FEMALE-BIASED SEX RATIO AT HATCHING IN THE GREEN WOODHOOPOE

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ABSTRACT.—In a population of Green Woodhoopoes (*Phoeniculus purpureus*) in the Rift Valley of Kenya, food abundance and breeding success varied greatly as a result of highly unpredictable patterns and abundance of rainfall. A given pair of woodhoopoes may breed successfully from zero to three times between May and December. We found a female-biased sex ratio in first nests of the year among those female breeders that had few (0–2) helpers. Apart from predation of entire broods, nestling mortality was extremely low (5%), and the bias was not based on differential starvation of male and female chicks. We examined several possible explanations for the female-biased sex ratio, and we suggest that production of female offspring by breeders in small groups is adaptive in that females are smaller and probably less expensive to rear than males. Young female nest helpers contributed significantly more feedings to subsequent broods than did their male siblings of the same age. The bias toward daughters could be effected either via nonrandom segregation of sex chromosomes or by differential mortality of eggs by sex. In several other bird species, larger eggs may give rise to males. This provides a possible means for the female parent to discriminate the sex of offspring before hatching. *Received 23 January 1990, accepted 12 May 1990.*

IN ANIMALS that reproduce sexually, each breeding individual should attempt to maximize its lifetime reproduction. One way parents might enhance their own reproductive advantage is through facultative control of the sex of their offspring. For vertebrates, this is a controversial and poorly understood subject. Although numerous explanations exist for why individuals should control the sex of offspring under specific conditions (Trivers and Willard 1973, Myers 1978, Williams 1979, Burley 1982, Charnov 1982, Clutton-Brock and Albon 1982, Clutton-Brock 1986), evidence for adaptive control of offspring gender in birds is scanty (Howe 1977, Williams 1979, Fiala 1981, Richter 1983, Clutton-Brock 1986, Breitwisch 1989) and usually ambiguous (cf. Ankney 1982 and Cooke and Harmsen 1983, and Blank and Nolan 1983 and Weatherhead 1985). In his review of sex ratio variation in birds, Clutton-Brock (1986: 326) concluded that "Sound evidence for sex ratio variation at hatching is thus scarce."

We report data that imply that in a cooperatively breeding bird (the Green Woodhoopoe, *Phoeniculus purpureus*), a female-biased sex ratio at hatching may occur under certain ecological and social conditions.

METHODS AND PERTINENT NATURAL HISTORY

We studied the social behavior and ecology of a marked population of Green Woodhoopoes near Lake Naivasha, Kenya, from mid-1975 through January 1982, and in June–July 1984 (Ligon and Ligon 1978, 1983, 1988, 1989a, b). Briefly, social units consist of 2–16 birds that contain no more than a single breeding pair, regardless of flock size. Each group defends a territory year-round, and territory size often is related positively to group size.

In each year breeding normally begins in late May or early June, following the "long rains" of March to May, and generally terminates in December or earlier. The number of successful nesting efforts per year appears to be controlled by food availability, which in turn is determined largely by patterns of rainfall. Two broods during the period June to December are common, and if environmental conditions are extremely favorable, three broods can be produced by one pair during this interval. When conditions are poor, breeding activity is limited, and only one or even no nesting attempt may occur. In such years, there is a lot of territory-to-territory variation both in the time of breeding and in the number of nests attempted.

Moth larvae make up the vast majority of food items of nestlings and adults during the six- or seven-month nesting season (unpubl. data), and numbers of these caterpillars through the year are related most directly to the amount of precipitation during the putative dry season, January to March. During this period, the moth caterpillars pupate in the ground and survive well only if the soil remains dry. If extensive rain falls during the "dry" season, mortality of the pupae is high, and few adults emerge to give rise to the generation of caterpillars that appears following the long rains. There is a significant inverse relationship between dry-season rainfall and subsequent repro-

ductive success in this population of woodhoopoes (Ligon and Ligon 1989a, b).

Nests are placed in tree cavities. We used an adjustable mirror and flashlight to inspect nest cavities after the eggs were laid. After determining clutch size, we generally did not inspect the nest again until the young began to hatch. This was indicated by changes in the behavior of the breeding female and helpers. After one or more eggs had hatched, the breeding female continued to eat large food items brought to her, but carried very small items into the nest cavity. As the eggs hatched, the helpers increased greatly the frequency of feeding visits and the number of minute food items brought to the nest. Unhatched eggs remained in the nest.

