 eggs for which all three variables had been measured. Nests were visited daily or twice daily during hatching and nestlings marked in the order in which they hatched. While many of the nestlings could be unambiguously assigned to specific eggs, others were assigned to eggs based on laying and hatching sequences. This was justified since Great-tailed Grackle eggs nearly always hatch in the sequence that they were laid. For 1,056 cases in which nestlings could be directly assigned to particular eggs, less than 1% (10) hatched out of order. When more than one egg had hatched between visits to a nest, the order of hatching was usually apparent from the plumage condition and size of nestlings. Any ambiguous cases were excluded. The gender of nestlings was determined by mass and tarsus length for individuals that were at least 7 days old or by dissection for those that were found dead or nearly dead.

Mass of eggs from which individuals of known sex hatched ranged from 6.47 to 10.46 g (Fig. 1) thereby providing adequate variation in size to detect any sex-size relationship that might exist. The overall mass of eggs decreased significantly in succeeding years consistent with data on egg-size variation taken from com-

plete clutches (Teather and Weatherhead, unpubl.). There was no evidence that eggs from which males hatched were heavier than those from which females hatched in any single year or for all years combined (Table 1).

Combining the data for all clutches could mask egg size-sex patterns within clutches, given greater variation in egg size among than within clutches. To account for egg-size variation among females, eggs in individual nests in which both males and females were present were ranked by size to determine if males came from the larger eggs more often. This was clearly not the case (Table 2). Indeed, the only observed trend was for females in three-egg clutches for which the size and sex of all eggs were known to come from larger eggs, a pattern opposite to that predicted. Three- and four-egg clutches for which I knew the size and sex of only two eggs similarly showed no pattern, with males and females coming from the larger egg in 20 and 21 cases, respectively.

These results may be confounded if there is sequence-related variation in egg size and if one sex comes more often from certain eggs in this sequence. However, while there are size differences between eggs of different laying sequence (Teather and Weatherhead, unpubl.), there is no tendency for one sex to come more often from eggs of a particular laying sequence in either three- or four-egg clutches (Table 3).

It is clear that female Great-tailed Grackles do not apportion energy reserves in eggs based on the gender of their offspring. This is somewhat surprising since the apparent degree of polygyny in this species would make it advantageous for females to produce large, healthy males. This contrasts markedly with the White-crowned Sparrows studied by Mead et al. (1987) that are primarily monogamous and for which male condition should be less important. However, although my data are not consistent with those of Mead et al.,

TABLE 2. Within-clutch egg size rank of males and females in clutches of three and four eggs. Size is ranked from largest (1) to smallest (4).

Clutch size	Sex	Sex of four eggs known				χ^2	<i>P</i>	Sex of three eggs known			χ^2	<i>P</i>
		1	2	3	4			1	2	3		
Four	Male	11	6	6	8	4.20	0.24	16	14	21	3.15	0.21
	Female	5	10	10	8			17	19	12		
Three	Male							32	40	47	5.62	0.06
	Female							48	40	33		

TABLE 3. Egg sex relative to sequence in three- and four-egg clutches for which the sex and sequence of all nestlings were known.

Clutch size	Sex	Sequence				χ^2	P
		1	2	3	4		
Four	Male	9	7	9	6	1.69	0.64
	Female	7	9	7	10		
Three	Male	39	39	41		0.13	0.94
	Female	41	41	39			

they are consistent with those of other studies. For example, Bancroft (1984) found no differences in the mass of eggs from which males and females hatched in Boat-tailed Grackles (*Quiscalus major*). Weatherhead (1985) found no tendency for males to come from larger eggs in Red-winged Blackbirds (*Agelaius phoeniceus*); this is supported by other studies of this species by Fiala (1981) and Blank and Nolan (1983). It is of interest that all of these species are highly polygynous and thus should be more appropriate than White-crowned Sparrows for testing the predictions arising from Trivers and Willard's model.

At this point I can offer no explanation as to why sexual dimorphism occurs in the eggs of White-crowned Sparrow but not in those of the dimorphic icterids that have been studied. It is possible that the difference in the size of eggs from which males and females hatch is not an adaptive response by adult females to produce higher quality sons but is a trait associated with some, as yet, unidentified character. Indeed, as pointed out by Mead et al. (1987), it is unclear whether the small differences in egg mass that they observed would affect survival and/or future reproductive performance. On the other hand, the difference in egg mass might be an adaptive response as indicated but is simply limited phylogenetically. It would be of interest to compare similar data for closely related species that exhibit higher levels of polygyny to see if predicted patterns emerge.

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