

Sibling Aggression and Siblicidal Tendencies in Birds

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Sibling aggression has long been observed in the class of Aves. Young chicks sometimes let their aggression go so far that it turns into siblicide, which occurs when dominant chicks of a brood kill their younger siblings. While siblicidal aggression is not widespread among birds, it has attracted much research. Most of this research seeks to find the cause of siblicide, and several hypotheses have been proposed. The most prominent of these is the food-amount hypothesis, which predicts a positive relationship between siblicidal aggression and deprivation of food (Drummond & Osorno, 2003). Another hypothesis offered is the prey-size hypothesis, which predicts an increase in sibling aggression as food becomes less easily monopolized (Mock, 1985). The brood-size hypothesis predicts that, as clutch size increases, there is a respective increase in siblicidal aggression (Lamey & Mock, 1991). Most recently, the challenge hypothesis has been proposed; it attempts to link siblicidal tendencies to the prevalence of certain hormones, namely testosterone, in the blood (Anderson et al., 2004). The role of parents, whether they encourage or attempt to impede siblicide, has also been studied (Anderson, 1995; Anderson & Loughheed 1999). The results of these studies show there is no single cause for avian siblicidal aggression. It is a complicated behavior with physiological, hormonal, and circumstantial causes.

The Food-Amount Hypothesis

The food-amount hypothesis (FAH) predicts a negative relationship in facultatively siblicidal bird species between food availability and siblicidal aggression

(Dewey et al, 1999). Drummond (2000) provides several associations of food amount and aggression which support the FAH. First, fighting occurs near feeding time and increases when food consumption is reduced; recently fed chicks are less likely to attack. Second, siblicide (by starvation or direct aggression) is more common when parents bring less food/ less food is available. Finally, in the same populations, when there is greater food stress compared to previous seasons, aggression is more frequent. Experimental studies with Blue-footed Boobies report the levels of dominance among chicks increased as food deprivation grew stronger. Studies on Black-legged Kittiwakes, Osprey, and Black Guillemot also showed increased siblicidal aggression with food deprivation, therefore supporting the FAH (Drummond, 2000).

Despite the logic of the food-amount hypothesis and support in many siblicidal species, several studies have found no variation in siblicidal aggression when food amount was manipulated. When Lamey et al. (1987) manipulated food amount with Great Egrets, Great Blue Herons, and Cattle Egrets, they found that food deprivation did not cause an increase in siblicidal aggression. While there were slight increases in fighting when food was at lower levels, the analysis interpreted it as not significant. Furthermore, when there was abundant food and chicks were fed until no longer hungry, Lamey et al. (1987) observed continued and sometimes increased, vigorous fighting. They speculated that these insensitivities to food deprivation resulted from the unpredictable nature of food availability in the wild, that is, young birds would not associate current food availability with future food availability. However, Drummond (2000) points out that in these studies different brood-sizes were pooled (some chicks were placed into larger/smaller broods than where they were found). This technique in

testing confounds the results because brood-size affects the level of siblicidal aggression (Lamey & Mock, 1991). In addition to this technique, in experimental studies done by Lamey et al. (1987) Drummond (2000) points out that the conditions were highly unnatural and there was no parental figure present as there would be in the wild.

The FAH has also been tested in obligately siblicidal species (the last born chick nearly always dies) by Drummond & Osorno (2003) in their study with Brown Boobies. Over two days of constant surveillance, all except one of the older chicks in the experimental groups attacked their younger nest mates. Although food deprivation caused older chicks to spend more time active, and therefore available to attack, there was no significant correlation between increased food amounts and reduced siblicidal aggression. Drummond & Osorno (2003) also compared Brown Boobies with Blue-footed Boobies (a facultatively siblicidal species) and found that food deprivation caused each species to intensify its natural behaviors. Blue-footed Boobies increased aggressiveness, and Brown Boobies more quickly expelled their nest mates. Although the FAH offers a logical and supported explanation of avian siblicidal aggression, in certain taxa food amount has no effect. For this reason, several other hypotheses have been proposed.