Clutch size in Green Woodhoopoes varied little; 88% were either three- or four-egg clutches. Despite this conservatism in clutch size variation, one third of the eggs in clutches of all sizes failed to hatch (see Ligon and Ligon 1988: table V). Separation of the data by year revealed a similar pattern: one third of all eggs laid in each year did not hatch (Ligon and Ligon 1988: table VI). Ligon and Ligon (1988) attribute this high rate of hatching failure to inbreeding depression.

In contrast to the high rate of hatching failure, starvation of nestlings was extremely rare (Ligon and Ligon 1988: table VI). Excluding losses of entire broods to predators, 95% (71/75) of the young woodhoopoes that hatched survived to fledge. The rarity of nestling starvation is probably related to the high hatching failure (i.e. a small number of nestlings initially may mean that each receives a larger proportion of the total food delivered than would be the case with a larger brood). The rarity of nestling mortality is important in that the number and sex of chicks fledged is 95% of the number and sex hatched (i.e. a sex ratio bias at fledging reflects the same bias at hatching).

RESULTS

Sex ratios of fledglings from first broods.—In small social units (i.e. a breeding pair with 0–2 helpers), more daughters are produced than sons in early (June to August) first broods of the year and in June to August broods of one (Table 1). Early broods are inevitably first broods, whereas first broods of the year are not necessarily produced early. Depending on the timing and amount of previous rainfall, first broods can appear either early (June–August) or late (after August) in the breeding season. In addition, the two "broods of one" categories (Table 1) are subsets of the two "all fledglings" categories. Broods of one are treated separately because if adaptive prehatching brood reduction occurs in conjunction with adaptive sex ratio manipula-

tion (see Discussion), such broods represent the extreme limit of adaptive reduction. The sex of single-chick broods thus is critical for evaluation of these ideas. The data for small flocks suggest that significantly more female than male offspring are produced in early first broods, regardless of size, and that the same is true for broods of one. When early and late broods of small flocks are combined, this sex bias disappears. In groups with more than two helpers, early broods were not significantly biased towards females.

This general pattern is illustrated in detail in the subset of data for 1981 (Table 2). These data are instructive because environmental conditions were unusually favorable: every mated pair in the study population initiated nesting in May or June (i.e. food resources were adequate to permit early breeding in all territories), most groups were small, and fledging success was high. Although the 1981 data are too few for statistical significance, they illustrate for one year the pattern of interest. Note that in the small groups three times as many daughters as sons were produced in first broods, and that broods of one also are strongly biased toward females. Second broods of those same breeding groups later in 1981 were not female-biased.

Female-biased sex ratio.—At least two possibilities should be considered to explain why breeding female Green Woodhoopoes in small flocks preferentially produce female offspring early in the June–December breeding period.

1. Trivers and Willard (1973: footnote 21) suggest that under some circumstances parents should produce the more "altruistic" sex, to help in the parents' subsequent reproductive efforts. To test this idea we compared young (≤2 yr of age), same-age, male and female full siblings with regard to the aid they provided to nestlings. Females made significantly ($P < 0.001$) more feeding visits than did their male siblings (Table 3), and females also tended to deliver more insect biomass per hour (Ligon and Ligon in prep.) than did males (not significant). This greater visitation effort by female helpers was apparent only in birds ≤2 yr of age. Among older helpers, males apparently contribute as much as females (Ligon and Ligon 1978).

Young female helpers often brought extremely small food items to nestlings at very high rates of delivery (Ligon and Ligon in prep.), a pattern not exhibited by their male counterparts. Thus a significant sexual difference exists

TABLE 1. Sex ratios of fledgling Green Woodhoopoes in small (0–2 helpers) and large (>2 helpers) groups, 1975–1981.

	Nests (*n*)	Females	Males	P^a
Small flocks				
All Fledglings	55	57	43	NS
All fledglings from early (June–Aug.) first broods	27	30	12	<0.005
Fledglings from all broods of one	20	14	6	NS
Broods of one, June–Aug. nesting	14	11	3	<0.05
Large flocks				
All Fledglings	73	70	63	NS
All fledglings from early (June–Aug.) first broods	59	30	28	NS
Fledglings from all broods of one	30	16	14	NS
Broods of one, June–Aug. nesting	16	6	10	NS

[a] Chi-square test; NS = not significant.

in the behavior of young helpers that could account, at least in part, for preferential production of daughters under the conditions we described. This suggestion is related to Fisher's (1930) hypothesis concerning cost of offspring of a particular sex (i.e. if young females are better helpers than males are, this in effect reduces the cost of producing daughters).

