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SEXUAL SIZE DIMORPHISM IN GREAT-TAILED GRACKLES:
THE COSTS OF SONS AND DAUGHTERS

by

Kevin L. Teather

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for
the degree of
Doctor of Philosophy
Department of Biology
Carleton University

1988

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ABSTRACT

I addressed three issues relevant to sex ratio theory as it applies to sexually dimorphic birds using a Texas population of great-tailed grackles (Quiscalus mexicanus). These were (i) the assumption that the larger sex is more costly to rear, (ii) the importance of sibling gender and the overall sex ratio of the brood on the growth and survival of nestlings, and (iii) the identification of factors which may contribute to biased fledgling sex ratios in certain populations.

Male energy requirements, as determined by oxygen and food consumption, were significantly greater than those of females between 5 and 12 days post-hatching. There was no evidence that males directed more of their energy into mass increase than females or that parents reduced the added costs of rearing males by feeding them larger or more nutritious, as opposed to more, food items.

Growth rates of nestlings suggested that the effects of sibling gender and/or the sex ratio of the brood, if present, were minimal. There was no evidence that starvation was more likely to occur if older siblings were males rather than females. Mass at fledging was influenced most strongly by the sequence of hatching with youngest nestlings weighing less. The mass of males at fledging, especially if they were the youngest in the brood, was more

variable than that of females while the growth of males was affected more strongly by both egg size and hatching date.

Fledgling sex ratios were one to one in 1985 but female biased in 1986 and 1987. Evidence from egg and clutch sizes, as well as levels of starvation, inferred that food was less abundant in the latter two years. This suggests that males may suffer higher mortality when food is limited. Two other lines of evidence support this idea. First, the fledgling sex ratio of a particular colony was correlated with the level of starvation in that colony. Second, patterns of growth and survival suggested that males were more likely to suffer than females when both were subjected to similar and potentially stressful conditions.

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GENERAL INTRODUCTION

It has been suggested that Fisher's (1930) theory concerning population sex ratio equilibria represents one of the few basic tenets of modern biology (Williams 1966). In fitting with any good scientific theory, it has generated a number of predictions that have resulted in experimental tests and subsequent modification and extension of the theory. Probably the most important development has been the shift in emphasis from the population sex ratio to a more detailed examination of individual strategies that result in population sex ratios. Here I present a brief overview of these ideas and relate them to both descriptive and empirical studies of altricial birds. In doing so, I hope to point out some of the weaknesses of the current theory as it applies to this taxon, and suggest ways in which these weaknesses might be addressed.

The sex ratio of adult populations in most organisms is close to unity (see review in Charnov 1982). Darwin (1871), while recognizing the potential evolutionary importance of this observation, was clearly puzzled when he noted:

"I formerly thought that when a tendency to produce the sexes in equal numbers was advantageous to the species, it would follow from natural selection,

but I now see that the whole problem is so intricate that it is safer to leave its solution for the future."

It was not until 1930 that Fisher put forth an explanation that fit within the framework of Darwin's ideas on natural selection. Quite simply, Fisher reasoned that since every offspring must have one mother and one father, the total reproductive value of males must equal that of females. This being the case, natural selection should favour parents that invest equally in sons and daughters.

The theoretical validity of this concept has been confirmed mathematically (Kolman 1960, Verner 1965, Leigh 1970, Charnov 1975, 1982) and was expressed most clearly by Shaw and Mohler (1953) as:

$$CM \times M = CF \times F$$

where CM = the cost of producing one male

M = the number of males at the end of parental care

CF = the cost of producing one female

F = the number of females at the end of parental care.

Empirical support for Fisher's ideas has come primarily from tests of three predictions generated by this model. First, given that males and females are equally expensive to rear, the sex ratio of most offspring groups should be 1:1. Second, greater mortality of one sex during the

period of parental care should result in more of that sex being produced initially to equalize the amount of investment in each sex. Third, any disparity in the costs of rearing sons and daughters should result in fewer of the more expensive sex by the end of parental care. For example, if males are twice as costly for parents to rear as females, and the average reproductive return for each is equal, then by the end of parental care females should outnumber males two to one.

While it is true that the sex ratio of most broods or litters is very close to unity (Charnov 1982), this is more easily explained as being the result of random segregation of sex chromosomes during the first (sex determining) meiotic division (Williams 1979). Thus, although often used as support for Fisher's theory, the predominance of even sex ratios is of little value in this regard. Tests of the other two predictions are more useful in examining Fisherian sex control.

Most of the evidence from this line of study has been obtained from investigations of invertebrates and I refer the reader to Charnov (1982) for detailed treatments of these groups. Among vertebrates, species of altricial birds that exhibit pronounced size differences between males and females (hereafter referred to as sexually dimorphic) are an obvious group in which to look for parental manipulation of the sex ratio because (a) there is

an extended period of parental care during which the offspring are completely dependent on parents for survival, (b) any size differences between males and females that are manifested before the end of parental care should be reflected in differing costs to parents, and (c) adult females contribute the sex-determining gamete and thus may be in a better position to influence the sex of their progeny. However, as I show below, investigations of possible sex ratio manipulation in this group have provided little support for Fisher's ideas.

Hatching and Fledging Sex Ratios in Sexually Dimorphic Altricial Birds

To my knowledge there have been no studies that have attempted to ascertain the primary sex ratio (i.e. at fertilization) in birds. However, unless there is differential mortality of eggs containing one sex, hatching sex ratios should be indicative of the proportions of males and females produced at fertilization. This could be accomplished by nonrandom chromosome segregation during the first meiotic division or by differences in the fertilizability of Z and W gametes. Unfortunately, because of the difficulty in sexing live nestlings at hatching, few data are available concerning secondary sex ratios. The most comprehensive data come from studies of domestic poultry in which there is no consistent difference in the

numbers of males and females at hatching (Foster and McSherry 1980). Unfortunately, since these species are generally precocial, costs of raising males and females are probably similar and biased sex ratios would not be expected. Reliable data for three species of dimorphic icterids - red-winged blackbirds (Agelaius phoeniceus, Fiala 1981a, Weatherhead 1983), yellow-headed blackbirds (Xanthocephalus xanthocephalus, Richter 1983) and boat-tailed grackles (Quiscalus major, Bancroft 1983) - and four species of raptors - American kestrels (Falco sparverius, Porter and Wienmeyer 1972), European sparrowhawks (Accipiter nisus, Newton and Marquis 1979), peregrine falcons (Falco peregrinus, Newton 1979), and bald eagles (Haliaeetus leucocephalus, Bortolotti 1984) - fail to reveal any deviation from a 1:1 sex ratio at hatching.

A significant bias in the sex ratio at fledging has been noted only in red-winged blackbirds (Fiala 1981b). One potential problem has been that statistical analysis requires very large samples to detect expected deviations from unity. For example, if females were 20% more numerous than males, a sample of over 600 nestlings would be required to statistically reject the null hypothesis of an equal sex ratio. Thus, it may be inappropriate to dismiss studies that have supported Fisher's predictions but have been rendered statistically inconclusive because of small samples. For example, Howe (1976) found that the sex ratio

of common grackles (Quiscalus quiscula), while 1:1 at hatching, became female biased by fledging. Bancroft (1983) noted that of nestlings hatching from the last egg in nests of boat-tailed grackles females were more likely to fledge than males. Cronmiller and Thompson (1981) showed that artificially enlarged broods of red-winged blackbirds fledged more females than males. These studies suggest that biased sex ratios may arise from differential mortality of males and females during the nestling period, especially when nestlings are placed in stressful or food limited conditions. Differential mortality of juvenile males and females in sexually dimorphic species of birds and mammals has also been documented and reviewed by Clutton-Brock et al. (1985).

Other studies have failed to support Fisher's ideas. Although Richter (1983) found a slight bias in favour of females at fledging in yellow-headed blackbirds (51:39), two other studies of the same species reported a fledging sex ratio of close to one (Willson 1966, Patterson and Emlen 1980). In addition, the slight but significant bias in favour of females in red-winged blackbirds noted by Fiala (1981b) does not reflect the degree of size dimorphism in the species. Despite the apparent bias in numbers of males and females fledging from the last egg, Bancroft (1983) found no overall bias in the sex ratio of boat-tailed grackles at the end of parental care. There is

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no evidence from raptors, that differ from icterids in that females are generally larger than males, of a male biased sex ratio at fledging (Newton 1979). Indeed, studies of golden eagles (Aquila chrysaetos) (Collopy 1980), hen harriers (Circus cyaneus) (Balfour and Cadbury 1979, Picozzi 1980), peregrine falcons (Hickey 1942), and European sparrowhawks (Mayr 1938 although see Newton and Marquis 1979) suggest that males may suffer slightly higher nestling mortality than females.

Any biases in fledgling sex ratios appear to be the result of differential survival of males and females during the nestling period. This has two implications with regard to Fisher's ideas. First, differential mortality of one sex should result in an overproduction of that sex at hatching. As noted above, this is not supported by available evidence. Second, differential mortality by one sex during this period may indicate that parents adaptively adjust the sex ratio of the brood after hatching. This might be the case if (1) females lay more eggs than they are capable of rearing and (2) females selectively remove (or at least do not feed) a proportion of male nestlings. In this way, females could "create" broods having the number of sons and daughters that they could efficiently rear. At the population level this would result in a fledgling sex ratio biased in favour of females while, as noted below, individual strategies would be expected to

vary depending on the condition of the adult female.

Strategies for Sex Ratio

Manipulation by Individuals

The most important extension of Fisher's ideas has been put forth by Trivers and Willard (1973) and suggests why and when individual females might manipulate the sex ratio of their brood even though the population sex ratio is 1:1. They suggested that if there is variance in the reproductive success of males and females, and if — successful breeding is at least partially dependent on the condition of the bird when it leaves the nest, females should preferentially rear those offspring that experience the greater variation in breeding success. In a highly polygynous system, for example, large, healthy sons should provide a better reproductive payoff than large, healthy daughters. This bias could be accomplished in a number of ways. First, the largest, healthiest females might produce more males than females. Second, all females might produce more males at times during the season when food is most abundant. Third, females might manipulate the laying sequence of eggs such that males hatch first and subsequently gain a competitive edge over nestmates.

Only one study of which I am aware has attempted to relate the sex ratio of the brood with naturally occurring variation in adult females. Blank and Nolan (1983) found

that older female red-winged blackbirds produced proportionately more male offspring than did younger females. It was proposed that older females, being more experienced parents, could produce higher quality offspring and that high quality sons had higher reproductive value than high quality daughters. Some of the best evidence for sex ratio manipulation in altricial birds has been provided by Burley (see review in Burley 1986). She has found that adult zebra finches (Poephila guttata) bias offspring production (probably after hatching) in favour of the sex of the more attractive parent with attractiveness being based on plastic leg-band colour.

Within season changes in the sex ratio of nestlings have been found to occur in both red-winged blackbirds (Weatherhead 1983) and common grackles (Howe 1976). Between season variation in the production of males was shown by Ryder (1983) who found that more males were produced in nests of ring-billed gulls (Larus delawarensis) in the earliest of three breeding seasons. In each of these studies the investigator suggested that males were being produced when resources were most abundant.

There is some evidence that suggests that nestling sex is not independent of egg sequence. Ankney (1982) found that males were more likely to hatch from the first two eggs in lesser snow geese (Chen caerulescens) while females were more likely to hatch from the last two (although see

Cooke and Harmsen 1983). Similarly, Ryder (1983) found that the first of three eggs in ring-billed gulls most often produced males while the second was more likely to produce females. It is interesting to note that neither of these species is highly dimorphic and advantages to producing high quality males should be less than in more dimorphic species. However, egg sequencing in dimorphic icterids, while sometimes showing nonrandom sex-sequence relationships, has failed to indicate any obvious adaptive trends. For example, Fiala (1981a) found that last eggs (in four egg clutches) of red-winged blackbirds most often produced females (although this may have been the result of differential mortality after hatch), while evidence provided by Weatherhead (1985) indicated that the percentage of males increases with laying order for four egg clutches. In addition, Weatherhead found the opposite tendency for three egg clutches. While small samples render the results of other investigations tentative, they too show contradictory trends. Thus, while Howe (1976) found that the first and second eggs of common grackles produced more females and males respectively (first egg - 6 males, 18 females; second egg - 22 males, 10 females), Bancroft (1983) found the reverse pattern in boat-tailed grackles (first egg - 20 males, 10 females; second egg - 9 males, 20 females). Consistent with the prediction that the first egg should produce the larger sex, Bortolotti

(1984) found that females most often hatch first in bald eagles.

To summarize, there are few data from either hatching or fledgling sex ratios that consistently support Fisher's prediction of an overproduction of the less expensive sex in sexually dimorphic altricial birds. Limited evidence suggests that individual strategies might be important in cases where parents produce males and females at either different times during the breeding season or in nonrandom hatching sequences. However it remains to be shown whether such patterns are adaptive in affecting the development and subsequent survival and/or reproductive success of nestlings.

Further Considerations

Three issues need to be addressed for a more complete understanding of adaptive sex ratio manipulation. First, the assumption that the larger sex is more costly for parents to rear needs to be more closely examined. Second, the importance of competition between nestlings and how it may affect reproductive success must be clarified. Third, given that males are often, although not always, underrepresented at fledging, it is important to identify potential factors that influence differential survival of sons and daughters.

There are few data concerning the relative costs to parents of raising nestlings of different sex. While Fiala and Congdon (1983) found that total energy requirements of male red-winged blackbird nestlings exceeded those of females, there was no indication that parents fed more at nests containing all males than nests containing all females (Fiala 1981b). In contrast, Newton (1978) found that male and female European sparrowhawks, despite large size differences, consumed similar amounts of food, and Collopy (1980) found no differences in energy requirements of male and female golden eagles. This suggests that costs of rearing male and female nestlings, if different, may not be directly proportional to their size. It has been suggested that differences in patterns of growth between the sexes may reduce the cost disparity of raising nestlings of different sex. Thus, while the energy of larger nestlings may be channelled into increasing body mass, that of the smaller nestling may be diverted into other physiological characters such as feather development. This has been proposed to explain the apparent similarity in energy requirements of yellow-headed blackbirds (Richter 1983), boat-tailed grackles (Bancroft 1984), and European sparrowhawks (Newton 1978).

The relative competitive ability of male and female nestlings has attracted little study. It has been established that the largest and most aggressive nestling

in swifts (Apus apus, Lack 1956) and common starlings (Sturnus vulgaris, Maxwell and Putnam 1972) is fed preferentially and that the first nestling to hatch in many arctic passerines later outcompetes its nestmates for parental attention (Hussel 1972). Lack (1954) and Yom-Tov and Ollason (1976) have suggested that females may often outnumber males at fledging in raptors because their size provides them with superior competitive ability. If the largest nestling consistently outcompetes its siblings, one might predict that males (in icterids), should realize higher nesting survival than females, not lower as predicted by Fisher (1930). On the other hand, evidence from a number of studies suggests that the smaller sex often develops locomotory skills and is able to fledge at an earlier age than the larger sex (e.g. Holcomb and Twiest 1970, Newton 1978, Picozzi 1980, Fiala 1981b, Richter 1983).