The Prey-Size Hypothesis

The prey-size hypothesis proposes that if food is limited, delivered in small units, and chicks have the ability to be a threat to each other, then siblicidal aggression will occur (Mock, 1985). This hypothesis was tested with Great Egrets and Great Blue Herons by Mock. In his study, siblicidal aggression included fighting and intimidation by means of monopolization of food. Mock found that Heron's prey was four times longer and 45

times heavier than that of Egret prey. The methods of feeding also differ between these two species. In the first week or so after hatching and in both species, food is regurgitated onto the floor of the nest before chicks eat it (indirect feeding). However, after this period, Egret chicks learned to intercept the boluses before they hit the nest (direct feeding), whereas Heron feeding methods remained indirect. Following the first three weeks after hatching, junior Egret chicks had a significantly greater chance of being deprived of food. In contrast, Heron junior chicks attained roughly the same amount as their senior nest mates. The small units of food provided by Egret parents were economically defensible and easily monopolized through direct feeding; therefore, siblicidal aggression held potential gain for dominant Egret chicks. On the other hand, the larger units of food provided by Heron parents, combined with the indirect method of feeding, held no potential gain for aggressive siblings. Furthermore, when Herons were fed on a small-prey diet by Egret foster parents in an experimental study, the Herons changed to direct feeding methods, fought at Egret-like rates, and killed most third-hatched chicks (Mock, 1985). The Herons behaved identically even when they were provided with ample amounts of the small prey. Lamey et al. (1987) also point out that the Great Blue Herons of Texas, which eat large fish, show relatively no siblicidal aggression, whereas the Heron population in Quebec, where they eat small fish, are eight times more aggressive.

Mock (1985) acknowledges the possibilities of food amount being a cause for siblicidal aggression, but he proposes that prey-size may trigger siblicidal aggression prior to food shortages. Mock offers three lines of evidence which attempt to discredit the FAH. First, that siblicidal aggression is present soon after hatching, when there is enough

food for all siblings. Second, in experimental captive groups of Egrets, in which all chicks were fed until full, numerous fights occurred. Lastly, wild Egret broods which were provided with sufficient food also continued to fight.

The Brood-Size Hypothesis

Lamey & Mock (1991) suggest that in siblicidal species where food levels are inconsistent, the FAH fails to explain all sibling aggression between nest mates. They offer the brood-size hypothesis as an alternative, proposing that as brood size is decreased, as a result of siblings' instinctive drive to ensure themselves sufficient nutrition, siblicidal aggression decreases. In their experiments with Cattle Egrets, Lamey & Mock experimentally removed the final hatched chick and then measured fighting rates. Cattle Egrets do not base chick aggression on current food amounts, and parents brought less food when the brood was reduced. Therefore, food was eliminated as a factor in the observed levels of siblicidal aggression (Lamey & Mock, 1991). Siblicidal aggression decreased dramatically by 95% after the youngest chick was removed, however, once the chick was reinstated, fighting resumed in full. Lamey & Mock (1991) report that most of the fighting in their control groups was between the middle and last hatched chick. Aggression between the first hatched and last hatched chicks virtually ceased after the first three day period of observation. This decline was almost identical to that of the experimental groups and caused Lamey and Mock to test the effect of the removed chick's rank.

In response, they experimentally removed the first hatched chick in further trials. The removal of the eldest chicks also resulted in a drastic decrease of siblicidal

aggression between the remaining chicks. In an interesting twist, when the eldest siblings were reinstated, the aggression levels were significantly higher than before the chick had been removed, due to the eldest chick's attempts to reestablish its superiority. The controls in these trials followed no such trend, and these findings suggest that rank of the removed chick is of no consequence. According to Lamey and Mock (1991), chicks obtain three benefits from a decrease in fighting: injuries resulting from aggression are no longer prevalent; fitness is saved by focusing energy solely on growth and maturing; and risk of predation, parental abandonment, and additional thermal stress is reduced by fifty percent with a brood of two versus a single chick brood.

Lamey and Mock (1991) do not exclude food amount or prey-size as proximate cues, but they add brood-size to the list of factors which contribute to siblicidal aggression. However, reduction of brood-size holds a disadvantage which food amount and prey-size do not: it is not reversible. Once a chick has been removed via death, it cannot be brought back if conditions improve.