2. Adult male woodhoopoes weigh almost 20% more than females (Ligon and Ligon 1978), and this size difference is apparent well before fledging. Presumably females are less expensive to produce than males and thus are more likely to be reared successfully when food is scarce

TABLE 2. First-brood reproduction in social units of Green Woodhoopoes 1981.

	Helpers		Experience of female breeders[a]	Offspring sex		
	Male (*n*)	Female (*n*)		Male (*n*)	Female (*n*)	? (*n*)
Small Flocks[b]						
DD	1	1	E	0	1	
MSG	0	0	N	0	1	
NLP	0	0	N	0	1	
3ST	0	1	N	0	1	
CR5	0	0	E	1	1	
WWH	1	0	E	1	2	
RFM	1	1	E	1	2	
Large Flocks[c]						
BRF	1	5	N	2	2	
AD	3	1	N	0	1	1
ST	1	2	E	1	0	
BF	1	3	E	1	2	
CF	1	2	E	1	1	
MM	1	1	E	0	2	

[a] Novice (N) or experienced (E) at first nesting of 1981.
[b] 0–2 helpers.
[c] 3–6 helpers.

(also see Richter 1983), or when nest helpers are few. In addition, brood sizes of early nests in small flocks are significantly smaller ($P = 0.0516$) than in later nests (1.64 [28 broods] versus 2.04 [27 broods]), which further suggests that food early in the nesting season may be scarcer than later in the year.

This explanation agrees with the hypothesis that disproportionate production of the less expensive sex (here, smaller females) occurs when resources required for rearing offspring are potentially or actually limited (Myers 1978). It is supported by the fact that in flocks with few or no helpers, female nestlings are significantly more common than males in early broods of one (Table 1). Trivers and Willard (1973) also predict decreased production of the more expensive sex, generally males, under conditions of food limitation. However, the focus of selec-

TABLE 3. Feeding visits (per hour of observation) by same age, full sibling novice helpers of opposite sex. Subscript indicates first or second nest of that year; where two sibling helpers of the same age and sex were present, their values were averaged.

Flock-Yr	Male helper(s)	Female helper(s)	Age (mo)
DD-1978	0.98	2.64 (2)	12
AD-1977	1.90	6.00	9
AD-1979$_1$	1.14 (2)	1.08	24
AD-1979$_2$	0.59 (2)	1.14	26
3ST-1979$_1$	1.73	0.87 (2)	20
3ST-1979$_2$	0.77	1.91 (2)	22
ST-1977	1.42	2.83	21
MS4-1978	0.34	5.25	20
HS-1978	1.67	1.93	12
3ST-1979	1.51	4.12	19

tion in the two hypotheses is not the same. Trivers and Willard suggest that a female in poor condition should produce offspring of the sex which, upon maturation, has the better chance of breeding successfully relative to others of its sex, when in suboptimal physical condition (generally females). In contrast, Myers emphasizes the overall reproductive success of the parent rather than that of the offspring.

DISCUSSION

We have addressed two possible adaptive explanations for the female-biased sex ratio: rearing the more helpful sex and rearing the less expensive sex. In addition, because Green Woodhoopoes are so dependent on allies of the same sex to maintain control of their territory (Ligon and Ligon 1983, 1989a), a female breeder with a few or no subordinate female flock mates might prefer to produce daughters before sons. That is, if a female woodhoopoe produces a daughter as soon as possible, her security relative to groups of females in neighboring flocks would be enhanced. Because the female breeder lays and incubates the eggs alone (Ligon and Ligon 1978), and therefore controls events within the nest, such a strategy could potentially be employed by a breeding female, even if this conflicted with the interests of her mate.

Females of simple pairs sometimes produce first offspring that are male, which is counter to the expectations of both the ally and more helpful sex hypotheses, and (assuming that female breeders never make mistakes) suggests that the "cheaper sex" explanation may be of most importance (i.e. when food on the territory is abundant, rearing a male nestling may be no more costly than rearing a daughter). In contrast, according to the other two hypotheses, in small groups, daughters should always be produced before sons, regardless of environmental conditions at the time of nesting.