As noted above, differential mortality of males has been noted to occur when nestlings are either naturally or artificially stressed in terms of food. This would explain why males apparently suffer higher mortality when they are the youngest nestling in both common grackles (Howe 1976) and boat-tailed grackles (Bancroft 1983). In addition, experimental enlargement of brood size has resulted in biased fledgling sex ratios in both red-winged blackbirds (Cronmiller and Thompson 1981) and rooks (Slagsvold and

Roskaft 1985). Thus, it has been suggested that males, because of increased food requirements, are more likely to starve when food becomes limiting (Bancroft 1983, Clutton-Brock et al. 1985).

Aims of the Study

The general aim of this study is to address the above considerations using a species that exhibits extreme sexual size dimorphism and in which size differences between males and females are expressed while nestlings are still under parental care. Each of these three topics - energy requirements of males and females, influence of sibling gender on growth and survival of nestlings, and factors associated with differential mortality of male and female nestlings - will be dealt with in a separate chapter.

In the first chapter I test the hypothesis that male and female nestlings have similar energy requirements but males divert more of this energy into characters that result in mass increase. Support for this hypothesis would indicate that costs of raising sons and daughters in sexually dimorphic species are similar and expected sex ratios would not be expected to deviate greatly from unity. However, assuming that energy demands of males exceed those of females, I also test whether parents reduce differences in costs between sons and daughters by differential

distribution of food.

In the second chapter I examine more closely factors that affect nestling growth and survival. In particular I attempt to ascertain whether the gender of a nestling's siblings affects its growth and survival. For example, if males receive more food than females then one would predict that a nestling that has two older males siblings would suffer decreased growth and survival in comparison to one having two older female siblings. This would be true if large size enabled males to monopolize most of the resources or if parents selectively fed larger nestlings at the expense of smaller ones when food was limiting.

In the final chapter I examine proximate factors that may be responsible for variation in fledgling sex ratios in this and other species. I subsequently discuss adaptive sex ratio manipulation in altricial birds in view of existing evidence and suggest that differential mortality of males and females, when it occurs, can be more appropriately explained within the context of the theory of sexual selection.

GENERAL METHODS

Study Area

This study was conducted between March and August 1985 to 1987, at the Welder Wildlife Refuge in southern Texas located approximately 12 km northeast of Sinton (Fig. 1). The area is considered to be humid subtropical to dry subhumid with average winter and summer temperatures of 13.9 and 30.0°C (Guckian and Garcia 1979). The average rainfall is 88.9 cm per year but extreme fluctuations occur (Drawe et al. 1978). The region has been classified as a transitional zone between South Texas Plains and Gulf Prairies and Marshes (Thomas 1975) with the general aspect of vegetation being a mixture of mesquite (Prosopis grandulosa), savannah, coastal prairies grassland, scrubland and chapparrel with areas of live oak (Quercus virginiana), woodlands, thickets and mottes.

Two oxbow lakes found on the 3158 h refuge, Big Lake and Pollita Lake, have areas of 52 and 32 h, respectively. Both lakes are generally less than 2 m deep although depths vary greatly with rainfall. Emergent vegetation found in and around the lakes consists primarily of cattail (Typha domingnesis and T. latifolia), bulrush (Scirpus californicus), spiny aster (Aster spinosus), and common reed (Phragmites australis). By July, much of the surface of the water is covered by lotus (Nelumbo lutea) and water lily (Nymphaea mexicana).

Figure 1. The Welder Wildlife Refuge.

Study Animal

Great-tailed grackles (Quiscalus mexicanus) belong to the subfamily Icterinae, a group noted for extreme variability in the level of sexual size dimorphism found among its members (Selander 1972). Measurements of adults taken by Selander (1958) show great-tailed grackles to be among the most dimorphic of this group with pronounced size differences between sexes occurring in tail length (203.8 vs. 144.5 mm), wing length (184.3 vs. 143.4 mm), bill length (31.3 vs. 24.2 mm), bill depth (12.6 vs. 10.4 mm), tarsus length (46.4 vs. 38.5 mm), and mass (227.1 vs. 121.6 g). Most importantly, for the purpose of this investigation, size dimorphism becomes apparent during the nestling period, with males being noticeably larger than females shortly after hatching (Gotie and Kroll, 1973).

Within the gulf coastal plain of southern Texas, great-tailed grackles have been found nesting in mesquite, huisache (Acacia farnesiana), hackberry (Celtis sp.), prickly ash (Zanthoxylum clava-hercularis), oak (Quercus sp.), cottonwood (Populus sp.), prickly pear cactus (Opuntia lindheimeri), Texas ebony (Pithecolobium flexicaule), willow (Salix sp.), yucca (Yucca sp.), and tall grass (Selander and Giller 1961). At the Welder Wildlife Refuge, grackles nest primarily in cattails, bulrushes and dead huisache trees (Tutor 1962). This wide range of potential nesting habitats combined with increased food availability associated with available agricultural land

has probably been responsible for the rapid spread of this species through the southern United States. Its present range extends east from New Mexico to Louisiana and north from northern South America to Kansas (Pruitt 1975, Gotie and Kroll 1973).

General Nest Checks

Beginning in late March of each year, potential nesting areas around Big Lake, Pollita Lake, and other smaller open bodies of water were searched daily and nests were numbered and classified according to their stage of construction (Teather et al., in press). In most cases nests were found prior to clutch initiation although later in the season nests were sometimes found during egg-laying, incubation, or after hatching.

Eggs were marked sequentially with a waterproof, felt-tipped marker and were checked daily to establish when incubation began. In a subsample of nests, the lengths and widths of all eggs were measured to the nearest 0.05 mm. After clutch completion, nests were visited every second or third day until hatching when they were visited daily or twice daily to establish hatching sequence. At this time, nestlings were marked with a felt-tipped marker on their tarsi according to the order in which they hatched. After nestlings had hatched, nests were visited every second or third day until all nestlings disappeared or fledged. Except where indicated, nestlings were assumed to have eventually fledged if they were

still present at 12 days post-hatching, the earliest age at which they were observed to leave the nest when disturbed. Nestlings that were present on one visit and absent the next were assumed to have disappeared at the midpoint between these two visits.

In a subsample of nests, generally containing either three or four nestlings, I took the following measurements of all nestlings in the brood on every second or third day: mass (to the nearest 0.1 g when nestlings were less than 10 g, to the nearest 0.5 g when nestlings were greater than 10 g), tarsus length (to the nearest 0.05 mm), and length of the 9th primary (to the nearest 0.05 mm). To supplement the decreased number of measurements of older nestlings due to nestling loss, I also measured previously unmeasured nestlings (of known age, sex and brood size) between 9 and 12 days post-hatching.

The sex of nestlings was determined using one of three methods. Mass differences between males and females were used if nestlings appeared healthy and had reached an age of at least 6 days post-hatching. When nestlings appeared to be suffering from reduced growth, I often used tarsus length, sometimes in conjunction with mass, which appeared to be less affected by food stress (see Chapter 2). Finally, when nestlings were too small to be sexed by external measurements (i.e. when they were found dead in nests) or when mass and/or tarsus length did not provide a clear indication of gender, sex was determined by dissection.

CHAPTER 1.

Sex-specific Energy Requirements of
Great-tailed Grackle Nestlings

INTRODUCTION

According to Fisher (1930), parents should invest equally in offspring of both sexes. When sons and daughters are equally costly to rear, the sex ratio at the end of parental care should be near unity. In species that exhibit large size differences between the sexes, it is generally assumed that the larger sex is more expensive. Under these conditions, one should find an overproduction of the smaller, or less expensive sex. While Fisher's theory has received relatively strong support from studies of certain groups of invertebrates (reviewed by Charnov 1982) and mammals (Clutton-Brock 1986), there is little evidence that birds adaptively manipulate the sex ratio of their broods (Clutton-Brock 1985) and there are no examples of sexually dimorphic birds that demonstrate a secondary (hatching) sex ratio biased as predicted by Fisher (references in Clutton-Brock 1985 and Slagsvold et al. 1986).

There are three possible explanations for the apparent lack of support for Fisher's theory among birds. First, the costs of raising sons and daughters in a dimorphic

species may be similar despite size differences. This would be the case if both sexes had similar energy demands but the smaller sex channelled resources into functions that require less mass increase. This hypothesis was originally proposed by Newton (1978) to explain food consumption similarities between dimorphic European sparrowhawk nestlings. Similarly, it has been suggested that females, the smaller sex among icterid nestlings, may direct more energy into feather growth than males and thus a similar amount of food would result in less absolute mass increase in this sex (Richter 1983, Bancroft 1984). Differences in energy allocation may thereby serve to reduce or eliminate any cost differences in rearing the two sexes.

Second, parents may reduce the difference in costs between sons and daughters by differential distribution of food such that the larger sex receives larger or more nutritious rather than a greater number of food items. This hypothesis assumes that most of the expense in raising nestlings is incurred while flying to and from foraging grounds and that capture costs do not vary greatly for different prey types or sizes. It also assumes that the smaller sex cannot consume the largest food items brought to the nest by parents. Although many studies have shown a positive correlation between prey size fed to nestlings and nestling age (e.g. Kessel 1957, Breitwisch et al. 1984), I

am not aware of any study that has documented differential distribution of prey to nestlings of different size or sex.

Third, if sex determination is random and primary sex ratios are not subject to selection, parents still might adaptively manipulate the sex ratio of their brood post-hatching such that investment in males and females is equal by the end of parental care (Charnov 1982). Thus, Fisher's (1930) prediction would be verified but by slightly different means. However, while a number of studies of sexually size dimorphic species have revealed biases in fledgling sex ratios (Howe 1977, Wegge 1980, Fiala 1981b, Roskaft and Slagsvold 1985, Chapter 3) there is no evidence that these biases are the result of parental manipulation.

Here I address the first two of these hypotheses by providing information on food requirements, metabolic demands, and diets of male and female great-tailed grackles. Specifically, this investigation was designed to answer the following questions. First, do sons have higher energy demands than daughters while under parental care and if so are these differences directly proportional to size differences between the sexes? Second, if energy demands among sons and daughters differ, do parents partially or wholly reduce this difference by feeding sons larger or more nutritious food items?

METHODS AND MATERIALS

Oxygen Consumption Rates

Determination of oxygen consumption rates of nestlings was carried out between 16 June and 5 July 1987. Oxygen consumption by 4 to 11 day old males and 5 to 11 day old females was determined using a constant volume manometric technique described in Davies (1966). The apparatus was modified to accomodate larger organisms (respiratory and control chambers were both 1 liter) and to allow a larger volume of oxygen to be introduced (two 20 ml syringes were attached to the respiratory chamber). All tests were conducted between 1500 and 1900 and the following procedure was used in each case. The nestling was removed from the nest and transferred to a portable O_2 monitoring station approximately 200 m away where mass, tarsus length and length of 9th primary were recorded. It was then placed in a respiratory chamber (containing 30 g of sodium hydroxide to absorb carbon dioxide) for a 20 min adjustment period with the entire apparatus submerged in a constant temperature (21°C) water bath. The temperature did not fluctuate more than 0.5 degrees throughout the testing period. Oxygen consumption was subsequently monitored until the nestling had consumed 20 ml (nestlings < 50 g) or 40 ml of oxygen (nestlings > 50 g). This was later converted to a rate per minute and corrected to standard temperature and pressure.

Food Requirements of Hand-Reared Nestlings

Groups of 5-6 day old nestlings were taken from nests on the evenings of 25 May ($N = 9$), 1 June ($N = 10$), and 15 June, 1986 ($N = 12$) and placed in pairs in natural nests which had been brought into the laboratory just prior to nestling collection. Nests were kept outside in the shade during the day with the exception of extremely hot or rainy conditions. During the evening, nestlings were returned to the laboratory in which the temperature was maintained between 22 and 26°C. Moist towels and a heating pad were placed over the nests to maintain humid conditions.

Nestlings were fed a homogeneous mixture of catfish chow, wild bird starter, egg, gelatin, vitamins, molasses and water (after Lanyon and Lanyon 1971) through syringes which contained measured (g) amounts of food. Feeding took place every 10 to 20 min from 0630 to 2030 and nestlings were fed until they stopped gaping. Thus, nestlings dictated how much food they received. Fecal sacs were collected from individuals after each feeding to calculate digestive efficiency.

Nestlings were weighed prior to feeding each morning and again at 2030. In addition, tarsus length (mm) and length of 9th primary (mm) were recorded each evening. All birds in the first group and birds of uncertain sex in groups two and three were sexed by dissection at the end of the 5-6 days in captivity. Birds whose sex was obvious by

their growth patterns were returned to natural nests.

Nestling Diets

Food samples of nestlings were collected between 27 May and 2 July 1986. To obtain samples from nestlings 5 to 11 days old, I used ligatures to restrict passage of food down the esophagus. Neck collars were placed on each nestling in a brood for 0.5 h between 1600 and 2000. Although food samples were sometimes collected from the same nestling more than once, these nestlings were never sampled on consecutive days. Food samples were collected and preserved in 30% alcohol for later measurement and identification. Each food item was subsequently oven dried at 40°C for 24 h and dry weights recorded.

Nestling Growth Rates

Overall growth rates of males and females were determined using measurements of mass, tarsus length, and length of 9th primaries of all nestlings in selected nests between 1985 and 1987. A more detailed description of the procedures used to collect and analyze data concerning nestling growth is presented in Chapter 2. Overall rates of growth were compared with (a) sizes of nestlings used for monitoring oxygen consumption rates and (b) growth rates of hand-reared nestlings.

RESULTS

Male grackle nestlings were significantly heavier and had significantly longer tarsi than females by the end of 2 days post-hatching as indicated by growth curves of healthy nestlings measured between 1985 and 1987 (Fig. 1-1A, B). The asymptotic masses of males and females, as determined by logistic curves, were 115.6 g and 73.7 g, respectively. Nestlings fledged as early as 12 days at which point female mass was 65.9% that of males. Development of 9th primaries was slightly more advanced in females, with primary lengths being significantly longer than those of males between 3 (first day of feather eruption) and 9 days post-hatching (Fig. 1-1C). After 10 days post-hatching, lengths of 9th primaries of males were slightly, although not significantly, longer than those of females.

Oxygen Consumption

Nestlings used in oxygen consumption experiments fell within the normal size range for their age groups (Fig. 1-1). Males had a higher rate of oxygen consumption than females in six of the seven age groups with differences being significant in four of these (Fig. 1-2). As with body mass, the difference between the sexes appeared to increase with age suggesting that the higher metabolic demands of males were correlated with size differences. Females, however, had a higher mass-specific rate of oxygen

Figure 1-1. Average sizes (± 1 std. dev.) of male (closed circles) and female (open circles) nestlings used in oxygen consumption experiments ($n = 2$ for 4 day old males and 4 for all others) compared to generalized growth curves for (A) mass, (B) tarsus length, and (C) length of 9th primary calculated from measurements taken over three years (males - solid lines, females - dashed lines). The number of measurements used to determine growth curves is shown for each line.