The Challenge Hypothesis

Most recently, a hypothesis has been proposed which attempts to explain siblicidal aggression as a result of increased testosterone levels: the challenge hypothesis. Anderson et al. (2004) compared testosterone blood levels in Nazca Boobies before times of aggression, during fights, and after siblicide of the youngest chick. In experimental broods of two, blood samples were taken from the younger chicks after they were first expelled from the nest. Chicks were then placed back into the nest, and, when they were expelled for a second time, blood samples from the older chicks were taken. Anderson et

al. (2004) found that, as predicted by the challenge hypothesis, testosterone levels were higher during fights. A-chicks also had significantly higher levels of testosterone during fights than they did in the two days following siblicide of their younger nest mate. The challenge hypothesis additionally predicts B-chicks' testosterone levels to be higher than A-chicks' during fights; A-chicks present a larger challenge to B-chicks than B-chicks to A-chicks, and thus B-chicks have more need for higher testosterone levels. The results of Anderson et al. (2004) support this prediction: B-chick testosterone levels measured during fights were significantly higher than that of A-chicks. The challenge hypothesis may offer a biological explanation for the causes of siblicidal aggression, not only in facultatively siblicidal species but in obligately siblicidal species of birds as well.

The Role of Parents in Siblicidal Aggression

Anderson (1995) has proposed that siblicidal aggression may hold certain advantages for parents; the chicks are able to judge their physiological states best, determine their competitive hierarchy, and maximize the effectiveness of brood reduction. This allows parents to fledge their most fit offspring, with the best chance of survival, and thereby secure the best chance of passing on their genes. However, there is a disadvantage to parental allowance of siblicidal aggression: the offspring may commit siblicide under less severe conditions than are most advantageous for the parents (Anderson, 1995). Due to these evolutionary relationships, it has been controversial whether parents play an active or passive role in regulating siblicidal aggression in their offspring. Generally, parents are thought to be passive in their regulation of siblicide once offspring hatch (Anderson & Loughheed, 1999).

Several studies on this subject have found, however, significant pre and post-hatching parental regulation of siblicidal aggression. In Anderson's (1995) comparative study of Blue-footed Boobies (facultatively siblicidal) and Masked Boobies (obligately siblicidal), it was found that parents influence the strength of siblicidal aggression within their broods through different hatching intervals and contrasting nest shapes. In obligately siblicidal species like the Masked Booby, parents hatch eggs at longer intervals than in facultatively siblicidal species such as the Blue-footed Booby (Anderson, 1995). This establishes a more biased competitive pecking order. It also increases the already substantial ability of the senior chicks to commit siblicide of junior chicks before or soon after they hatch. The differences in the nest shapes of Masked Boobies and Blue-footed Boobies also contribute to Masked Boobies' successful siblicide of junior chicks. Anderson (1995) observed that Blue-footed Boobies have nests with steeper sides than those of Masked Boobies, and these hinder senior chicks' ability to eject their younger nest mates. Masked Boobies, on the other hand, have flat nests that make ejection of younger nest mates quite easy. Although Masked Booby nesting sites are less capable of forming a bowl-shaped nest, Anderson (1995) found only a 20% handicap from the soil, whereas the differences measured in depths between the two species approached 100%. These findings produce substantial support for partial parental regulation of siblicidal aggression.

Anderson & Loughheed (1999) also conducted studies of these two species which tested what he referred to as the nestling-influence hypothesis (only offspring influence siblicidal aggression), the parental-influence hypothesis (only parents influence siblicidal aggression), and the joint-influence hypothesis (both offspring and parents influence

siblicidal aggression). The post-hatching regulatory influence of parents was examined through a series of cross-fostering experiments in which Blue-footed Booby hatchlings were cared for by Masked Booby parents and vice versa. Results of this study supported the joint-influence hypothesis while disagreeing with the offspring-influence hypothesis and parent-influence hypothesis (Anderson, 1995). In short, Anderson (1995) found that when Blue-footed Booby and Masked Booby nestlings were under the care of Masked Booby parents, siblicide was significantly higher than when both species of nestlings were cared for by Blue-footed Boobies. These results may be explained by the parents' behaviors: Masked Booby parents spend up to eight hours away from the nest searching for food, which allows unsupervised time to fight, and they make nests that seem to facilitate siblicidal aggression (Anderson, 1995). It appears that the characteristics of the parents (how much time they spend away from the nest), along with the nests which they prepare, influence the likelihood of siblicide. Blue-footed Booby parents/nests restrict siblicide, and Masked Boobie parents/nests foster it (Anderson, 1998). While these parental techniques may contribute to regulation of siblicidal aggression, the offspring and many other factors discussed previously affect the final outcome, whether it is intimidation or death.