In several species of cooperatively breeding birds, males are more likely than females to serve as helpers (Brown 1987), but until recently there has been no evidence that production of male offspring is favored. In the Red-cockaded Woodpecker (*Picoides borealis*), virtually all helpers are male. A significant bias toward producing males occurs in groups in which the breeding female is a newcomer to the territory (i.e. has not previously bred there), whether or not she is helped (Gowaty and Lennartz 1985). This situation resembles that of the woodhoopoes: in both species a female breeder with few or no helpers (typically a new arrival to the territory or a novice breeder) produces significantly more offspring of the more helpful sex (daughters in the woodhoopoes, sons in the woodpeckers). However, in these woodpeckers, unlike the woodhoopoes, males and females are similar in size (Ligon 1968, Ligon and Ligon 1978).

Proximate causes of the biased sex ratio in Green Woodhoopoes.—We have considered four possible mechanisms responsible for the female-biased sex ratio described here.

1. *Sex-biased mortality of nestlings.* In general, biased sex ratios of nestlings are a result of posthatch nestling mortality (Clutton-Brock 1986). However, in the woodhoopoes, post-hatch starvation of nestlings is so rare that it cannot be the mechanism producing the female bias.

2. *Age of female breeder.* Blank and Nolan (1983) found that older female Red-winged Blackbirds (*Agelaius phoeniceus*) produced a preponderance of sons. We have no record of any female woodhoopoe breeding successfully at <3 yr of age. We examined the numbers of sons and daughters produced by females of ages 3–4, 5–6, and 7–9 yr, and we found no relationship between sex of offspring and age of the female breeder.

3. *Females are the heterogametic sex.* In birds, females are the heterogametic sex and it is possible that the sex-ratio bias described here is based on a modification of the primary sex ratio. We have not been able to investigate this possibility.

4. *Differential mortality of one sex in the egg stage.* Sex of hatchlings possibly could be determined by the female parent during the incubation period, as she alone incubates the eggs. In some species of birds, egg size apparently correlates with sex; either those eggs that produce males are larger than those that produce females (Howe 1976, Ankney 1982, Ryder 1983, Mead et al. 1987) or vice versa (Fiala 1981; but cf. Blank and Nolan 1983 and Weatherhead 1985). In the woodhoopoes, considerable intraclutch variation exists in egg size and shape (See Ligon and Ligon 1978: fig. 7). Either the size or shape of eggs could provide the incubating female with a simple means of "choosing" offspring sex (i.e. by selectively denying incubation to some eggs).

Several observations of single eggs off to one side of the nest cavity suggested to us that this might occur, but we were unable to obtain sufficient data (based on marked and measured eggs that hatched) to investigate this notion. In short, we speculate that if inbreeding depression is not the sole cause of the high level of embryonic mortality (Ligon and Ligon 1988), both it and the biased sex ratio may be interrelated, as previously suggested for birds (Charnov 1982: 111).

Other evidence for parental control of offspring sex in birds.—In addition to the sex ratio manipulation of offspring in Red-cockaded Woodpeckers (Gowaty and Lennartz 1985), some of the findings of Patterson et al. (1980) appear to parallel the pattern for Green Woodhoopoes described here. Patterson et al. found a significant male bias in first broods of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), but not in the second or third broods. Conditions of food availability are better early in the season, and in the blackbirds the male feeds only first broods. Here 'ι appears that under the optimal conditions of abundant food and paternal provisioning, the more costly male offspring are favored. Similarly, when food availability and assistance are limited, female woodhoopoes produce an excess of females, the less expensive sex to rear. In each case it appears that the sex of offspring produced is gauged to the availability both of food and the amount of provisioning assistance the female parent is likely to receive.