Figure 1-2. Average oxygen consumption (± 1 std. dev.) of male and female nestlings. Asterisks above bars denote significant differences at $p < 0.05$ (t-tests). Sample sizes are the same as in Fig. 1-1.

consumption suggesting that differences in metabolic rates between the two sexes were less than would be expected based on size differences alone (Fig. 1-3).

Using age-mass and mass-oxygen consumption relationships, it is possible to estimate the relative difference in total energy demands by male and female grackles during the nestling period (Fig. 1-4). For this analysis I assume that equations describing oxygen consumption versus body mass in Figure 1-3 can be applied to 0 to 4 day old nestlings. I also assume that my estimates of oxygen consumption were close to average daily values. While these assumptions may increase the error of absolute metabolic estimates, they should not affect estimates of relative differences between males and females. According to this analysis, metabolic demands of female nestling grackles are estimated to be 1181 kJ (where $1\text{ l of O}_2 = 20.08\text{ kJ}$, Nagy 1980) or approximately 83% those of males (1420 kJ) between 0 and 12 days post-hatching.

Food Requirements of Hand-Reared Nestlings

Hand-reared males were significantly heavier and had significantly longer tarsi than females from days 6 through 11 (Fig. 1-5A, B). Females, however, had significantly longer 9th primaries than males on days 6 through 9 (Fig. 1-5C). While these results are similar to differences between the sexes in natural nests growth of all three

Figure 1-3. Mass-specific oxygen consumption by male and female nestlings. Regressions for females ($y = -4.18 + 1.40x$, $r^2 = 0.912$) and males ($y = -4.02 + 1.30x$, $r^2 = 0.857$) are significantly different ($F = 36.81$, $p < 0.01$).

Figure 1-4. Estimated energy requirements of male (open bars) and female (closed bars) nestlings between 0 and 12 days post-hatching. Curves represent cumulative differences.

CUMULATIVE ENERGY REQUIREMENTS (kj)

1400
1200
1000
800
600
400
200
0

DAILY ENERGY REQUIREMENTS (kj)

AGE (days post-hatching)

Figure 1-5. Differences in (A) mass, (B) tarsus, and (C) 9th primary (± 1 std. dev.) in hand-reared male (●) and female (○) nestlings. Sample sizes are the same in (B) and (C) as in (A). Asterisks indicate significant differences at $p < 0.05$ (t-tests).

variables was depressed in hand-reared nestlings (Fig. 1-6A, B).

The relationship between body weight and the energy requirements generally follows a power function (reviewed in Power 1983). However, over the range of weights used in this study, I found that the amount of food consumed versus body mass was best described by a linear relationship (food consumed = $7.26 + 0.44 * \text{mass}$, $r^2 = 0.624$, $p < 0.001$, $n = 132$). Consequently, because males were larger, they consumed more food than females of similar ages throughout the study period (Fig. 1-7). The average amount of food consumed by males between days 5 and 12 was 272.5 g, or 15.8% more than the amount consumed by females (235.4 g). During the same period, males weighed 30.0% more than females. Therefore, although males consumed more food than females, this difference was not directly proportional to the difference in body size. Females, in fact, consumed slightly more food than males of equal mass (Fig. 1-8).

To determine whether males and females differed in the amount of food consumed per unit mass gained each day, I calculated (dry weight of food consumed (g) - dry weight of feces (g)) / weight gained (g). No consistent differences were found between values obtained for males and females over the study period (Table 1-1).

Figure 1-6. Mass (solid lines), tarsus length (dashed lines) and 9th primary length (dotted lines) shown as a percentage of normal growth for (A) males and (B) females. Normal growth was determined from naturally reared nestlings and sample sizes range from 5 to 35. Sample sizes for hand-reared nestlings are as in Fig. 1-5A.

AGE (days post-hatching)

Figure 1-7. Average amount of food consumed per day (± 1 std. dev.) by male and female nestlings from 6 to 12 days post-hatching. Asterisks above each day indicate the level of significance (* $0.1 > p > 0.05$, ** $0.05 > p > 0.01$, *** $p < 0.01$; t-tests). Sample sizes are as in Fig. 1-5A.

Figure 1-8. Food consumed per day as a function of body mass. Regressions for females (crosses: $y = 0.39x + 10.16$, $r^2 = 0.329$) and males (dots: $y = 0.52x + 1.03$, $r^2 = 0.658$) are significantly different ($F = 3.30$, $p = 0.04$).

Table 1-1. Relationship between amount of food consumed and weight increase for males and females. Values represent $[(\text{dry weight of food consumed (g)} - \text{dry weight of feces (g)}) / \text{weight increase per day (g)}] \pm 1 \text{ std. dev.}$ Probability values were calculated from t-tests on arcsine transformations. Sample sizes are as in Fig. 1A.

DAYS			
POST-HATCHING	MALES	FEMALES	p
6	1.63 $\pm$ 0.62	2.63 $\pm$ 1.57	0.236
7	1.61 $\pm$ 1.21	1.82 $\pm$ 1.39	0.688
8	1.30 $\pm$ 0.42	1.14 $\pm$ 0.17	0.201
9	1.13 $\pm$ 0.47	1.09 $\pm$ 0.24	0.782
10	1.14 $\pm$ 0.18	1.32 $\pm$ 0.21	0.030
11	1.59 $\pm$ 1.27	1.43 $\pm$ 0.47	0.731
12	0.94 $\pm$ 0.16	1.44	0.236

Nestling Diets

Approximately 80% of the 283 individual prey items collected from nestlings were either orthopterans (45%) or arachnids (35%). Conocephalus (10%) and Melanocephalus (26%) were the most common genera of orthopterans while most spiders were from the genus Lycosa. Lepidopteran larva (9%) and various other species, including dipterans, one small mammal, and one Anolis lizard (total 9%) were the other constituents of nestling's diet. Approximately 2% of all food items could not be identified.

Although there was a great deal of variation in the amount of food individual nestlings received per one-half hour (Fig. 1-9), the absolute amount of food received by both sexes increased with age (males: food consumed = $-0.05 + .036(\text{age})$, $r^2 = 0.158$, $p < 0.01$, $n = 74$; females: food consumed = $0.07 + 0.015(\text{age})$, $r^2 = 0.071$, $p < 0.05$, $n = 74$) with the slopes between these regressions being significantly different ($F = 5.53$, $p < 0.05$). While the amount of food received did not differ significantly for any one age group, males received significantly more food than females when samples for all age groups were combined ($0.242 \text{ g} \pm 0.194$ (std. dev.) versus 0.190 ± 0.100 , $t = 2.02$, $p < 0.05$, $d.f. = 136$).

Differences in the amount of food received by males and females could be the result of parents either feeding males larger or more food items. The weights of food

Figure 1-9. Amounts of food consumed by 4 to 12 day old nestlings. Sample sizes are shown above bars. There are no significant differences between males and females for any one day.

samples showed a large amount of variation with dry weights ranging from 0.015 g (Conocephalus) to 1.135 g (Cicada). Thus, there existed the potential for parents to preferentially feed male nestlings larger food items. However, while dry weights of individual food items received by males were slightly larger, the difference was not significant ($0.128 \text{ g} \pm 0.145$ versus 0.108 ± 0.089 , $t = 1.38$, $p > 0.10$, d.f. = 265). Similarly, males received slightly more food items, but again the difference was not significant (1.88 ± 1.04 versus 1.77 ± 1.04 , $t = 0.589$, $p > 0.10$, d.f. = 136).

Parents might also defray costs of raising males by feeding them more nutritious food. While per gram caloric value has been found to vary little among small arthropods (Kale 1965), it is possible that orthopterans have a higher amount of undigestible chiton than do arachnids or lepidopteran larvae. Thus, I predicted that males should receive proportionately more of the latter two prey types in their diet. Contrary to the prediction, the diets of males and females were essentially the same (Table 1-2). When the analysis was restricted to nestlings greater than 8 days old (i.e. the most dimorphic group), diets remained similar.

Table 1-2. Number of food items by prey types fed to 5-11 day old male and female great-tailed grackle nestlings.

PREY TYPE	MALES		FEMALES	
	ALL	>8 DAYS	ALL	>8 DAYS
Orthoptera	65	36	66	35
Arachnida	40	20	51	20
Lepidoptera	10	6	14	0
Other	8	3	3	0
Unknown	5	1	8	2
Total	128	66	142	57

DISCUSSION

Based on oxygen consumption rates, female energy requirements were estimated to be only 83% of those by males over the total nestling period. Recall that female mass is only 65.9% of male mass by 12 days post-hatching. Thus, while female energy demands are substantially less than those of males, the difference is not proportional to the difference in mass between the sexes. Interspecific comparisons have shown that metabolic requirements vary with the 0.724 power of mass (Lasiewski and Dawson 1967). Applying this value intraspecifically, female grackle nestlings would be expected to require 69% of the total energy needed by males. Thus, the 83% of male energy required by females is greater than predicted by mass differences between the sexes. Absolutely then, male nestlings have higher metabolic costs than females but, relative to body size, females are more costly.

Reliable estimates of total energy requirements by nestlings are difficult to obtain. For example, it is probably not realistic to assume that oxygen consumption rates estimated over a short period each day are average daily values. Fiala and Congdon (1983) circumvented this problem by calculating energy requirements using doubly labelled water over a number of days. Thus, it is interesting to note that their estimates of metabolic rates of nestling red-winged blackbirds were approximately twice

that of earlier estimates (Brenner 1968, Dyer 1968). More specifically in terms of this study, we have no data concerning the demands of nestlings between 0 and 4 days post-hatching. However, because mass-specific oxygen consumption by great-tailed grackles increased between 5 and 11 days post-hatching, an observation consistent with studies of other altricial nestlings (e.g. Dawson and Evans 1957, Blem 1975, Bryant and Gardner 1979, Bucher 1983), I felt justified in extending the regression describing this relationship to predict values for younger nestlings. Despite these potential sources of error, estimates of gross energy requirements agree quite closely with those of Fiala and Congdon (1983) who estimated that female red-wings required 797 kJ of energy or 79% of that required by males (1014 kJ). In that female and male red-wings fledge at approximately 30 g and 40 g, respectively (Fiala 1981b), my estimates of 1182 kJ for females (fledging weight $\approx$ 70 g) and 1400 kJ for males (fledging weight $\approx$ 115 g), while slightly low, seem reasonable.

In addition to this study and that of Fiala & Congdon (1983), results from a study of rooks indicated that energy demands of male nestlings were higher than those of females, with the difference corresponding to size differences between the sexes (Slagsvold et al. 1986). Taken together, these investigations provide strong evidence that male nestlings, in sexually dimorphic icterid

species, have higher metabolic demands than females.

These results are in agreement with intersexual differences in food consumption by hand-reared great-tailed grackle nestlings. This study indicated that male nestlings consume more food than females of equal age and therefore require a greater absolute amount of food to be reared to fledging. The difference in food consumption over the 5-6 day study period is probably a minimum estimate for two reasons. First, the growth of hand-reared males was more depressed than that of females and thus differences in food requirements of nestlings reared in natural nests are probably larger. Second, since the disparity in size between the sexes continues to increase while the nestlings are under parental care (approximately another two weeks after fledging), food consumption differences probably continue to increase. These results agree closely with those of Fiala and Congdon (1983) showing that the gross energy intake of male red-winged blackbirds, from days 0 through 10, was approximately 1.3 times that of females. Therefore, the hypothesis that energy demands of male and female nestlings are similar, despite size differences, can be rejected for these species. It should be noted, however, that among raptors, a group in which females are larger than males, there is no evidence that size differences between male and female nestlings results in differing energy demands. Newton

(1978) found that male and female European sparrowhawk nestlings, despite large size differences, consumed similar amounts of food, and Collopy (1986) found no differences between male and female golden eagle nestlings in food consumption or energy metabolized. On the other hand, size differences between adult raptors does appear to lead to differences in energy demands (Mosher and Matray 1985; Kaiser and Bucher 1985). Further investigation concerning energy demands of nestlings that exhibit reversed sexual size dimorphism need to be conducted before generalizations can be applied to this group.

Results presented here suggest that females consumed slightly more food than males of similar weight. This is consistent with mass-specific oxygen consumption and confirms that, per unit mass, females have higher energy requirements than males. These results differ from those found for red-winged blackbirds in which males consumed slightly more food than females of similar weight (Fiala 1981b). However, because hand-reared nestlings in both studies suffered from reduced growth rates, energy requirements determined by oxygen consumption rates are probably more reliable.

It has been suggested that dimorphic nestlings might channel energy into different characters. Thus, while energy of the larger nestling is directed to structures which result in increased body weight, that of the smaller

sex may be diverted into other physiological characters which enable it to compete with its larger broodmates. Both Richter (1983) and Bancroft (1984) have implemented this hypothesis in explaining why feather development is more advanced in females than males in yellow-headed blackbirds and boat-tailed grackles. Data from this study do not support this interpretation. Despite more advanced feather development in females, the amount of weight gained per unit food consumed was similar for both sexes. Although it might be argued that the variability between nestlings masked potential differences, it is more likely that feather growth is not more costly to females than males. Female feather development, although initiated earlier, proceeds at a rate similar to males. Thus, on a daily basis, both sexes probably direct similar amounts of energy into feather development. Any added costs to the female should occur only during the initial stages of feather growth.

The results of this study did not support the possibility that parents could invest equally in sons and daughters, despite size differences, by feeding sons larger or more nutritious prey items. For these conditions to have been met would require that the energy expended during search and capture of the larger or more nutritious prey is not significantly greater than for the smaller or less nutritious prey. A second, although less stringent

assumption, is that daughters are unable to consume prey types or sizes fed to males. If this were not so, parents would be expending more energy than necessary in feeding the smaller sex. While the first assumption appears reasonable, the second seems less likely. If parents foraged opportunistically, however, one would expect some variance in the size and quality of prey types brought back to the nest. Subsequent differential distribution of prey types to nestlings could reduce or eliminate any differences in costs in rearing them. Because males and females received similar types of food, while males received more food than females, it appears that parents were not manipulating the distribution of prey types to balance investment in the sexes.

