

A Study in Skew

Sex Allocation Bias in Birds

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*You have a funny feeling
And you think your mind's infirm.
You check your breeder records
And these results confirm
The patterns male and female
Of the chicks your pairs have raised.
For chance they're quite unlikely,
And frankly, you're amazed.
You shake your head and wonder
How it really could be true –
Relax Dear Aviculturist!
What you've just seen is SKEW!*

Skew is a term used to describe something that is “more developed on one side than the other” or is distorted “from a true value or symmetrical form” [1]. For the purposes of this brief discussion, skew refers to sex allocation bias or sex ratio adjustment, which is variance of a population or its progeny from the evolutionarily stable 50:50 (male:female) sex ratio [28]. Skew is much more than individual nests or groups having more males or females by chance.

A Little Background Gender Biology

Before beginning a discussion of skew in birds, it may be helpful to review some basic gender biology.

Animals such as mammals and birds are “chromosome dependent” [28] species, which means gender results from sex chromosomes. The cells of most animals contain a complete paired set of chromosomes, one set inherited from each parent. These cells are called “diploid” (“di” meaning “two” and “ploid” from “ploidy” which refers to the basic number of an organism’s chromosomes). In a two-phased process called meiosis, which occurs in the gonads, reproductive cells (gametes) are formed. Each gamete contains half of a complete set of chromosomes and is “haploid” (“ha” meaning “half”). Fertilization occurs when a gamete from the male organism combines with a mature gamete from the female, called an oocyte, to form an offspring with a complete paired set of chromosomes (diploid).

Chromosomes contain genes. The combinations of the genes of the sets of chromosomes comprise the genetic “blueprint” for the organism. Genes even determine how an organism may be able to react to its environment.

The set of all of an organism’s genes, regardless of whether a gene is expressed, dominant or recessive is called its genotype. The observable outward characteristics of the organism, including attributes such as color patterns and

behavior resulting from the interaction of the individual’s genotype with its environment are called its phenotype.

In animals such as mammals and birds, where both males and females are normally diploid, gender results from combining two sex chromosomes. Because of their general shape, mammalian sex chromosomes are designated “X” and “Y”. In mammals, the father, who has X and Y sex chromosomes, determines the gender of the offspring. He is the heterogametic parent (“hetero” meaning “different”), which means he can form gametes with either an X or Y sex chromosome. The mother is the homogametic parent as both of her sex chromosomes are X (“homo” meaning “same”). Therefore, unfertilized mammal ova can only contain X chromosomes, and gender cannot be determined until fertilization. If an X gamete of the father fertilizes an egg, the resulting offspring will be female (XX). If a Y gamete fertilizes an egg, the resulting offspring (XY) will be male.

In birds, the chromosomes are designated Z and W and the heterogametic parent is the mother [13]. A female bird has ZW sex chromosomes, and a male has ZZ. This means that the female bird determines the gender of her offspring.

Biological Mechanism for Avian Sex Determination [21, 22]

Avian research indicates that maternal sex steroids such as testosterone, androstenedione, 5-alpha-dihydrotestosterone and beta-oestradiol [21] influence the segregation of the sex chromosomes in the oocytes. The female appears to adjust the amounts of these sex steroids delivered to the yolk of the forming gametes, determining gender during the first of the two phases of meiosis [2, 12, 22], just a few hours before ovulation and prior to fertilization [8, 13, 21, 24]. This appears to be accomplished in part via two layers of steroidogenic cells that make up the follicular walls; these layers are known as the theca (outer layer, in direct contact with the female’s bloodstream) and granulosa (inner layer, closer to the yolk of the gamete) [22]. Research indicates that this adjustment occurs in response to factors in the mother’s current environment [22]. As such, response of the mother bird to her environment appears to be part of the mechanism for determining the sex of her young.

This implies two things important to skew. First, it implies that avian sex ratios are not constrained by fixed numbers of male or female oocytes within the ovary.