Summary

Many hypotheses have been formulated to explain the causes of the relatively uncommon phenomenon of siblicidal aggression. All have been supported by evidence, however, no single hypothesis can fully explain the cause of avian siblicidal aggression. The most researched of these is the food-amount hypothesis, which predicts that

siblicidal aggression will increase as abundance of food decreases (Dewey et al., 1999). Due to such high interest and inspection, it has become the most generally accepted hypothesis as well. Studies on Blue-footed Boobies, Black-legged Kittiwakes, Osprey, and Black Guillemot have supported this hypothesis (Drummond 2000). However, several studies have found no variance in siblicidal aggression when food amount was manipulated in Cattle Egrets, Great Egrets, Great Blue Herons, and obligately siblicidal species (Lamey et al., 1987; Drummond & Osorno, 2003). Although the FAH appears to be the ultimate cause in most species, in some taxa and certain circumstances it cannot fully explain the occurrence of siblicidal aggression.

Several other hypotheses have been put forth. The prey-size hypothesis predicts that siblicidal aggression will increase as food becomes more easily monopolized/smaller (Mock, 1985). In his study with Great Egrets (which are fed smaller fish) and Great Blue Herons (which are fed larger fish), Mock saw that the size of regurgitated boluses and the methods of feeding, direct or indirect, influenced the levels of siblicidal aggression. While prey size may be a proximate cause of siblicidal aggression, not all siblicidal species are fed on small prey and not all non-siblicidal species are fed on larger prey. Thus, the prey-size hypothesis can offer only a partial explanation for siblicidal tendencies in birds.

The brood-size hypothesis has also been offered as an explanation for siblicidal aggression. It predicts that siblicidal aggression will intensify as the number of chicks in a clutch increases (Lamey & Mock, 1991). In experimental studies with Cattle Egrets, when brood size was reduced from three to two, fighting virtually ceased; when the sibling previously taken out of the nest was returned, fighting elevated to normal levels.

This evidence supports the idea that in siblicidal species the number of chicks vying for resources and attention affects the level of siblicidal aggression. However, this only appears to be a proximate cause, due to the fact that species vary in what number of chicks produces siblicidal aggression and non-siblicidal species often have equal to or a greater numbers of chicks than siblicidal species.

The newest hypothesis which has been offered is the challenge hypothesis. With this hypothesis, Anderson et al. (2004) attempt to link increased testosterone levels with times of increased siblicidal aggression. After taking blood samples from Nazca Boobie chicks before and after fights, Anderson et al. (2004) found that levels of testosterone in the chicks were higher surrounding the time of the fights. They also found that junior chicks' testosterone levels were higher than senior chicks; this is explained by the observation that junior chicks are more threatened by senior chicks than senior chicks are by junior chicks. This new hypothesis is an interesting and different way of explaining the origins of avian siblicidal aggression. This biological perspective could put an interesting twist on the new studies done pertaining to siblicidal aggression, perhaps even revealing that certain species have inherited genetic dispositions to siblicidal aggression.

Studies which focused on the role of parents in regulating siblicidal aggression found that parental influence on varying hatching intervals and nest shapes can facilitate or hinder siblicidal aggression in Masked Boobies and Blue-footed Boobies, respectively (Anderson, 1995). Cross-fostering studies done by Anderson (1998) also support the idea that parents have a part in regulating siblicidal aggression. Masked Boobie and Blue-footed Boobie chicks raised by Masked Boobie parents had higher levels of sibling aggression than when they were raised by Blue-footed Boobie parents. The parental

influence on siblicidal aggression is certainly one of many proximate causes. Further research in this direction might look for a genetic basis on which avian parents encourage or discourage siblicidal tendencies among their young.

While a great deal of research has already been done on siblicidal aggression, much remains to be learned. By testing the various hypotheses put forth and using different species, more secure conclusions can be made. In addition, the challenge hypothesis represents the new type of research questions that should be put forth. Studies that seek to explain the relationship between testosterone and siblicidal aggression, along with other internal biological causes, should be the next step in the exploration of siblicidal aggression. This research could not only identify the causes of aggression in siblicidal birds but also discover what, if any, genetic differences distinguish between siblicidal and non-siblicidal species.

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