It is possible that despite cost differences in raising sons and daughters, parents simply cannot adjust the primary sex ratio as predicted by Fisher (1930), nor do they adaptively reduce the costs of raising sons by differential provisioning of food. Fisher's prediction of equal investment in sons and daughters might still be upheld if parents manipulate the sex ratio of their brood post-hatching such that fewer of the more costly sex are reared to independence. While there is evidence of non-random fledgling sex ratio biases in the predicted direction for a number of dimorphic species (see General Introduction), one should be cautious in invoking adaptive

explanations where none are warranted. Assuming that adults have a finite capacity for bringing food back to the nest, and that food is divided among nestlings more or less evenly, one would predict that males should suffer higher mortality than females, especially during times of food stress. This stress may be influenced by the sex ratio of the brood such that individuals having male siblings are under more stress than those having female siblings, as well as by environmental food shortages. I address these possibilities in the following two chapters.

CHAPTER 2

The Influence of Sibling Gender and the Sex Ratio
of the Brood on the Growth and Survival
of Great-tailed Grackle Nestlings

INTRODUCTION

The ability to gain access to parental resources should be an important factor in determining the relative success of individual nestlings and ultimately the entire brood. Available evidence suggests that the oldest nestling, because of its larger size, is in a better position to secure those resources. However, differences in size between nestlings need not be age-related. In many species that exhibit sexual size dimorphism, males may be significantly larger than females within a few days of hatching. If increased size provides a competitive advantage to males, one would predict that a nestling having all males siblings would receive less food than one having all female siblings. In addition, the overall sex ratio of the brood may affect the growth and survival of nestlings if the increased costs to parents in rearing broods containing proportionately more males result in nestlings obtaining less than sufficient food. However, while the growth and survival of altricial nestlings is known to be influenced by many factors, including habitat

(e.g. Quinney et al. 1986), time of the breeding season (e.g. Peterson et al. 1986), food abundance and quality (e.g. Bryant 1978), brood size (e.g. Coulson and Porter 1985), egg size (eg. Williams 1980) and hatching sequence (eg. Wilson et al. 1987), the possible effects of sibling gender and the sex ratio of the brood have been largely overlooked.

In the only study that has addressed this problem, Fiala (1981b) found that red-winged blackbird nestlings grew equally well in nests containing either predominantly males or females. Two considerations make a re-examination of this problem necessary. First, differences in growth would be most apparent in the youngest nestling. Since Fiala did not assess growth with respect to sequence, an effect of sibling gender on last-hatched nestlings may have been masked by lumping them with their older nestmates. Second, if females adaptively adjust the sex ratios of their broods prior to hatching to match their capabilities of rearing nestlings, then no differences in growth rates would be expected. For example, it is generally assumed that the number of eggs produced by a female is directly related to her ability to rear them. A finer level of control would be to vary the sex ratio of the brood such that a female in relatively good condition, for example, would produce all males while one in relatively poor condition, while still able to rear three offspring, could

only do so if they were females. If this were true, one would expect the sex ratio of the brood to influence neither the growth rate of individual nestlings nor the success of the nest.

In this investigation I examined the possible influence of sibling gender on the success of individual nestlings and entire broods in great-tailed grackles, a species in which pronounced differences in body sizes of males and females shortly after hatching result in sex-specific differences in energy demands (Chapter 1). To determine whether females produce broods having the number of sons and daughters that they can optimally rear, they were provided with foster broods that had a similar number of nestlings but with a potentially different proportion of males. If females do adjust the sex ratios of their broods, one could make the following predictions. First, overall growth rates of foster nestlings should be lower and more variable than those of controls. This would follow since the nestlings of females getting more males than expected should do more poorly than controls, while those of females getting fewer or the same number of males should do equally well. For similar reasons, starvation should be more pronounced in foster broods. Finally, the growth of males should be depressed when, because of nestling switches, they occur in a brood in which a female had been expected for that position in the hatching

sequence.

If females do not adjust the sex ratio of their broods then one would predict that (i) growth rates of male or female nestlings should be inversely correlated with the number of male siblings they have with this relationship being most apparent among youngest nestlings, (ii) the chance of all nestlings surviving in a brood should be inversely correlated to the proportion of males such that nests fledging all females should be more numerous than those fledging all males, and (iii) nests in which the last nestling is lost, presumably to starvation, should be characterized by a higher number of males among surviving nestlings.

METHODS

Clutch Switches

Forty-three three-egg clutches laid between 30 April and 17 May, 1987 were chosen from two separate colonies to monitor females' ability to raise broods with unexpected sex ratios. Twenty-two experimental females (11 pairs) had their entire clutches exchanged just prior to hatching with those of another female in the same colony whose first egg was due to hatch on the same day. While sex of these nestlings was unknown to me at the time switches were made, the resulting broods had to contain fewer, the same, or more males than originally expected. Sex was determined by mass and/or tarsus length after nestlings were at least five days old, an age at which there was little overlap for either of these variables between males and females (see Chapter 1). Nesting success and nestling growth (see below) for the 22 experimental nests were subsequently compared with those for 21 control nests located in the same colonies and having similar hatching dates. Measurements of nestlings in all nests took place on the day that the last nestling hatched and on every third day for nine more days. The last nestling was measured once more two days later. Thus, in nests in which all nestlings fledged, four sets of measurements were obtained for the first two nestlings and five measurements for the youngest nestling with the last set being obtained when it was 11

days old

Nestling Growth Rates

To determine the relative importance of sibling gender and other factors in affecting nestling growth rates, I measured all nestlings in selected nests over the three year period. I attempted to measure each nestling at least three times in 1985 and at least four times in 1986 and 1987 with the final measurements taken when nestlings were at least 8 days old. However, since predation during the nestling period resulted in larger samples for younger nestlings, I often measured previously unmeasured nestlings (of known age) that were 9 to 12 days old. Mass was determined to the nearest 0.1 g for nestlings less than 10 g and to the nearest 0.5 g for heavier nestlings while tarsus length was determined to the nearest 0.05 mm.

Analysis of Growth Rates

Two data sets were used to determine if sibling gender or the sex ratio of the brood affected nestling growth. The first consisted of measurements of all nestlings over the entire nestling period, regardless of the number of measurements taken for each individual. These data were subsequently subdivided such that growth rates of nestlings of different hatching sequence from broods of different sizes and sex ratios could be compared. The second data

set consisted of growth rates of individual nestlings that were measured at least four times with the last measurements being taken on or after 8 days post-hatching. This data set, although less extensive, allowed for control of other factors that might have affected growth rates that was not possible in the first analysis. To be included in this analysis, nestlings had to come from nests in which all eggs had hatched and in which siblings survived long enough to be sexed.

Preliminary analyses indicated that increases in mass and tarsus length fit a logistic curve as described in Ricklefs (1967). Estimates of the asymptote (A), maximum rate of growth (K), and day of inflection (I) for these curves were determined using the nonlinear curve fitting program (AR) in BMDP (Ralston 1985). To generate a biologically more meaningful (or at least more easily understood) parameter for comparisons of different groups of nestlings, I used values for A, K and I to estimate mass and tarsus length at day 12 (earliest fledging date) and present only these estimates in the Results. All values for A, K and I from which these values were derived can be found in Appendix 1. To test for differences for variability in natural growth rates, either between males and females or between individuals of the same sex but a different hatching sequence, I calculated $F_{\max}$ values from the ratios of the coefficients of variation for predicted

asymptotes (Lewontin 1966).

RESULTS

Clutch Switches

There was no evidence that females produced broods having sex ratios that reflected their own condition. Fledging success of experimental nests was slightly, although not significantly, higher than control nests (1.72 ± 1.28 versus 1.29 ± 1.35 , $t = 1.07$, $p > 0.10$, d.f. = 41) and starvation rates were similar for both experimental nests (7/22) and controls (5/21). If females produce broods having sex ratios that coincided with their own rearing capabilities, starvation should have been most likely when the last nestling to hatch was a male when a female was expected. However, in the seven cases of starvation in experimental nests, females expected a daughter twice and a male twice, with the sex of the other three expected nestlings unknown because of depredation at an early age.

There were no consistent differences in overall growth rates of nestlings raised in experimental ($n = 38$) and control ($n = 45$) nests and only one difference between groups of nestlings of similar hatching sequence (Table 2-1). Thus, while oldest males in control nests were significantly heavier than those from experimental nests, this pattern was not evident in other nestlings. Also, there were no significant differences in the variability of growth between control and experimental nestlings.

Table 2-1. Mass (± 1 std. dev.) at 12 days post-hatching for nestlings reared by their own (control) and by foster (experimental) parents. Significant differences between groups (* $0.05 < p < 0.10$, ** $p < 0.05$) were determined using t-tests for means and F-tests for variances.

	<u>FIRST TO HATCH</u>		<u>SECOND TO HATCH</u>		<u>THIRD TO HATCH</u>	
	M	F	M	F	M	F
CONTROL	109.9	68.1	113.7	72.3	93.7	65.4
	± 7.61	± 6.45	± 12.50	± 3.96	± 7.64	± 8.17
(N)	(9)	(7)	(6)	(11)	(8)	(4)
EXPERIMENTAL	98.9	70.4	106.9	71.3	95.6	68.9
	± 7.49	± 4.06	± 6.75	± 4.00	± 14.83	± 5.46
(N)	(4)	(11)	(8)	(6)	(5)	(4)
MEANS	**	NS	NS	NS	NS	NS
VARIANCE	NS	NS	*	NS	*	NS

Factors Affecting Nestling Growth Rates

(i) Measurements of All Nestlings

Based on the combined measurements of mass and tarsus length of all nestlings over three breeding seasons, individuals from broods of four grew as well as those from broods of three (Table 2-2A, B). The first two nestlings in broods of three and the first three nestlings in broods of four showed similar patterns of growth in mass and tarsus length, while growth of the youngest nestling for each brood size was depressed. In addition, coefficients of variation for predicted asymptotes of both mass and tarsus increased with hatching sequence indicating more variable growth among the youngest nestlings. For example, variation in mass was significantly different between nestlings of all hatching sequences with the exception of the first two females in both brood sizes and the first two males in broods of four. It is also apparent that males were more variable in growth than females. Differences between the sexes are significant for nestlings of all but the first nestlings in each brood size. Because tarsus growth varied little among nestlings of different hatching sequence, subsequent analyses will be restricted to mass.

The sex ratio of the brood appeared to have little effect on the growth rates of nestlings (Table 2-3). While males from broods of three appeared to grow somewhat better as the ratio of male to female siblings decreased, this

Table 2-2. Mass and tarsus length at 12 days post-hatching for (A) males and (B) females as a function of brood size and hatching sequence. N refers to the number of measurements used to derive logistic growth curves. Coefficients of variation are in parentheses.

(A) Males

HATCHING SEQUENCE	BROOD SIZE = 3			BROOD SIZE = 4		
	MASS	TARSUS	N	MASS	TARSUS	N
1	108.6 (.0104)	57.3 (.0077)	299	110.1 (.0150)	57.2 (.0083)	173
2	109.1 (.0149)	57.3 (.0072)	335	111.2 (.0171)	57.3 (.0099)	155
3	98.4 (.0215)	55.6 (.0121)	283	110.9 (.0312)	57.4 (.0165)	134
4				99.3 (.0669)	56.2 (.0327)	85
MEAN	106.3	56.8	917	110.0	57.3	545

(B) Females

HATCHING SEQUENCE	BROOD SIZE = 3			BROOD SIZE = 4		
	MASS	TARSUS	N	MASS	TARSUS	N
1	72.3 (.0078)	48.6 (.0047)	383	73.7 (.0127)	48.5 (.0088)	122
2	69.7 (.0103)	48.7 (.0063)	324	71.1 (.0103)	48.8 (.0088)	147
3	68.7 (.0159)	48.4 (.0081)	301	71.6 (.0164)	48.8 (.0107)	153
4				61.1 (.0341)	47.6 (.0179)	99
MEAN	70.7	48.6	1008	71.2	48.7	521

Table 2-3. Mass at 12 days post-hatching as a function of the sex ratio of the brood (males:females), brood size and hatching sequence. Number of measurements that curves are based on is given in parentheses.

(A) Males

Hatching Sequence	BROOD SEX RATIO						
	Brood Size = 3			Brood Size = 4			
	3:0	2:1	1:2	4:0	3:1	2:2	1:3
1	106.9 (55)	109.0 (129)	110.2 (68)	111.2 (14)	111.9 (33)	114.2 (35)	108.0 (13)
2	105.1 (52)	109.7 (140)	110.3 (100)	119.5 (15)	112.0 (29)	112.7 (31)	110.6 (17)
3	98.9 (49)	97.1 (149)	100.7 (85)	114.6 (14)	110.0 (26)	107.0 (31)	110.6 (11)
4				82.6 (19)	105.5 (26)	100.0 (26)	102.3 (11)

(B) Females

Hatching Sequence	BROOD SEX RATIO						
	Brood Size = 3			Brood Size = 4			
	2:1	1:2	0:3	3:1	2:2	1:3	0:4
1	73.4 (86)	72.6 (182)	70.1 (64)	73.4 (7)	72.0 (25)	73.5 (41)	77.0 (11)
2	68.0 (69)	70.4 (144)	68.8 (68)	72.7 (9)	71.4 (33)	72.2 (36)	70.9 (11)
3	65.7 (59)	70.5 (168)	66.1 (68)	69.4 (11)	73.1 (31)	71.0 (40)	73.6 (13)
4				69.0 (14)	55.6 (34)	63.0 (38)	72.8 (13)

trend was not as apparent in nestlings from broods of four. Note, however, that the lightest male nestlings at 12 days post-hatching were those having three older male siblings. There was little evidence that female growth rates were influenced by the overall sex ratios of the brood. One possible exception was that oldest females in broods of four were heavier in nests containing fewer males.

Growth Rates of Individual Nestlings

To examine the possible effects of the sex ratio on the growth of nestlings while controlling for variation in growth due to year and hatching sequence, the mass at day 12 of each nestling was expressed as the number of standard deviations from the average for individuals from its year and sequence cohorts. The sex ratio (expressed as the number of males in a brood) did not affect female growth in either broods of three ($y = 0.108x - 0.127$, $r^2 = 0.074$, $p = 0.370$, $n = 148$) or broods of four ($y = -0.190x + 0.326$, $r^2 = 0.164$, $p = .190$, $n = 66$). There was a small, but significant correlation between the sex ratio of the brood and mass of males at day 12 in broods of three ($y = -0.243x + 0.476$, $r^2 = 0.177$, $p = 0.033$, $n = 145$) but not four ($y = 0.007x + 0.008$, $r^2 = 0.007$, $p = .958$, $n = 61$).

Two other variables, egg mass and hatching date, were examined for possible influence on nestling growth while, again, controlling for year and sequence related variation.

While the size of eggs contributed significantly to variation in male mass at day 12 ($r^2 = 0.275$, $p < 0.001$, $n = 150$), it did not influence female mass ($r^2 = 0.130$, $p = 0.133$, $n = 134$). The relationship between hatching date and variation in growth was somewhat more confusing. While hatching date did not influence growth for males in 1985 ($r^2 = -0.017$, $p = 0.877$, $n = 81$) there was a weak negative correlation in 1986 ($r^2 = -0.200$, $p = 0.078$, $n = 81$) and a weak positive correlation in 1987 ($r^2 = 0.191$, $p = 0.084$, $n = 79$). Hatching date was not correlated with growth of females in either 1985 ($r^2 = -0.132$, $p = 0.240$, $N = 81$) or 1986 ($r^2 = -0.144$, $p = 0.310$, $n = 81$) while the two variables were positively correlated in 1987 ($r^2 = 0.257$, $p = 0.019$, $n = 81$).