Second, avian mothers may be able to adjust the sex ratio of their progeny based on their genetic ability to respond to factors in the environment (facultative adjust-

ment). These factors, which may include territory and food quality and availability, adequate appropriate nesting sites, availability of suitable mates, actions of weather, predators, parasites and diseases, etc., are called selection pressures [28, 29].

Brief Discussion of

Sex Allocation Theory [15, 28, 29]

Sex allocation, or sex ratio bias is theorized to be a result of an organism's response to various selection pressures that suggest greater success for passing on its genetic material if the offspring are predominantly one gender versus the other [28]. Further, "facultative sex ratio variation will only be favored when the fitness benefits of this behavior are greater than its costs [29]". [15]

If the factors influencing the success of an individual are relatively equal to its needs, then selection favors the environmentally stable sex ratio of 50:50. However, the more the pressures vary from parity, and the more the success of offspring of different gender may be influenced by these pressures, the more selection favors parents who can skew the sex of their progeny to accommodate it [28].

Models of sex allocation theory attempt to identify these factors and predict their influence on the gender ratio of offspring. Conversely, sex ratio bias may be observed, and a model developed in an attempt to determine the factors influencing it.

Mechanisms For Sex Ratio Adjustment in Birds

There are two basic ways that parent birds might control the sex ratio of their offspring. In the first, one or both parents adjust the sex ratio after the young have hatched. This might be accomplished by allowing chicks of the unwanted gender to die through such means as neglect, direct destruction, or even tossing them out of the nest [7, 8, 12]. Methods of this type are called Secondary sex ratio adjustment. This can be expensive for the mother, as at minimum she has expended her body

resources [13] to form and incubate eggs of chicks that will ultimately be purposefully destroyed.

The second, much more efficient [28] mechanism for sex ratio skew is Primary adjustment. In birds, this kind of skew occurs before the fertilization of the egg. As previously discussed, the female avian may be able to skew her clutch to the most successful gender ratio [8] in response to the prevailing selection pressures from her environment prior to investing her resources [13] in eggs and chicks.

Examples of Skew Pressures and Strategies

Some of the selection pressures on and skew strategies of avian species are illustrated in the following summaries of sex allocation studies. These summaries just touch the surface of the depth of information contained in the studies. Also, these are just a few of the studies of avian sex ratio bias that have been done (Hasselquist and Kempenaers [7] have compiled convenient reference charts of some of the avian skew research that has been done, arranged by factors and strategies studied.)

Maternal condition; egg quality

Tree Swallow (*Tachycineta bicolor*) [30]. In this study, all members of the clutches, including unhatched eggs and dead nestlings (210 young in 40 broods) were tested to determine the sex ratio at laying (Primary sex ratio). The condition of the mother was determined by age, body mass and her ectoparasite burden as indicated by the number of parasite holes in her feathers.

The study found that females in better condition produced more male eggs. "Further, females in better condition produced more male offspring that were also in better condition." Researchers theorize that the high frequency of extra-pair paternity (fathering chicks with other females in other pairs in addition to those of his social mate) in this socially monogamous species may indicate that reproductive success is more strongly influenced by

selection pressures (more variable) for male offspring than for female. It also found that young who fledged in better condition appeared to have a greater survivability rate, as they returned to breed the following season. Consequently, a Tree Swallow in good condition would have a greater chance of distributing more of her genes into future generations by producing a male offspring. This offspring would be more likely to be in good condition and survive to successfully compete with other males for the opportunity to mate with more females. A female in less good condition might benefit from producing female chicks, as it would be less likely that her male offspring (in less good condition themselves), could successfully compete with stronger males to father chicks.

Lesser Black-backed Gull (*Larus fuscus*) [20]. In this study, the condition of female Lesser Black-backed Gulls was experimentally manipulated using egg removal, food supplementation and cross fostering. Both the hatching sex ratio and ratio of chicks surviving to fledging were analyzed. "Males in this species are larger on average than females, grow faster, and are more susceptible to starvation as chicks." Also, "males apparently carry smaller reserves at hatching, a situation that adversely affects early survival rate."