In a population of Common Grackles (*Quiscalus quiscula*), five-egg clutches (the most common clutch size) showed a decreasing proportion of females as the breeding season progressed, and presumably as the dependability of the food supply increased (Howe 1977). Howe suggested that this reflected a seasonal change in primary sex ratio probably controlled by nonrandom segregation of the sex chromosomes. Fiala (1981) also described a seasonal pattern of variation in sex ratio in Red-winged Blackbirds, with the proportion of females rather than males increasing for a time as the season progressed. Fiala (1981) surmised that young female Red-winged Blackbirds, which typically initiate nesting later than older birds, might produce an excess of female offspring and that this could account for the significant portion of the seasonal trend he observed. Blank and No-

lan (1983), in part confirming Fiala's suggestion, demonstrated that young females do indeed produce a majority of daughters, but via differential nestling starvation. In addition, Blank and Nolan showed that the progeny of old females is biased toward sons, probably as the result of differential hatching of the sexes. As mentioned earlier, Patterson et al. (1980) found a male-biased sex ratio in first broods of the season in Yellow-headed Blackbirds. In this species male breeders help to provision only first broods. All of these temporal trends suggest maternal control of nestling sex ratio.

Other possible means of controlling offspring sex are related to correlations between laying sequence and sex, and between egg size and sex. Within Common Grackle clutches, egg weight increases with laying sequence, and mortality from last-laid eggs is less for females (Howe 1976). Fiala (1981) discovered a female bias in last eggs among the Red-winged Blackbirds he studied, and last eggs were largest in clutches of four (cf. Weatherhead 1985). In both of these North American blackbirds, significant trends have been described between increasing egg size and laying sequence, and with sex of last-laid eggs. However, Blank and Nolan (1983) found no indication that position in the laying sequence was associated with sex or that eggs from which males and females hatched differed in their energy content (also see Weatherhead 1985). In four-egg clutches of the Lesser Snow Goose (*Chen c. caerulescens*), Ankney (1982) reported that the first two eggs laid were larger than the last two, and that first eggs gave rise to males significantly more often than to females, but Cooke and Harmsen (1983) were unable to confirm this. Ryder (1983) described a relationship between egg sequence and sex in the Ring-billed Gull (*Larus delawarensis*). Like Ankney (1982), Ryder found more males produced by first-laid eggs than by last-laid eggs. Mead et al. (1987) determined that in White-crowned Sparrows (*Zonotrichia leucophrys*), egg size correlates with sex: male eggs are larger. (See Mead et al. [1987] for additional discussion of the relationship between egg size and sex.) All of these studies taken together (Table 4) suggest that sex-ratio adjustment does occur in birds and that the mechanism we have suggested for woodhoopoes, although not previously described, is plausible. They also point out that at the population level sex ratios usu-

TABLE 4. Possible factors involved with sex-ratio adjustment in the Green Woodhoopoe and in some other avian species (sources listed).

Green Woodhoopoe (this study)	Other Studies
1. Population nestling sex ratio not significantly biased.	Howe (1977), Fiala (1981), Ankney (1982), Ryder (1983), Blank and Nolan (1983), Richter (1983), Weatherhead (1985)
2. Seasonal variation in sex ratio.	Howe (1977), Fiala (1981)
3. Sex ratio biased when female breeder novice or with little or no help at the nest.	Gowaty and Lennartz (1985), Blank and Nolan (1983), Patterson et al. (1980)[a]
4. Smaller sex (female) produced when food less abundant.	Howe (1977), Blank and Nolan (1983), Patterson et al. (1980)[b]
5. Sex produced that will contribute more help at subsequent nests.	Gowaty and Lennartz (1985)
6. Suggestion that variation in egg size may be related to offspring sex.	Howe (1977), Fiala (1981), Ankney (1982), Mead et al. 1987

[a] Sex ratio biased when help (male parent) is present.
[b] Sex ratio biased when food is more abundant.

ally will not be biased (Fisher 1930, Richter 1983).

Finally, four species for which a sex-ratio bias has been described (i.e. Common Grackle, Red-winged Blackbird, Yellow-headed Blackbird, and Green Woodhoopoe) share certain important features which, taken together, strengthen the likelihood that adaptive manipulation of the hatching sex ratio occurs under certain conditions. First, all exhibit strong sexual dimorphism; male nestlings are considerably larger and thus more costly to feed than females. Second, there is seasonal or temporal variation in food abundance, which changes the costs of rearing offspring over time. Third, there is variation in the amount of provisioning assistance the female breeder will receive. In the grackle and blackbirds, the male parent may or may not feed nestlings, whereas in the woodhoopoes the variation in provisioning appears to be related in large part to number of helpers.

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