Sex Ratio of Broods and Nesting Success

Patterns of starvation provide little support for the prediction that nestlings would be more likely to starve when older siblings are males than when they are females. Thus, while the youngest nestling was lost least frequently when its older siblings were both females in broods of three, starvation appeared to be most frequent in nests that contained a male and a female, rather than two males, as the oldest nestlings (Table 2-4). In broods of four, starvation was, in fact, slightly (although not significantly) higher when the oldest three nestlings

Table 2-4. Sex-specific hatching sequence of broods in which the youngest nestling starves. The sex of the nestling that starved is denoted by parenthesis. Nestlings that starved before their sex was determined are designated as 'U'.

SEX SEQUENCE	1985	1986	1987	Σ
M M (M)	0	0	2	2
M M (F)	0	0	2	2
M M (U)	0	6	4	10
M F (M)	1	0	1	2
M F (F)	0	1	1	2
M F (U)	1	10	8	19
F M (M)	0	1	1	2
F M (F)	0	0	0	0
F M (U)	1	12	4	17
F F (M)	1	0	1	2
F F (F)	0	0	1	1
F F (U)	1	2	6	9

contained proportionately more females (Table 2-5).

It is apparent, however, that broods of three that contained mostly males were less likely to fledge all nestlings than those that contained mostly females (Table 2-6). Although the differences are not significant, of 163 nests in which all nestlings fledged, 98 contained two or three females while only 65 contained two or three males. When broods of four were considered, however, sex ratios at fledging did not differ from those expected if nestling loss occurred randomly (Table 2-7).

Table 2-5. Sex-specific hatching sequence of the first three nestlings of four-nestling broods for nests in which the youngest nestling starved.

SEQUENCE	1985	1986	1987	Σ
M M M (-)	4	4	2	10
M M F (-)	1	6	1	8
M F M (-)	4	4	2	10
F M M (-)	1	3	2	6
M M U (-)	0	4	3	7
M F F (-)	3	6	3	12
F M F (-)	2	8	4	14
F F M (-)	2	9	5	16
F F F (-)	0	8	2	10
F F U (-)	0	3	0	3

Table 2-6. Sex-specific hatching patterns for three-nestling broods in which all nestlings fledge or are depredated at the same time. Initial clutch size was three in each case. Observed frequencies did not differ significantly from random ($\chi^2 = 10.02$, $p > 0.10$).

SEX SEQUENCE	ALL FLEDGE				ALL DISAPPEAR			
	1985	1986	1987	Σ	1985	1986	1987	Σ
M M M	2	10	1	13	2	1	2	5
M M F	3	11	3	17	1	3	0	4
M F M	3	7	8	18	3	1	4	8
F M M	5	7	5	17	0	0	4	4
M F F	4	11	5	20	0	1	2	3
F M F	4	16	10	30	1	4	1	6
F F M	3	13	9	25	3	1	0	4
F F F	2	13	8	23	1	2	1	4

Table 2-7. Sex ratios of four-nestling broods in which all nestlings fledged or were depredated at the same time. Initial clutch size was four in each case. Observed frequencies did not differ significantly from random ($\chi^2 = 3.94$, $p > 0.10$).

SEX RATIO	ALL FLEDGE	ALL DEPREDATED	OBS
4 : 0	4	0	4
3 : 1	12	2	16
2 : 2	18	7	25
1 : 3	15	0	15
0 : 4	2	1	3

DISCUSSION

Providing females with broods having potentially different numbers of male and female offspring than expected did not affect the growth or the survival of nestlings. Although sample sizes were small, these data support other studies that suggest sex determination in birds is random and that females cannot adjust primary sex ratios in order to produce broods having the number of sons and daughters that they are most capable of rearing. For example, in the most detailed analysis of natural variation in offspring sex ratios, Fiala (1981a) found that sex ratios of red-winged blackbird broods deviated little from a binomial distribution of the sexes and that sex ratios were not correlated with laying sequence, egg size, clutch size or harem size. In addition, neither Patterson and Emlen (1980) nor Weatherhead (1983) found evidence of adaptive sex ratio manipulation in studies designed specifically to detect it. On the other hand, slight seasonal correlations with sex ratio variation have been noted by Howe (1977), Fiala (1981) and Weatherhead (1983) although it is unclear whether these represent adaptive responses by females.

Given that the proportion of males produced in a brood is random, and that males are more costly to rear than females, one might predict that nestlings in nests containing mostly males would grow less well than in nests

containing mostly females. Evidence provided here, however, suggests that any effects of the overall sex ratio of the brood on individual nestling growth is minimal. While male mass at day 12 was significantly correlated with the proportion of males in broods of three, the sex ratio accounted for very little of the overall variation in mass even after controlling for variation due to year and hatching sequence. There was no correlation between mass and the sex ratio of the brood for males in broods of four nor females in either brood size. Most importantly, youngest nestlings grew equally well regardless of whether older siblings were predominantly male or female and there was no tendency for starvation to occur more frequently when the oldest nestlings were males rather than females. Thus, there was little evidence that the food demands of older siblings influenced the growth or survival of the youngest nestlings. While these results do not support the above prediction, they do agree with those of Fiala (1981b) who found that the proportion of males in broods of red-winged blackbirds did not influence the growth of nestlings. It is possible that any potential effect of sibling gender on nestling growth in both of these species is reduced by variation due to hatching sequence.

Hatching asynchrony might effectively buffer older nestlings from the potential effects of other variables that might affect growth, including the sex ratio of the

brood, by concentrating these effects on the youngest nestling. This notion is, in fact, central to Lack's (1954) adaptive explanation of hatching asynchrony. That is, asynchronous hatching of eggs when food conditions are limiting should result in the youngest nestling being quickly eliminated from the nest so that the food demands of the remaining nestlings can be adequately met. Great-tailed grackle eggs hatch asynchronously (Chapter 3) and the mass of nestlings at 12 days post-hatching was influenced most strongly by sequence of hatching. Thus, while the first two nestlings in broods of three and the first three nestlings in broods of four did equally well, the youngest in each brood size, regardless of its sex, grew more slowly. In addition, variability in growth increased with hatching sequence. These results agree with those found by Bancroft (1984) for boat-tailed grackles. Bancroft also noted that at least some of this variability could be attributed to variation in hatching spread of the eggs. If clutches were manipulated to reduce or eliminate hatching asynchrony, one would predict that the growth of all nestlings would be influenced more by environmental variables, including the sex ratio.

Richter (1983) suggested that male offspring might receive more food than female offspring only when conditions are favourable. If this is true, then male growth should be more dependent than female growth on

favourable conditions and therefore should be more variable than that of their sisters. The growth of males in great-tailed grackles, especially among youngest nestlings, is more variable than female growth. Comparisons between male and female growth in a number of other sexually dimorphic species reveal a similar pattern (Howe 1979, Moss 1979, Fiala 1981b, Bancroft 1984). In addition, besides the effect of the sex ratio on males in broods of three, both egg mass and hatching date appear to affect male growth to a greater degree than they affect female growth. Males grew somewhat better earlier in the breeding season in 1986 while the opposite trend was apparent in 1987. This was probably a function of differing patterns of rainfall between the two years (Chapter 3). In any case, this further supports the idea that males, because of higher food demands, are more likely to be influenced by environmental factors than are females.

Finally, the likelihood that all nestlings in a nest will fledge, at least for broods of three, appeared to be influenced by the proportion of males in the brood. This is surprising given the above results as it suggests that the sex ratio of the brood does, in fact, influence nestling survival. One possibility is that male nestlings, because of increased food demands, may be more likely to vocalize their needs to parents. If these vocalizations can be used as cues by predators, complete broods

containing all or mostly males would be underrepresented at fledging (Charnov 1982). It is still not clear, however, why broods of four did not show a similar trend. It is possible that females that lay four-egg clutches are in much better condition than those laying three eggs and thus are more capable of meeting their food demands.

Alternatively, the sample of four-nestling broods may have been too small to reveal any biases. It is clear that well designed experiments are needed to address this problem further. In particular, studies concerning the begging rates of male and female nestlings when under food stress and the response by predators to these calls would be valuable.

CHAPTER 3

Biased Fledgling Sex Ratios in Great-tailed Grackles:
Nonadaptive Sex-Specific Mortality

INTRODUCTION

Differences in the amount of energy that parents invest in sons and daughters should be reflected in the sex ratio at the end of parental care (Fisher 1930). Thus, species in which males are larger, and presumably more costly to rear, should be characterized by a fledgling sex ratio biased in favour of females with the extent of this bias reflecting the relative size disparity between the two sexes. Altricial species of birds in which size differences between males and females develop soon after hatching should be an appropriate group in which to search for evidence of adaptive sex ratio manipulation. However, while investigations of these species have not generally supported Fisher's theory, a number of studies have shown that, under certain conditions, males may be underrepresented at independence (e.g. Howe 1976, Wegge 1980, Cronmiller and Thompson 1981).

Since there is little evidence of skewed secondary (hatching) sex ratios in birds (reviewed by Clutton-Brock 1986 and Slagsvold *et al.* 1986), it has been suggested that any bias at the time of fledging is the result of

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differential mortality of males and females. In particular, it appears that males may suffer higher mortality when placed in food-limited or stressful situations such as those that would be found in enlarged broods (Cronmiller and Thompson 1981, Roskaft and Slagsvold 1985) or faced by youngest nestlings (Howe 1976, Bancroft 1983). However, no investigations have directly examined the effect of naturally occurring starvation on fledgling sex ratios.

It is clear that levels of food availability, whether measured directly (e.g. Bryant 1975, Quinney et al. 1986) or indirectly (e.g. Murphy 1985, Peterson et al. 1987), affect the growth and/or survival of nestlings. However, it is important to note that food shortages may not affect all nestlings in the brood equally. In many altricial species incubation begins before the final egg and, as a result, eggs hatch asynchronously and pronounced size differences are established between nestlings. This results in the youngest (and subsequently smallest) nestling being most likely to starve during periods of food shortage (e.g. Howe 1976, Clark and Wilson 1981, Bancroft 1983).

Higher food requirements of males, in conjunction with variation in food abundance and within brood patterns of mortality due to asynchronous hatching, lead to a clear prediction concerning potential sex ratio biases in

sexually dimorphic species. Specifically, when food is limiting, sex ratios at fledging should be biased in favour of females with much of this bias being the result of differential mortality among youngest nestlings. In this investigation I provide information on (i) possible variation in food abundance over a three year investigation of great-tailed grackles, (ii) the degree of asynchronous hatching in this species and how it influences size disparity among nestlings, and (iii) the relationship between fledgling sex ratios and levels of starvation occurring between years or between colonies within years. In addition, I present the results of an experiment designed to reduce the effects of asynchronous hatching such that the two youngest nestlings were both subjected to similar and potentially stressful conditions. In doing this, my aim was to determine whether males were more likely than females to be negatively affected by such conditions.

METHODS

Nest Checks

Great-tailed grackle nests were monitored from April to August, 1985 to 1987 on the Welder Wildlife Refuge as described in the general methods. Eggs were marked sequentially as they were laid and checked to see if they were being incubated. Preliminary analyses showed length and width of eggs (measured to the nearest 0.05 mm) to be highly correlated with egg mass ($r^2 = 0.962$) as determined by measurements of all three variables for 100 eggs in 1985. Thus, all egg masses reported here are estimated from the equation:

$$M = 0.0036L^2 + 0.07174W - 11.1211$$

Starvation Indices

Nestlings that were present on one visit and missing the next were assumed to have disappeared at the midpoint between these two visits. While it was often possible to predict which nestlings were going to starve based on their relative size and behaviour (hungry nestlings were extremely vocal), infrequent nest visits during the nestling period increased the chance of making an error in determining the cause of death of an individual. Thus, I objectively estimated rates of starvation using two methods. First, assuming that only the youngest nestling was likely to starve, I examined the frequency at which the

youngest nestling disappeared between subsequent nest checks. Since it was possible that some of these nestlings were lost to predators, I subtracted from this value the rate of predation estimated from the average frequency that older nestlings disappeared. Thus, theoretical values for this index range from zero to one with higher values indicative of higher rates of starvation.

Because the potential effect of starvation on fledgling sex ratios may have been at least partially masked by the effect of predation before nestlings left the nest, I also estimated starvation using the proportion of fledglings that hatched from the last egg. Therefore, while the first index more accurately reflects the actual level of starvation in a year or area, the second should more accurately reflect the influence that starvation has on fledgling sex ratios. Of course, if predation is equally likely to occur on nests regardless of sex ratio or starvation, there should be a high (negative) correlation between these two indices.

Experimentally Induced Hatching Synchrony in the Two Youngest Nestlings

In order to compare the growth and survival of males and females when placed under similar and potentially stressful conditions, I conducted a series of egg and nestling switches between 2 and 30 June 1987. Clutches or

broods were manipulated, within a day of hatching, to create 56 nests in which the youngest two nestlings were the same age (to the nearest $1/2$ day). While the sex of nestlings was unknown at the time experimental nests were created, it was assumed that manipulations should result in two males (MM), a male and a female (MF), and two females (FF) in a 1:2:1 ratio. Growth of the two youngest nestlings in each nest (hereafter referred to as experimental nestlings) was determined by recording mass (to the nearest 0.5 g), tarsus length, and length of the 9th primary (both to the nearest 0.05 mm) on every second day until they disappeared or fledged. Nestlings were assumed to fledge if they were still in the nest at 11 days post-hatching.

RESULTS

Potential Variability in Food Abundance Between Years
as Indicated by Clutch Size, Egg Size and Rainfall

Although food abundance was not measured directly, evidence from other studies suggest that both egg and clutch sizes often reflect local resource abundance (e.g. Murphy 1985, Hessel and Quinney 1987). Clutch size ranged from one to five eggs with three and four-egg clutches being most frequent in all years (Fig. 3-1). The average number of eggs laid by females, however, differed significantly between years. Average clutch size in 1985 (3.45 ± 0.65 (std. dev.)) was significantly greater than that in 1986 (3.34 ± 0.62 ; $t = -2.47$, $p < 0.05$) and 1987 (3.18 ± 0.61 ; $t = 6.23$, $p < 0.01$) while clutches in 1986 were larger than those in 1987 ($t = 4.81$, $p < 0.01$).