Maternal condition has a direct effect on the quality of the contents (provisioning) of the egg she produces. As the researchers had predicted, the study found that females in good condition would produce high-quality eggs and result in a larger proportion of surviving male chicks than would females under greater nutritional stress. Also, it found that as the laying season progressed, the females that were not receiving supplementary food tended to increasingly skew the sex ratio of their eggs toward females. The supplemented females did not skew the primary gender ratio.

Paternal condition; paternal ability

Collared Flycatcher (*Ficedula albicollis*) [5]. In this study of the

Collared Flycatcher, researchers attempted to determine if a secondary sex characteristic of the male, a white forehead patch, influenced brood sex ratio. The size of the white forehead patch appears to be a "badge of status" with a larger patch indicating greater success in finding food during the non-breeding season. This makes him more attractive to females during the breeding season, and increases the likelihood that he may be polygynous. The size of the patch appears to be subject to both genetic and environmental factors, so a large patch might indicate to a potential mate that a male has both good genetics and is a good provider.

The study found that the sex ratios of Collared Flycatcher offspring appeared to be adjusted in response to the observable characteristics (phenotype) of the father. Females who mated with males having the largest forehead patches showed the most brood bias toward male chicks.

Blue Tit (*Parus caeruleus*) [10, 23, 24]. Studies of Blue Tits have also shown sex ratio bias toward males in response to the phenotype of the father. Two phenotypic factors that have been analyzed in relation to skew are the vividness of the male's yellow feathers, and another very special trait: The ultraviolet intensity of his crest [24].

As with the Collared Flycatcher, these factors appear to be indicative of the abilities and condition of the male, and females tend to produce more male offspring for fathers exhibiting superior characteristics. Caterpillars are a high quality food source for Blue Tits during the breeding season. These caterpillars contain carotenoid pigments that are infused unchanged into the feathers of the bird [23]. The more of the caterpillars (with their carotenoid pigments) the male consumes, the brighter the yellow in his feathers will be. A male with brighter yellow feathers signals to potential mates that he has been more successful than less brightly colored males at foraging for this nutritious food source. As such, "it would direct-

ly benefit the female to pair with a very yellow male." [23]

The ultraviolet brightness of the crest appears to be an indicator of the male's condition based on his success in foraging for food in the previous year; the brighter the crest, the greater his success and the better his condition. Males with crests bright in the ultraviolet are therefore more attractive to potential mates. This is an important reminder to researchers that birds may be strongly influenced by factors that they can clearly discern, but are undetectable to unaided human senses [10].

**Food resources;
response to environment**

Zebra Finch (*Taeniopygia guttata*) [12]. In the wild, "Zebra Finches breed opportunistically when there is sufficient food available, often rapidly mobilizing their reproductive systems in response to an ephemeral boom in grass seed production." A chick's average life expectancy at hatching is only 51 days, and surviving birds can breed as early as two months of age. As a result, the birds must develop and mobilize resources quickly if they are to breed successfully. Because of this very short life expectancy, birds with higher fledging weight have a better chance of reaching the threshold to breeding success more quickly than fledglings of lower weight.

Study of captive, domestic-raised Zebra Finches has determined that the success of females is more dependent on fledging weight than that of males, as it has been linked to their attractiveness to mates, survival to breeding age, and to the number of chicks they produce. In males, only attractiveness to mates has been linked to fledging weight. Sex allocation theory would indicate that parents with better resources should skew the sex ratio of their clutches to the more variable sex, in this case, females.