The mass of eggs generally increased over the first two eggs (in three-egg clutches) or three eggs (in four-egg clutches) with the last laid egg being slightly lighter than the penultimate (Fig. 3-2). Although within clutch variation in egg mass was similar for three and four-egg clutches in all three years, there were significant differences in the sizes of eggs between years (ANOVA for repeated measures, three-egg clutches: $F = 7.26$, $p < 0.001$; four-egg clutches: $F = 4.88$, $p < 0.01$). Eggs were smaller in 1987 than the previous two years for both clutch sizes while eggs were lighter in 1986 than in 1985 for four-egg

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Figure 3-1. Distribution of clutch sizes in 1985, 1986,
and 1987.

Figure 3-2. Variability in egg mass (mean $\pm$ 1 std. err.)
between years (1985 - ●, 1986 - o, 1987 - *)
for clutches of (A) three and (B) four eggs.

LAYING SEQUENCE

clutches.

Variation in egg and clutch size may have been related to the pattern of rainfall over the three years and its accompanying effect on insect abundance. Rainfall between January and May was greater than normal (31.4 cm, average from 1956 to 1987) in 1985 (45.8 cm) while below normal in 1986 (21.6 cm) and 1987 (27.4 cm). The amount of rainfall in the months directly preceding egg-laying may be most important in terms of limiting egg and clutch size. While 21.7 cm of rain fell between March and April of 1985 (with more than 15 cm occurring a few days after the initiation of nest-building), total precipitation in March and April of 1986 and 1987 amounted to only 4.4 and 2.0 cm, respectively, well below the average of 9.00 cm.

Water levels of the lakes in which grackles nested provide another index of moisture-related environmental conditions that may be more indicative of differences in water availability over the three years. Because of the heavy rainfall in April noted above, water levels were substantially higher in 1985 than either of the other two years (Fig. 3-3). Between April and August, lake levels generally decreased with the exception of 1987 in which heavy rainfall in June resulted in rising water levels. However, as this occurred during the latter part of the nesting cycle, and any effects on insect abundance would have experienced some time-lag, it is questionable whether

Figure 3-3. Lake levels in 1985 (+), 1986 (x), and 1987 (*).

DATE

- it would have affected food levels significantly.

Asynchronous Hatching

Incubation of three-egg clutches usually began after the second or third egg was laid while that for four-egg clutches began after the second, third or fourth eggs (Fig. 3-4). Variability in the onset of incubation affected the synchrony of egg hatching with early incubation resulting in a longer period between the hatching of the first and last egg (Fig. 3-5). Not surprisingly, the amount of time between hatching of the first and last eggs is positively correlated with the difference in masses of the youngest and oldest nestlings on the day the last egg hatches (Fig. 3-6).

Fledgling Sex Ratios

Significantly more females than males fledged over the three years of the study (Table 3-1). While the sex ratio did not differ from unity in 1985, proportionately more females fledged in 1986 and 1987. While the difference is significant only in 1986, it should be noted that a similar proportion of fledglings were males in 1987, but a smaller sample size rendered the difference insignificant.

Eggs almost always hatched in the order that they were laid. For 1056 eggs from three and four-egg clutches for which laying and hatching order were both known, less than

Figure 3-4. Day on which incubation begins for three and four-egg clutches.

Figure 3-5. The number of days between the hatching of the first and last egg in clutches of (A) three and (B) four as a function of when incubation had begun.

Figure 3-6. The difference in mass between the oldest and youngest nestlings in clutches of (A) three and (B) four on the day that the youngest nestling hatched.

Table 3-1. Yearly fledgling sex ratios. Totals include all fledglings from Table 2 as well as 11 males and 5 females which fledged from nests for which the clutch size was unknown.

YEAR	MALES	FEMALES	UNKNOWN	% MALES	p
1985	168	163	8	50.8	NS
1986	419	495	20	45.8	<0.01
1987	180	210	0	46.1	NS
TOTAL	767	888	28	46.7	<0.01

1% hatched out of sequence (5 of 513 in three-egg clutches and 5 of 533 in four-egg clutches). Thus, subsequent discussion of sequence-related hatching trends is applicable to both laying and hatching sequence. It should be noted, however, that if males and females differed in their patterns of mortality, then sequences of males and females at fledging may not directly reflect laying sequences.

When the numbers of males and females that fledged are examined with respect to the order in which they hatched (hereafter referred to as the sex-sequence), it appears that most of the bias in the overall sex ratio is due to more females fledging from the last egg (or youngest nestling) (Table 3-2). In two egg-clutches, for example, nearly twice as many females fledged from the second egg, resulting in an overall fledgling sex ratio of 24 males to 36 females. However, neither the sex-specific hatching sequence nor the overall sex ratio differed significantly from random (sequence: $G = 1.16$, $p > 0.05$; sex ratio: $G = 1.72$, $p > 0.05$). In three-egg clutches, more females fledged from all three eggs, particularly the first and third (sequence: $G = 0.62$, $p > 0.05$; sex ratio: $G = 5.12$, $p < 0.05$). The overall sex ratio from four-egg clutches is slightly, although not significantly skewed in favour of females with the difference again being most apparent in the youngest nestling (sequence: $G = 3.70$, $p > 0.05$; sex

Table 3-2. Fledgling sex ratios broken down by hatching sequence.
 Individuals whose sex or hatching sequence was unknown
 are designated as 'U'.

CLUTCH SIZE	SEX	HATCHING SEQUENCE						Σ
		1	2	3	4	5	U	
1	M	2					0	2
	F	2					0	2
	U	0					0	0
2	M	14	10				0	24
	F	15	19				2	36
	U	0	0				0	0
3	M	129	138	101			23	391
	F	152	152	128			25	457
	U	1	2	5			1	9
4	M	93	85	92	38		21	329
	F	83	93	92	55		26	349
	U	4	2	4	7		2	19
5	M	1	4	1	2	1	1	10
	F	6	3	4	2	0	4	19
	U	0	0	0	0	0	0	0

ratio: $G = 0.36$, $p > 0.05$).

As three and four-egg clutches were most common in all three years it is useful to compare yearly sex-sequence patterns in these two clutch sizes (Table 3-3). While sex-sequence patterns only approach significance for broods of four in 1985, a number of points are worth mentioning. In 1985, for example, males and females were randomly spread among hatching sequence in broods of three while a higher proportion of males fledged from the first and third eggs and more females fledged from the second egg in broods of four (sequence: $G = 6.76$, $0.1 > p > 0.05$). In 1986, overall female biases were largely the result of a greater proportion of females fledging from the last egg of both brood sizes. In 1987, on the other hand, the overall female bias appeared to be the result of proportionately more females fledging in broods of three, regardless of hatching sequence, with no apparent difference in clutches of four. Unfortunately, the paucity of four-egg clutches in 1987 (see above) makes it difficult to assess sex ratios in this category.

In summary, equal numbers of males and females fledged in 1985, a year characterized by above average rainfall, large clutch sizes, and heavy eggs. In both 1986 and 1987, when rainfall was below average, and clutch and egg sizes were significantly smaller, fledgling sex ratios were biased in favour of females. This suggests that in years

Table 3-3. Annual variation in sequence-related fledgling sex ratios from clutches of three and four.

YEAR	SEX	CLUTCH SIZE = 3				CLUTCH SIZE = 4				
		1	2	3	U	1	2	3	4	U
1985	M	20	20	17	1	30	20	31	16	4
	F	22	22	17	3	15	27	21	18	5
1986	M	68	78	55	11	48	50	48	19	13
	F	79	79	76	16	51	51	56	32	18
1987	M	41	40	29	11	15	15	13	3	4
	F	51	51	35	6	17	15	15	5	3

of low food abundance, males may be less likely to survive than females. In addition, most of this bias was apparently the result of more females than males fledging from the last-hatched nestling although data for three-nestling broods in 1987 suggest that biases may sometimes occur in the first two nestlings.

Starvation and Biased Sex Ratios

Potential differences in food availability in 1986 and 1987 suggest that starvation may be responsible for female-biased sex ratios in those two years. Recall that higher levels of starvation are indicated by higher values for the first index and lower values for the second. Starvation indices for the three consecutive years were .114, .223 and .303 when calculated on the basis of individual nestling losses (Index 1). The proportion of all fledglings that hatched from the last egg were similar in 1985 (.234) and 1986 (.236) but were substantially lower in 1987 (.209) (Index 2). Thus, the first index of starvation correlates well with the proportion of males that fledged in each year while, somewhat surprisingly, this pattern was not as obvious from the second index.

As mentioned previously, grackle nests were aggregated in stands of cattails or bulrushes found near open bodies of water. While some nests were more widely dispersed, colonies were, for the most part, clearly defined on the

basis of location and nesting synchrony. As a consequence, different colonies exhibited unique levels of starvation and predation. Therefore, because of the difficulty in drawing conclusions on the basis of three points representing yearly sex ratios and starvation rates, I also examined whether variation in colony fledgling sex ratios was influenced by the degree of starvation in those colonies.

Levels of starvation as determined by patterns of individual nestling loss were strongly correlated with colony sex ratios (Fig 3-7A). Thus, in areas in which starvation was high, the proportion of fledglings that were males decreased. As with the yearly comparison, however, this pattern is less obvious when starvation rates are calculated on the basis of sequence-related fledgling success (Fig. 3-7B). While the relationship conforms to the prediction that fewer males should fledge in colonies in which the last nestling is less likely to fledge, the correlation is not as strong as when the index is determined by patterns of nestling loss throughout the nestling period.

Are Females Better Survivors than Males?

If it is assumed that the secondary (hatching) sex ratio is randomly determined, biased fledgling sex ratios must be the result of differential mortality of males and

Figure 3-7. The proportion of fledglings which are male as a function of the level of starvation in a particular colony. Points represent colonies in which at least 50 nestlings fledged. Refer to text for details of starvation indices. The correlation is significant for the first index ($r_s = -0.872$, $p < 0.01$) but not the second ($r_s = 0.374$, $p > 0.05$).

females. In order to examine this more closely, I conducted a series of nestling switches resulting in the two youngest nestlings being the same age. In doing so, I hoped to create a situation in which any potential growth and/or survivorship differences were gender rather than age-related. If males are more likely to starve because of increased food demands, then one would predict that (a) differential mortality in these nests would result in female-biased sex ratios by fledging in experimental but not older nestlings, and (b) growth of males should be more severely affected than growth of females.

Predation on artificially created broods was high with 35 of 56 manipulated broods being depredated before any nestlings fledged. Of the remaining 21 broods, 12 fledged all young and 9 fledged some young. A total of 24 non-experimental nestlings (the oldest nestling in each brood) and 31 experimental nestlings (switched nestlings of the same age) fledged.

Although the small number of fledglings makes statistical analysis difficult, the predicted trends are apparent. Thus, while there were no differences in the numbers of males and females that fledged from non-experimental nestlings, males were apparently under-represented at fledging among experimental nestlings (Table 3-4). Growth rates of experimental nestlings lend further support to the hypothesis that, because of increased food

Table 3-4. Fledgling sex ratios in artificially manipulated broods in which the two youngest nestlings (experimentals) are the same age.

	BOTH	ONE	NEITHER	
	EXPERIMENTAL	EXPERIMENTAL	EXPERIMENTAL	
	NESTLINGS	NESTLINGS	NESTLINGS	
	FLEDGE	FLEDGE	FLEDGE	Σ
OLDEST	5 : 8	4 : 4	3 : 0	12 : 12
EXPERIMENTAL	9 : 15	3 : 4	-----	12 : 19
TOTAL	13 : 23	7 : 8	3 : 0	24 : 31

demands, males suffer more than females under food limiting conditions. When both experimental nestlings fledged, they consisted of two males (MM) once, a male and female (MF) seven times, and two females (FF) four times. The two males from MM broods suffered greatly reduced growth compared to those having female siblings (Fig 3-8A). In addition, both males were losing weight at the time they were last measured and did not likely survive to independence. Females, on the other hand, while growing slightly better when placed with other females, appeared to be less affected by the gender of their siblings (Fig 3-8B).

Figure 3-8. Growth rates of experimental (A) males and (B) females in nests containing a similar aged nestling of the same (●), or opposite (○) sex.

AGE (days post-hatching)

DISCUSSION

The results of this study suggest that food abundance varied between years with resources being more plentiful in 1985 than in either 1986 or 1987. Although food abundance was not measured directly, egg and clutch sizes are known to reflect existing levels of food availability. A number of studies have found clutch size to be positively correlated with natural food abundance during the period of egg formation (Perrins 1965, Southern 1970, Bryant 1975, Andersson 1981, Hessel and Quinney 1987) and a predicted increase in clutch size has been demonstrated in at least two species when provided with supplemental food (Newton and Marquiss 1981, Hogstedt 1981). Similarly, egg mass is considered to be influenced by female body condition at the time of egg-formation and laying (Murphy 1986) resulting in a positive correlation between egg size and food availability (Murphy 1985, Mills 1979, Winkler and Walters 1983, Pierotti and Bellrose 1986, Jarvinen and Ylimaunu 1986). Given this, and the below average rainfall in both 1986 and 1987, it is probable that food was more limiting in these years than in 1985.

In great-tailed grackles, as with many other species, the initiation of incubation before egg laying has been completed results in initial size disparities between nestlings. Subsequently, the youngest nestling in a brood is most likely to suffer when food is limiting. If males

are more prone to starvation because of increased metabolic demands, then hatching asynchrony, combined with environmental food scarcity, should result in biased fledgling sex ratios in the last nestling to hatch. Evidence presented here suggests that this is the case. It must be noted, however, that biased sex ratios in 1987 were also the result of more females fledging from earlier hatching eggs. In addition, in 1987 the youngest nestling in broods of four was equally likely to fledge as its older siblings. While the latter may simply be the result of sampling bias due to a small number of four-egg clutches in 1987, it is more difficult to understand why female fledglings outnumber males from hatching sequences that are less prone to food stress. In chapter two, I proposed that a higher proportion of males in a nest might result in a higher level of food stress because of the increased demands of the total brood. If nestlings actively voiced their hunger levels to parents, and if predators used these vocalizations to find nests, then broods containing more males would be more prone to predation (Charnov 1982). This would result in a decrease in the number of males that fledged regardless of hatching sequence. This might also explain why the two starvation indices were not more highly correlated.

By manipulating broods such that the two youngest nestlings were the same age, I hoped to expose males and

females to similar and potentially stressful conditions.

Because the sex of nestlings was unknown at the time that switches were made, I assumed that males and females were equally represented. Given that there have been no studies that have documented biased sex ratios at hatching (see General Introduction) and that the fledging sex ratio of the nonmanipulated nestlings for this experiment was one to one, this assumption is probably valid. Although high levels of predation greatly diminished the expected number of fledglings, the greater number of females than males reaching independence in experimental nests, supported the hypothesis that differential mortality due to food limitation may result in biased fledgling sex ratios.

With the exception of broods of four in 1985, there was no evidence to suggest that females adaptively) manipulated the order in which males and females were produced. Sequence-related biases in the number of males and females that reach independence may be the result of nonrandom hatching patterns, differential mortality of one sex hatching from certain eggs, or both. Nonrandom production of males and females from eggs of different laying sequence has been found in snow geese (Ankney 1982), ring-billed gulls (Ryder 1983), red-winged blackbirds (Weatherhead 1985) and bald eagles (Bortolotti 1984).