The data in this study support the prediction of sex allocation theory. The study indicated "zebra finches manipulate the primary and secondary sex ratios

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of their broods in relation to the resources they are likely to receive...Sex ratios at hatching were male biased when food was restricted, but female biased when food was abundant." During periods of low food availability, clutch ratios were skewed towards males, and female survival rate was low. During periods of unrestricted food supply, female chicks hatched and fledged earlier, with a higher survival rate than males.

Territory quality, nest availability and helpers

Seychelles Warbler (*Acrocephalus sechellensis*) [13,14]. The Seychelles Warbler is endemic to one small (29 hectares) island, Cousin, in the Seychelles chain and many generations of the population have been studied. Territories of the warblers living there vary from those high in their insect food resources, to those low in these resources. The warblers employ a "helper" strategy, where mature offspring, usually daughters [13], may assist their parents in raising young, including incubation and feeding. This strategy was most successful when no more than two helpers were present on high-quality territories. The benefits of the helper strategy were reduced when more than two helpers were in the territory, due in part to the benefit of the helpers being offset by the additional competition for food resources. Low quality territories presumably contained sufficient resources only to support the pair and its young, as helpers there reduced the parents' reproductive success [13].

During the study, pairs on low-quality territories who had no helpers had 77% sons (the non-helping sex). Unhelped pairs on high-quality territories had 13% sons (i.e. produced more of the helping sex). "Breeding pairs occupying high-quality territories switched from producing female eggs when no or one helper was present, to producing male eggs when two helpers were present in the territory." [13]

Populations were moved to two islands where no Seychelles Warblers existed before, including Aride, a larger

island with abundant insect prey resources, to observe how they responded to completely new territories. Breeding pairs that had occupied low-quality territories on Cousin Island that now had high-quality territories on a new island switched from producing mostly male to producing mostly female eggs. Pairs that had been on high-quality territories on Cousin and had high-quality territory on a new island produced female (helper) eggs and those that changed from high to low territories switched from more female to more male eggs. Ongoing, success and skew of nests and helpers operated in the same way as on Cousin Island.

Additionally, studies of the birds on Aride (86 clutches produced by 19 females over a three year period between October 1988 and November 1991) [14] found that not only were the clutches strongly female biased, but concluded that the skew resulted from pre-ovulation (Primary) mechanisms [14].

"By biasing offspring sex ratios towards sons, which disperse, in low-quality territories and daughters in high-quality territories, breeding birds avoid having competing offspring on low-quality territories, and gain helpers on high-quality territories." [13]

Eclectus Parrot (*Eclectus roratus*) [8, 9, 19]. The Eclectus parrot demonstrates a most unusual and puzzling sex ratio skew. This is an example of science observing what appears to be sex ratio bias, and then attempting to understand it. At this time, researchers do not understand the function of skew in the Eclectus. It may be connected with several factors, including the scarcity of appropriate nest hollows [9, 19] and what appears to be a polyandrous social structure (or perhaps a male helper strategy) where at least one of the several males attending a female at her nest hollow is the father of the chicks [9, 19].

Eclectus are unique in that they are strongly sexually dimorphic virtually from hatching [9]. Eclectus females stake out and defend nesting hollows,

and even inadequate depressions on a tree trunk (potential future hollows?) from an early age [9]. Her brilliant red and blue plumage coloration is cryptic within the recesses of her hollow, yet the intensity of her red head and face feathers appear to signal "ownership" of a nest hollow when she is positioned within with her head framed at its entrance [19]. This signals occupancy of the hollow to competitive females, and to potential male helpers/mates. Females remain close to their nest hollows even outside of breeding season to discourage competing females from attempting to usurp this "prize real-estate" [9].

The male's green plumage is cryptic in the environment of the leafy canopy, where he spends much of his time foraging. It is also bright in the ultraviolet [9, 19]. The efforts of several males are required to support the female and maximize the potential for the survival of even one of the normal clutch of two chicks [9, 19].

How might Eclectus skew the sex ratio of their young? Toward the helping sex in times of want? Toward females in times of plenty?