Others, however, have found no sequence related biases when looking at closely related or the same species (snow geese,

Cooke and Harmsen 1983), herring gulls (Larus argentatus, Ryder and Termaat 1987), Canada geese (Branta canadensis, Leblanc 1987). Among species closely related to great-tailed grackles, there were no significant sequence-related trends in either common grackles (Howe 1976) or boat-tailed grackles (Bancroft 1983).

Are Biased Fledgling Sex Ratios Adaptive?

Fisher (1930) predicted that the ratio of males to females at the end of parental care should reflect their relative costs. Subsequently, studies that have found female biased fledgling sex ratios have been used as evidence in support of Fisher's model (e.g. Cronmiller and Thompson 1981, Slagsvold et al. 1986). I suggest, however, that there is no reason to invoke an adaptive explanation concerning skewed sex ratios in dimorphic species and that high mortality among male nestlings may simply be a cost of increased size. To properly evaluate these hypotheses, it is necessary to state specifically the predictions of each and examine the evidence in light of these predictions.

The basic premise put forth by Fisher is that natural selection should favour females that invest equally in sons and daughters. One way that this could be accomplished in a species in which males are more costly to produce than females is through differential segregation of chromosomes such that there is an overproduction of females at

fertilization. Assuming that males and females are equally likely to survive, this would result in the total investment in both sexes being equal at the end of parental care with the sex ratio being biased in favour of females. However, there is no evidence that this occurs in birds (Charnov 1982, Clutton-Brock 1986). Therefore, any adaptive response by females that is meant to equalize investment in sons and daughters must occur after hatching. This would require that (1) females are able to recognize the gender of their offspring and (2) that they actively remove male offspring from nests with this selective elimination of certain offspring presumably occurring before substantial investment had already been made. Gender recognition would be most likely to occur in species in which males are visually distinguishable, either because of size or plumage differences, from females. While I know of no studies that have examined this problem directly, it has been suggested that parents might divide broods on the basis of nestling gender (see Price and Gibbs 1987). However, brood reduction in altricial birds is generally considered to be a passive phenomenon and active manipulation of brood sizes by females is probably rare (although see Burley 1986). Note also that this manipulation should be independent of environmental conditions since its function is to create broods in which overall investment in males and females is equal regardless

of overall food demands or availability. Evidence presented in this and the previous chapter, however, suggests that male great-tailed grackle nestlings suffer higher nestling mortality than female nestlings only when placed in stressful or food-limiting situations.

It is interesting that Selander (1960, 1961) found no evidence of a biased sex ratio in nestling great-tailed grackles. Unfortunately, Selander's data are of little use in this analysis for two reasons. First, sex ratios were examined only during a brief period and it is unknown if food was limited during that period. Second, sex ratios were based on nestlings of all ages. This would reduce any potential bias since sex-specific mortality would be more pronounced later in the nestling period.

It is clear that patterns of nestling mortality in other species that exhibit sexual size dimorphism are not independent of sex or food availability. Lower proportions of males fledging from the youngest nestling in both common grackles (Howe 1976) and boat-tailed grackles (Bancroft 1983) have been attributed to a higher starvation rate among males hatching from the last egg. Higher mortality among nestling males has also been noted in rooks (Slagsvold et al. 1986), western gulls (Larus occidentalis, Sayce and Hunt 1987) and capercaillies (Capercaillie capercaillie, Wegge 1980). Experiments in which brood size was increased in an effort to induce stressful conditions

have resulted in lower proportions of males fledging in both red-winged blackbirds (Cronmiller and Thompson 1981) and rooks (Roskoff and Slagsvold 1985). Also, males have been found to exhibit more variable growth than females in common grackles (Howe 1976), hooded crows (Corvus corone cornix, Slagsvold 1982), and yellow-headed blackbirds (Willson 1966, Richter 1983). All of these studies suggest that biases in fledgling sex ratios are the result of differential mortality of one sex when placed under adverse conditions and are not an adaptive response by females to equalize investment in sons and daughters. Thus, while I cannot reject an adaptive explanation for the periodic occurrence of biased fledgling sex ratios in some sexually dimorphic species, I suggest that these cases are more easily explained as being a nonadaptive consequence of differential food requirements of males and females.

Differential Mortality of Male Offspring and Its Possible Role in Sexual Selection

Darwin (1858) suggested that large size would be selected for in males because of the advantage it conveys, when competing with other males for access to females, the resources to attract females, or in attracting females directly. An upper limit to male size is reached when the cost associated with it equals the benefits. Thus far, however, it has been difficult to establish how and when

this cost might be manifested. It has generally been assumed that size is negatively correlated with survival in adult males. Evidence for this has come through interspecific comparisons suggesting that adult males of highly dimorphic species experience higher mortality than males of less dimorphic species (Searcy and Yasukawa 1981). Within species comparisons, however, have been less fruitful. Searcy (1979a, b) and Weatherhead et al. (1987) found no selection against large males within yellow-headed or red-winged blackbirds. Yasukawa (1987), on the other hand, found a weak but significant correlation between size and mortality for redwings. The problem is confounded by the possibility that large size may be advantageous under certain conditions while disadvantageous under others (Weatherhead et al. 1984).

Size differences between males and females are expressed much earlier in development than most other sexually selected characters, with these differences often becoming pronounced while offspring are still under parental care. Among birds, for example, males are significantly heavier than females in great-tailed grackles by 2 days post-hatching. The upper limit to male size could be imposed at this life history stage if (1) males suffer higher mortality than females during this period, (2) size is heritable, and (3) selection is size-dependent among males. It is clear from evidence presented here and

elsewhere (references cited above) that male nestlings do, under certain conditions, suffer higher mortality than female nestlings. In addition, general body size has been shown to have high heritability (e.g. Boag and Grant 1978, Smith and Zach 1979). However, I have no evidence of size-selective mortality among males and expect that this information would be extremely difficult to obtain.

In conclusion, biased fledgling sex ratios exhibited by a number of sexually dimorphic species might incidentally result in females investing equal amounts of energy into sons and daughters during the period of parental care. However, this should not necessarily be interpreted as an adaptive response by females as predicted by Fisher (1930) and others. Sex ratio biases, instead, may simply be a passive result of differential mortality of males because increased energy demands of this sex make it more susceptible to starvation during periods of food shortage. A second, but more speculative, mechanism that might account for fewer males among the oldest nestlings is that broods containing more males may be more vocal (because food demands could not be adequately met) thereby attracting more predators. If predators removed all nestlings, then biased fledgling sex ratios would not be limited to the youngest nestling. In either case, sex ratios at independence should reflect the level of food availability.

CONCLUSIONS

Chapter 1

1. Great-tailed grackle nestlings exhibit pronounced size differences between the sexes which become apparent shortly after hatching. At twelve days post-hatching, female mass is 65.7% that of males.
2. Female energy requirements over the first twelve days post-hatching, as determined by rates of oxygen consumption, were estimated to be 83% those of males. Thus, while male nestlings required more energy absolutely, female nestlings required proportionately more energy per unit body mass.
3. Intersexual differences in energy requirements as determined by food consumption, of hand-reared nestlings agree with those determined by measurement of oxygen consumption. Thus, males consumed significantly more food than did females between 5 and 12 days post-hatching.
4. There was no evidence that males directed more of their energy into mass increase than females or that parents reduced the added costs of rearing males by feeding them larger or more nutritious, as opposed to more, food items.

Chapter 2

1. Sibling gender or the overall sex ratio of the brood appeared to have little effect on nestling growth. There was limited evidence that broods of three that contained two or three males were less likely to fledge all nestlings than those containing two or three females.
2. There was no evidence that starvation was more likely to occur if the oldest nestlings were males rather than females.
3. Mass at fledging for both males and females was influenced most strongly by the sequence of hatching such that nestlings which hatched last weighed less than their older siblings. The mass of males at fledging, especially if they were the youngest in the brood, was more variable than that of females while the growth of males was affected more strongly by both egg size and hatching date.

Chapter 3

1. In this study, both egg and clutch sizes were significantly higher in 1985 than in 1986 or 1987 suggesting that food abundance may have been limited in the latter two years. The idea that food was less abundant in the second two years was supported by increased rates of starvation in these years.

2. Fledgling sex ratios were significantly female-biased in 1986 and 1987 but not in 1985. The relative proportion of males and females that fledged in a particular colony was strongly correlated with the fledgling sex ratio of that colony; where starvation was high, fewer males than females fledged.
3. Finally, when broods were manipulated so that the youngest two nestlings were both subjected to similar and potentially stressful conditions, patterns of growth and survival suggested that males were more likely to suffer than females.

Taken together, these results support the hypothesis that biased sex ratios, when they occur, may be more easily explained as being a consequence of differential mortality of the larger sex under food limiting conditions rather than an adaptive response by females to maximize their reproductive output. This being the case, then increased male mortality in sexually dimorphic species may be a cost to males of increased size due to sexual selection.

LITERATURE CITED

- Andersson, M. 1981. Reproductive tactics of the long-tailed skua Stercorarius longicaudus. Oikos 37: 287-294.
- Ankney, C.D. 1982. Sex ratio varies with egg sequence in lesser snow geese. Auk 99: 662-666.
- Bancroft, G.T. 1983. Reproductive tactics of the sexually dimorphic boat-tailed grackle (Aves). Ph.D dissertation, Tampa, Univ. South Florida.
- Bancroft, G.T. 1984. Growth and sexual dimorphism of the boat-tailed grackle. Condor 86: 423-432.
- Balfour, E. and C.J. Cadbury. 1979. Polygyny, spacing and sex ratio among hen harriers Circus cyaneus in Orkney, Scotland. Ornis Scand. 10: 133-141.
- Blank, J.L. and V. Nolan, Jr. 1983. Offspring sex ratio in red-winged blackbirds is dependent on maternal age. Proc. Nat. Acad. Sci. 80: 6141-6145.
- Blem, C.R. 1975. Energetics of nestling house sparrows, Passer domesticus. Comp. Biochem. Physiol. 52: 305-312.
- Boag, P.T. and P.R. Grant. 1978. Heritability of external morphology in Darwin's finches. Nature 274: 793-794.
- Bortolotti, G.T. 1984. Evolution of the growth rate and nestling sex ratio in bald eagles (Haliaeetus leucocephalus). Ph.D dissertation, Toronto, Univ. of

Toronto.

Brenner, F.J. 1968. Energy flow in two breeding populations of red-winged blackbirds. Amer. Midl. Natur. 79: 289-310.

Breitwisch, R., Merritt, P.G. and G.H. Whitesides. 1984. Why do northern mockingbirds feed fruit to their nestlings? Condor 86: 281-287.

Bryant, D.M. 1975. Breeding biology of house martins Delichon urbica in relation to aerial insect abundance. Ibis 117: 180-216.

Bryant, D.M. 1978. Environmental influences on growth and survival of nestling house martins Delichon urbica. Ibis 120: 271-283.

Bryant, D.M. and A. Gardiner. 1979. Energetics of growth in house martins (Delichon urbica). J. Zool. (London) 189: 275-304.

Bucher, T.L. 1983. Parrot eggs, embryos, and nestlings: patterns and energetics of growth and development. Phys. Zool. 56: 465-483.

Burley, N. 1986. Sex-ratio manipulation in colour-banded populations of zebra finches. Evolution 40: 1191-1206.

Charnov, E.L. 1975. Sex ratio selection in an age-structured population. Evolution 29: 366-368.

Charnov, E.L. 1982. The theory of sex allocation. Princeton University Press, Princeton.

- Clark, A.B. and D.S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Quart. Rev. Biol.* 56: 253-277.
- Clomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* 58: 1-124.
- Clutton-Brock, T.H. 1985. Sex ratio variation in birds. *Ibis* 128: 317-329.
- Clutton-Brock, T.H. 1986. Sex ratio variation in mammals. *Quart. Rev. Biol.* 61: 339-374.
- Clutton-Brock, T.H., Albon, T.H., and F.E. Guinness. 1985. Parental investment and sex differences in juvenile birds and mammals. *Nature* 313: 131-133.
- Collopy, M.W. 1980. Food consumption and growth energetics of nestling golden eagles. Ph.D. dissertation, University of Michigan, Ann Arbor.
- Collopy, M.W. 1986. Food consumption and growth energetics of nestling golden eagles. *Wils. Bull.* 98: 445-458.
- Cooke, F. and R. Harmsen. 1983. Does sex ratio vary with egg sequence in lesser snow geese? *Auk* 100: 215-217.
- Coulson, J.C. and J.M. Porter. 1985. Reproductive success of the kittiwake (*Rissa tridactyla*): the roles of clutch sizes, chick growth rates, and parental quality. *Ibis* 127: 450-466.
- Cronmiller, J.R. and C.F. Thompson. 1981. Sex ratio adjustment in malnourished red-winged blackbird broods. *J. Field Ornith.* 52: 65-67.

- Darwin, C. 1859. The origin of species. Murray, London.
- Darwin, C. 1871. The descent of man and selection in relation to sex. Murray, London.
- Davies, P.S. 1966. A constant pressure respirometer for medium-sized animals. *Oikos* 17: 108-112.
- Davies, D.C. and J.K. Payne. 1982. Variation in chick sex ratios during hatching. *Anim. Behav.* 30: 931-932.
- Dawson, W.R. and F.C. Evans. 1957. Relation of growth and development to temperature regulation in nestling chipping sparrows. *Phys. Zool.* 30: 315-327.
- Drawe, D.L., Chamrad, A.D., and T.W. Box. 1976. Plant communities of the Welder Wildlife Refuge. Contribution No. 5, Series B, Revised. Welder Wildlife Foundation, Sinton.
- Dyer, M.I. 1968. Respiratory metabolism studies on red-winged blackbird nestlings. *Can. J. Zool.* 46: 223-233.
- 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. In: Natural selection and social behavior: Recent research and new theory (R.D. Alexander & D.W. Tinkle, eds.), pp. 198-214. Chiron Press, New York.
- Fiala, K.L. and Congdon, J.D. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* 64: 642-647.

- Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
- Foster, W.H. and D.M.G. McSherry. 1980. A search for genetic variation in the sex ratio at hatching. Br. Poult. Sci. 21:131-134.
- Gosling, L.M., Baker, S.J. and K.M.H. Wright. 1984. Differential investment by female coypus (Myocastor coypus) during lactation. Zool. Soc. Lond. Symp. 51: 273-300.
- Gotie, R.F. and J.C. Kroll. 1973. Growth rate and ontogeny of thermoregulation in nestling great-tailed grackles, Cassidix mexicanus prosopidicola (Icteridae). Condor 75: 190-199.
- Guckian, W.J. and R.N. Garcia. 1979. Soil survey of San Patricio and Aransas Counties, Texas. USDA, SCS.
- Hickey, J.J. 1942. Eastern populations of the Duck Hawk. Aux 59: 176-204.
- Hogstedt, G. 1981. Effect of additional food on reproductive success in the magpie Pica pica. J. Anim. Ecol. 50: 219-229.
- Holcomb, L.C. and G. Tweist. 1968. Red-winged blackbird nestling growth compared to adult size and differential development of structures. Ohio J. Sci. 68: 277-284.
- 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. 1979. Evolutionary aspects of parental care in the common grackle, Quiscalus quiscula L. *Evolution* 33: 41-51.
- Hussel, D.J.T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* 42: 317-364.
- Hussel, D.J.T. and T.E. Quinney 1987. Food abundance and clutch size of tree swallows Tachycineta bicolor. *Ibis* 129: 243-258.
- Jarvinen, A. and J. Ylimaunu. 1986. Intraclutch egg-size variation in birds: physiological responses of individuals to fluctuations in environmental conditions. *Auk* 103: 235-237.
- Kaiser, T.J. and T.L. Bucher. 1985. The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation, and water loss in relation to ambient temperature in the prairie falcon, Falco mexicanus. *Phys. Zool.* 58: 748-758.
- Kessel, B. 1957. A study of the breeding biology of the European starling (Sternus vulgaris) in North America. *Amer. Midl. Natur.* 58: 257-331.
- Kolman, W. 1960. The mechanism of natural selection for the sex ratio. *Amer. Nat.* 94: 373-377.
- Lack, D. 1954. The natural regulation of animal numbers.

Oxford University Press, London.

- Lack, D. 1956. Further notes on the breeding biology of the swift, Apus apus. Ibis 98: 606-619.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London.
- Lanyon, W.E. and V.H. Lanyon. 1971. A technique for rearing passerine birds from the egg. Living Bird 8: 81-93.
- Lasiewski, R.D. and W.R. Dawson. 1967. A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13-23.
- Leblanc, Y. 1987. The relationship between sex of gosling and position in the laying sequence, egg mass, hatchling size, and fledgling size. Auk 104: 73-76.
- Leigh, E.G. 1970. Sex ratio and differential mortality between the sexes. Amer. Nat. 104: 205-210.
- Lewontin, R.C. 1966. On the measurement of relative variability. Syst. Zool. 15: 141-142.
- Maxwell, G.R. and L.S. Putnam. 1972. Incubation, care of young, and nest success in the common grackle (Quiscalus quiscula) in northern Ohio. Auk 89: 349-359.
- 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.

- Mills, J.A. 1979. Factors affecting the egg size of red-billed gulls Larus novaehollandiae. Ibis 121: 53-67.
- Mosher, J.A. and P.F. Matray. 1974. Size dimorphism: a factor in energy savings for broad-winged hawks. Auk 91: 325-341.
- Moss, D. 1979. Growth of nestling sparrowhawks (Accipiter nisus). J. Zool. Lond. 187: 297-314.
- Murphy, M.T. 1985. Nestling eastern kingbird growth: effects of initial size and ambient temperature. Ecology 66: 162-170.
- Murphy, M.T. 1986. Body size and condition, timing of breeding, and aspects of egg production in eastern kingbirds. Auk 103: 465-476.
- Nagy, K.A. 1980. CO₂ production in animals: analysis of potential errors in the doubly-labelled water method. Amer. J. Physio. 238: 466-473.
- Newton, I. 1978. Feeding and development of sparrowhawk Accipiter nisus nestlings. J. Zool. (London) 184: 465-487.
- Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.
- Newton, I. and M. Marquiss. 1979. Sex ratio among nestlings of the European sparrowhawk. Am. Nat. 113: 309-315.
- Patterson, C.B. and J.M. Emlen. 1980. Variation in nestling sex ratios in the yellow-headed blackbird.

- Amer. Nat. 115: 743-747.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit. J. Anim. Ecol. 34: 601-647.
- Peterson, K.L., Best, L.B., and B.M. Winter. 1986. Growth of nestling sage sparrows and Brewer's sparrows. Wils. Bull. 98: 535-546.
- Picozzi, N. 1980. Food, growth, survival and sex ratio of nestling hen harriers, Circus c. cyaneus in Orkney. Ornith. Scand. 11: 1-11.
- Pierotti, R. and C.A. Bellrose. 1986. Proximate and ultimate causation of egg size and the "third chick disadvantage" in the western gull. Auk 103: 401-407.
- Porter, R.D. and S.N. Weinmeyer. 1972. Reproductive patterns in captive American kestrels (Sparrowhawks). Condor 74: 46-53.
- Power, R.H. 1983. Ecological implications of body size. Cambridge University Press, Cambridge.
- Price, T. and H.L. Gibbs. 1987. Brood division in Darwin's ground finches. Anim. Behav. 35: 299-301.
- Pruitt, J. 1975. The return of the great-tailed grackle. Amer. Birds 29: 985-992.
- Quinney, T.E., Hessel, D.J.T., and C.D. Ankney. 1986. Sources of variation in growth of tree swallows. Auk 103: 389-400.
- Ralston, M. 1985. Derivative-free nonlinear regression. In: BMDP Statistical Software Manual (W.J. Dixon, ed.),

- pp. 305-314. University of California Press, Berkeley.
- Richter, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Amer. Nat.* 121: 158-171.
- Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48: 978-983.
- Ricklefs, R.E. 1974. Energetics of reproduction in birds. In: *Avian energetics* (R.A. Paynter, ed.), pp. 152-192. Publ. Nuttall Orn. Club 15.
- Ricklefs, R.E. 1977. A note on the evolution of clutch size in altricial birds. In: *Evolutionary ecology* (B. Stonehouse and C. Perrins, eds.), pp. 193-214. MacMillan, London.
- Roskaft, E. and T. Slagsvold. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. *J. Anim. Ecol.* 54: 261-266.
- Ryder, J.P. 1983. Sex ratio and egg sequence in ring-billed gulls. *Auk* 100: 726-728.
- Ryder, J.P. and B.M. Termaat. 1987. Secondary sex ratios and egg sequence in herring gulls. *Auk* 104: 526-528.
- Sayce, J.R. and G.L. Hunt, Jr. 1987. Sex ratios of prefledging gulls. *Auk* 104: 33-37.
- Searcy, W.A. 1979a. Sexual selection and body size in male red-winged blackbirds. *Evolution* 33: 649-661.

- Searcy, W.A. 1979b. Size and mortality in male yellow-headed blackbirds. *Condor* 81: 304-305.
- Searcy, W.A. & Yasukawa, K. 1981. Sexual dimorphism and survival of male and female blackbirds (Icteridae).--
Auk, 98, 457-465.
- Selander, R.K. 1958. Age determination and molt in the boat-tailed grackle. *Condor* 60: 353-376.
- Selander, R.K. 1960. Sex ratio of nestlings and clutch size in the boat-tailed grackle. *Condor* 62: 34-44.
- Selander, R.K. 1961. Supplemental data on the sex ratio in nestling boat-tailed grackles. *Condor* 63: 504.
- Selander, R.K. 1972. Sexual selection and dimorphism in birds. In: Sexual selection and the descent of man (B. Campbell, ed.), pp. 180-230. Aldine, Chicago.
- Selander, R.K. and D.R. Giller. 1961. Analysis of sympatry of great-tailed and boat-tailed grackles. *Condor* 63: 29-86.
- Shaw, R.F. and J.D. Mohler. 1953. The selective significance of the sex ratio. *Amer. Nat.* 87: 337-342.
- Slagsvold, T. 1982. Sex, size, and and natural selection in the hooded crow Corvus corone cornix. *Ornis Scandinavica* 13: 165-175.
- Slagsvold, T. and E. Roskaft. 1985. Differential mortality of males and female offspring in experimentally manipulated broods of the rook. *J. Anim. Ecol.* 54:

261-266.

Slagsvold, T., Roskaft, E. and S. Engen. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scand.* 17: 117-125.

Smith, J.N.M. and R. Zach. 1979. Heritability of some morphological characters in a song sparrow population. *Evolution* 33: 649-661.

Southern, H.N. 1970. The natural control of a population of tawny owls Strix aluco. *J. Zool. Lond.* 162: 197-285.

Teather, K.L., Muma, K. and P.J. Weatherhead. (in press). Estimating settlement patterns from nest data. *The Auk*.

Thomas, G.W. 1975. Texas plants - an ecological summary.

In: Texas Agricultural Experimental Station, MP - 585, Revised.

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

Tutor, B.M. 1962. Nesting studies of the boat-tailed grackle. *Auk* 79: 77-84.

Verner, J. 1965. Selection for the sex ratio. *Amer. Nat.* 99: 519-421.

Weatherhead, P.J. 1983. Secondary sex ratio adjustment in

- red-winged blackbirds (Agelaius phoeniceus). Behav. Ecol. Sociobiol. 12: 57-61.
- Weatherhead, P.J. 1985. Sex ratios of red-winged blackbirds by egg size and laying sequence. Auk 102: 298-304.
- Weatherhead, P.J., Greenwood, H. and R.G. Clark. 1984. On the use of avian mortality patterns to test sexual selection theory. Auk 101: 134-139.
- Weatherhead, P.J., Greenwood, H. and R.G. Clark. 1987. Natural selection and sexual selection on body size in red-winged blackbirds. Evolution 41: 1401-1403.
- Wegge, P. 1980. Distorted sex ratio among small broods in a declining capercaillie population. Ornis Scand: 11: 106-109.
- Williams, A.J. 1980. Variation in weight of eggs and its effect on the breeding biology of the great skua. Emu 80: 198-202.
- Williams, G.E. 1966. Adaptation and natural selection. Princeton University Press, Princeton.
- Williams, G.E. 1979. The question of adaptive sex ratios in outcrossed vertebrates. Roy. Soc. Lond. Proc. 205: 567-580.
- Willson, M. F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Mongr. 36: 51-77.
- Wilson, R.T., Wilson, M.P. and J.W. Durkin. 1987. Growth of nestling barn owls. Ibis 129: 305-318.

Winkler, D.W. and J.R. Walters. 1983. The determination of clutch size in precocial birds. Current Ornith. 1: 33-68.

Yasukawa, K. 1987. Breeding and nonbreeding season mortality of territorial male red-winged blackbirds (Agelaius phoeniceus). Auk 104: 56-62.

Yom-Tov, Y. and J.G. Ollason. 1976. Sexual dimorphism and sex ratios in wild birds. Oikos 27: 81-85.

APPENDIX

Appendix 1. Values of A (asymptote), K (maximum rate of growth), and I (day of maximum growth) used to estimate values for mass and tarsus length at 12 days post-hatching in Table 2-2.

(A) MALES - MASS

HATCHING SEQUENCE	BROOD SIZE = 3		
	A	K	I
1	115.5±1.20	.450±.010	5.87±.068
2	117.4±1.75	.434±.012	6.05±.096
3	104.4±2.24	.453±.019	5.82±.134
MEAN	113.8±1.11	.440±.008	5.98±.063

HATCHING SEQUENCE	BROOD SIZE = 4		
	A	K	I
1	118.0±1.77	.445±.014	6.08±.098
2	118.7±2.03	.446±.014	5.96±.107
3	121.6±3.81	.411±.019	6.33±.199
4	107.5±7.51	.430±.042	6.21±.416
MEAN	119.2±1.62	.428±.010	6.19±.087

(B) FEMALES - MASS

HATCHING SEQUENCE	BROOD SIZE = 3		
	A	K	I
1	75.2±0.59	.455±.009	4.91±.054
2	72.0±0.74	.474±.012	4.81±.069
3	72.0±1.15	.441±.015	5.09±.106
MEAN	73.6±0.48	.454±.007	4.95±.044

HATCHING SEQUENCE	BROOD SIZE = 4		
	A	K	I
1	76.4±0.97	.465±.017	4.88±.083
2	73.4±0.76	.474±.014	4.76±.071
3	74.6±1.22	.449±.017	4.91±.107
4	62.5±2.13	.496±.038	4.41±.208
MEAN	74.1±0.71	.453±.010	4.90±.063

Appendix 1 - cont.

(A) MALES - TARSUS

HATCHING SEQUENCE	BROOD SIZE = 3		
	A	K	I
1	62.0±0.48	.333±.006	4.48±.060
2	62.2±0.45	.329±.005	4.55±.057
3	60.6±0.78	.322±.008	4.49±.102
MEAN	61.8±0.34	.326±.004	4.53±.044

HATCHING SEQUENCE	BROOD SIZE = 4		
	A	K	I
1	61.5±0.50	.343±.007	4.49±.062
2	61.6±0.61	.345±.007	4.47±.073
3	62.7±1.04	.322±.010	4.60±.127
4	62.3±2.04	.312±.015	4.90±.253
MEAN	62.2±0.43	.331±.005	4.60±.053

(B) FEMALES - TARSUS

HATCHING SEQUENCE	BROOD SIZE = 3		
	A	K	I
1	50.9±0.24	.361±.005	3.55±.036
2	51.1±0.32	.357±.006	3.56±.048
3	51.6±0.42	.331±.006	3.76±.065
MEAN	51.2±0.19	.350±.003	3.61±.028

HATCHING SEQUENCE	BROOD SIZE = 4		
	A	K	I
1	50.6±0.44	.371±.011	3.54±.064
2	51.1±0.40	.366±.009	3.60±.059
3	51.3±0.55	.353±.009	3.62±.079
4	50.5±0.91	.336±.012	3.66±.135
MEAN	51.2±0.27	.354±.005	3.63±.040

Appendix 2. Values of A (asymptote), K (maximum rate of growth), and I (day of maximum growth) used to estimate values for mass at 12 days post-hatching in Table 2-3.

(A) MALES

SEX RATIO	BROOD SIZE = 3		
	A	K	I
3:0	114.4±2.53	.414±.018	6.21±.152
2:1	111.1±1.95	.451±.015	5.84±.110
1:2	117.7±2.20	.427±.014	6.21±.123

SEX RATIO	BROOD SIZE = 4		
	A	K	I
4:0	118.0±9.23	.424±.017	6.13±.480
3:1	120.6±3.03	.434±.017	6.24±.154
2:2	122.0±4.05	.415±.026	6.25±.281
1:3	116.3±3.54	.454±.027	5.96±.196

(A) FEMALES

SEX RATIO	BROOD SIZE = 3		
	A	K	I
2:1	73.2±1.28	.452±.019	4.95±.118
1:2	74.7±.708	.449±.010	5.03±.064
0:3	70.5±1.03	.466±.018	4.82±.100

SEX RATIO	BROOD SIZE = 4		
	A	K	I
3:1	75.5±2.71	.443±.033	5.09±.231
2:2	71.7±2.00	.462±.033	4.79±.185
1:3	74.3±1.21	.451±.018	4.92±.109
0:4	76.2±2.30	.442±.032	4.92±.199

END

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