Aviculturists have recorded long sequences of male and of female chicks produced by individual females in captivity. In a study of Eclectus chick gender sequence in aviculture [8], twelve females produced a total of 216 fledglings in about 160 clutches. Overall, parity was represented as 46% of the fledglings were male. However, the genders were produced in long sequences of same-gender chicks. For example, one female produced 20 males in a row followed by 13 females in a row. Another female produced 40 fledglings, only 9 of which were male (and 5 of the nine were in a row). The study cites a reference to a comment from Low (1986, p. 143) [8] which indicates that these sequences do not appear to be uncommon in Eclectus. "...a predominance of chicks of one sex is not at all unusual...One Eclectus in Chester Zoo produced 30 sons before the first daughter was produced." [8]

The study demonstrated that these "runs" of one sex and then another are

unlikely to have occurred by chance, and seem to somehow be determined by the female bird prior to laying [8]. In nature, observers have noted a strong tendency to see few females compared to males. This may be due to several factors not related to skew, including the female behavior of staying with her nest hollow even when not breeding. But, the observation may also be due in some part to sex ratio bias that is not understood. Studies of wild *Eeclctus* are being conducted which may determine if the skew observed in aviculture is repeated in the natural environment, or what the natural sex allocation strategy in wild *Eeclctus* may be [9, 19].

Season; hatching order

Crimson Rosella (*Platycercus elegans*) [16, 17, 18]. The effects of season were observed in a population of Crimson Rosellas. While overall, there was an approximately 50:50 sex ratio during the breeding season, researchers observed that the proportion of first-hatched males increased as the breeding season progressed. In the Crimson Rosella, studies have shown that hatching rank does not appear to relate to chick survival success except in years of low food availability. This is because the behavior of the male and female parents operates to maximize the probability that all chicks within a brood are fed equally.[17, 18]

Researchers consider that one possible reason for bias toward female chicks during the early part of the breeding season may be that yearling females can be recruited into the breeding population and yearling males cannot [16]. (For a picture of a female Crimson Rosella in juvenile plumage with her chicks, see Krebs 2002 [17].)

House Finch (*Carpodacus mexicanus*) [2]. The effects of hatching order in two distinct environments were studied in two populations of House Finch in Montana and Alabama. In these groups, growth rate of each sex of chick varied according to hatching order within the brood. Additionally, "hatching order had a large effect on juvenile morphology,

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which in turn was the main determinant of juvenile survival.”

During the study, first-laid eggs produced mostly females in Montana but mostly males in Alabama. The actual survival rate of sons and daughters in each hatching position was tested statistically against a “what if” scenario. In this scenario, the gender in each hatching position was compared against what would happen if a chick of the opposite gender were hatched in that position instead. The test indicated that “males hatched in male biased positions had higher survival than males hatched in female biased positions.” The study determined that by skewing the broods’ sex ratios, the populations increased the survival of male and female offspring by 10 to 20% in both environments.

The study also tested what happened if young in one hatching order in the original nest were cross fostered into a different nest such that they were in a different hatching order in the foster nest. The test indicated that the original hatching order “strongly affected the morphology at the end of growth,” and therefore the survival of the chick, regardless of the change.

An Application for Sex-Ratio Theory Conservation Biology [3, 4, 6, 11, 25, 26, 27]

The Kakapo (*Strigops habroptilus*) is endemic to New Zealand [6] and is the largest of all parrots (1.5-4 kg) [6, 27]. This nocturnal, terrestrial parrot is unique in its extreme sexual size dimorphism, lek breeding system, the female caring for herself and her eggs and chicks with no participation from the male [4, 26, 27], and breeding in cycles coincident with the heavy fruiting cycles (masting) of area Podocarp trees [11, 25]. This timing means the breeding cycles can be separated by 2-5 years [6, 27] or more, with no breeding activity between cycles [3].

The Kakapo is among the most critically endangered [4] parrots in the world and is considered to be extinct in its natural range [26].

Management and conservation

efforts began during the 1970s and were intensified during the late 1980s and early 1990s [6]. These efforts included translocation of all known Kakapo to four islands on which eradication techniques had been employed against introduced mammalian predators and competitors such as rats and possums [3, 4, 6, 11, 25, 26]. Female Kakapo are located on three of the islands, including Whenua Hou (Codfish Island) [6]. Efforts also include radio-transmitter tracking, protection from predation, human interference to ensure the success of nests/chick survival and supplementary feeding [6]. Not all females utilize the supplementary food [3, 4, 6, 11].

As of 2001, the total known population of the Kakapo was 62 [3, 6] individuals with an adult sex ratio heavily skewed toward males at 31:19 [4]. This skew may represent influence of predation by introduced mammals and habitat destruction since European settlers arrived in New Zealand in the nineteenth century. It may also represent natural sex ratio bias [27]. Kakapo numbers are so small and their environment so intensely managed and changed that at this time data cannot support any firm conclusions [4, 6, 27] in this regard. However, the 2001 sex ratio is important to an understanding of how few breeding females vs. males existed with which to increase the population. This group included 47 surviving original translocated birds and 15 offspring fledged since 1991 [11, 25].

Of the 15 offspring, 6 were produced during the 1999 breeding season and 9 were produced prior to that time. The sex ratio of fledglings produced prior to 1999 is 7:2 [26]. The sex ratio of the 6 fledglings produced in the 1999 breeding season is 2:4 [11].

As recruitment of more females into the population is critical to the Kakapo recovery plan [3, 4, 25], the difference in the sex ratio of the 1999 fledglings drew the attention of Kakapo researchers [4].

Evidence indicates females select large mates who are able to hold central

or high ground at leks, and male young tend to grow faster and become larger more quickly than female young. Thus, in Kakapo, males are the more variable gender. Sex allocation theory would predict that female Kakapo in better condition would tend to skew the sex ratio of their clutches toward males [4, 25].

Examination of the supplementary feeding program revealed that one female who had not been supplemented had produced three of the four female chicks. The Kakapo who had produced the fourth female chick had accepted supplementary food. Her clutch was comprised of 1 female and 2 male chicks [4, 11].

In considering this data, historical sex ratios and supplementary feeding data prior to 1999, and papers discussing sex allocation theory, [3, 4, 26], the Kakapo research team proposed and implemented a revised supplementary feeding program. This program included reducing supplemental food during the breeding season to a threshold that would not endanger the physical health of the females, yet would encourage the production of female vs. male chicks [3, 4, 25, 26].

The 2002 breeding season was particularly productive, coinciding with an extraordinarily heavy masting of a plentiful Podocarp tree, the Rimu (*Dacrydium cupressinum*) on Whenua Hou [11, 25]. To take advantage of the mast to trigger a Kakapo breeding cycle, all 21 females then of breeding age had been translocated to Whenua Hou and the new skew-based supplemental feeding program implemented [3, 25].

Thirteen of the females produced a total of 24 fledglings, 19 of which were female, as the sex allocation theory-inspired conservation plan had predicted [3, 11, 25]. This raised the total population of Kakapo to 86 [3] individuals. Researchers are hopeful that the incorporation of skew-based strategies into the conservation plan will continue to be successful in producing female chicks in future breeding seasons [3, 4]. Skew may play a critical role in bringing the Kakapo back from the brink of extinction.

Skew and Aviculture

Sex allocation bias in birds appears to be a response to many inter-related factors. Aviculturists may observe skew from their breeding birds as chick sex ratios or patterns of gender that are unlikely to have occurred by chance. Skew may also be observed at different times from different birds depending on the species and the genetic abilities of the individuals to respond to the pressures of their environment.

So, Dear Aviculturist,

There's nothing wrong with you.

We don't yet understand it

Although we're trying to.

Sex ratio adjustment, gender bias,

SKEW.

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