Avian Siblicide

Killing a brother or a sister may be a common adaptive strategy among nestling birds, benefiting both the surviving offspring and the parents

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Occasionally, the pen of natural selection writes a murder mystery onto the pages of evolution. But unlike a typical Agatha Christie novel, this story reveals the identity of the murderer in the first scene. The mystery lies not in "whodunit," but in why.

The case at hand involves the murder of nestling birds by their older siblings. Observers in the field have frequently noted brutal assaults by elder nestmates on their siblings, and the subsequent deaths of the younger birds. The method of execution varies among different species, ranging from a simple push out of the nest to a daily barrage of pecks to the head of the younger, smaller chick. Such killings present a challenge to the student of evolutionary biology: Does siblicide promote the fitness of the individuals that practice it, or is such behavior pathological? In other words, are there certain environmental conditions under which killing a close relative is an adaptive behavior? Moreover, are there other behaviors or biological features common to siblicidal birds that distinguish them from nonsiblicidal species?

Avian siblicide holds a special interest for several reasons. First, because nestling birds are relatively easy to observe, a rich descriptive literature exists based on field studies of many species. Second, because birds tend to be monogamous, siblicide is likely to involve full siblings. (Although recent DNA studies suggest that birds may not be as monogamous as previously thought, most nestmates are still likely to be full siblings.) Third, young birds require a large amount of food during their first few weeks of development, and this results in high levels of competition among nestlings. The competitive squeeze is exacerbated for most species because the parents act as a bottleneck through which all resources arrive. Fourth, some avian parents may not be expending their maximum possible effort toward their current brood's survival (Drent and Daan 1980, Nur 1984, Houston and Davies 1984, Gustafsson and Sutherland 1988, Mock and Lamey in press). Parental restraint may be especially common in long-lived species, in which a given season's reproductive output makes only a modest contribution to the parents' lifetime success (Williams 1966).

Siblicide—or juvenile mortality resulting from the overt aggression of siblings—is not unique to birds. It is also observed, for example, among certain insects and amphibians; in those groups, however, the behavioral pattern is rather different. Most siblicidal insects and amphibians immediately consume their victims as food, whereas in birds (and mammals) siblicide rarely leads to cannibalism. For example, tadpoles of the spadefoot toad acquire massive dentition (the so-called "cannibal morph") with which they consume their broodmates (Bragg 1954), and fig wasps use large, sharp mandibles to kill and devour their brothers (Hamilton 1979). In contrast, among pronghorn antelopes, one of the embryos develops a necrotic tip on its tail with which it skewers the embryo behind it (O'Gara 1969), and piglet littermates use deciduous eyeteeth to battle for the sow's most productive teats (Fraser 1990). Among birds and mammals it seems that the goal is to secure a greater share of critical parental care.

Although biologists have known of avian siblicide for many years, only recently have quantitative field studies been conducted. The current wave of such work is due largely to the realization that siblicide occurs routinely in some species that breed in dense colonies; such populations provide the large sample sizes needed for formal testing of hypotheses.

Models of Nestling Aggression

Our examination of siblicidal aggression focuses on five species of birds. Two of these, the black eagle (*Aquila verreauxi*) and the osprey (*Pandion haliaetus*), are raptors that belong to the family Accipitridae. A third species, the blue-footed booby (*Sula nebouxii*) is a seabird belonging to the family Sulidae. We also present studies of the great egret (*Casmerodius albus*) and the cattle egret (*Bubulcus ibis*), both of which belong to the family Ardeidae. Each of these species exhibits a distinct behavioral pattern; the range of variation is important to an understanding of siblicide.

The black eagle is one of the first birds in which siblicide was described. This species, also called Verreaux's eagle, lives in the mountainous terrain of southern and northeastern Africa, as well as the western parts of the Middle East. Black eagles generally build their nests on cliff ledges and lay two eggs between April and June. The eaglets hatch about three days apart, and so the older chick is significantly larger than the younger one. The black eagle is of particular interest for the study of

Figure 1. Two cattle egrets peer down at their recently evicted younger sibling. For several days before the eviction, the elder siblings pecked at the head of their smaller nestmate. Here the younger bird holds its bald and bloodied head out of reach. Soon after the photograph was made, the bird was driven to the ground and perished. (Photograph courtesy of the authors.)

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siblicide because the elder eaglet launches a relentless attack upon its sibling from the moment the younger eaglet hatches. In one well-documented case, the senior eaglet pecked its sibling 1,569 times during the three-day lifespan of the younger nestling (Gargett 1978).

Among ospreys, sibling aggression is neither so severe nor so persistent as it is among black eagles. Ospreys are widely distributed throughout the world, including the coastal and lacustrine regions of North America. The nests are generally built high in trees or on other structures near water. A brood typically consists of three chicks, which usually live in relative harmony. Nevertheless, combative exchanges between siblings do occur in this species; comparisons between the fighting and the pacifist populations offer insights into the significance of aggression.

The blue-footed booby lives exclusively on oceanic islands along the Pacific coast from Baja California to the northern coast of Peru. Blue-footed boobies are relatively large, ground-nesting birds that typically form dense colonies near a shoreline. Two or three chicks hatch about four days apart, and this results in a considerable size disparity between the siblings. As in many other siblicidal species, the size disparity predicts the direction of the aggression between siblings.

Young nestmates also differ in size in the two egret species we have studied. The larger of these, the great egret, is distributed throughout the middle latitudes of the world, and also throughout most of the Southern Hemisphere. Great egrets make their nests in trees or reed beds in colonies located near shallow water. The cattle egret also nests in colonies, but not necessarily close to water. Cattle egrets live in the middle latitudes of Asia, Africa and the Americas. As their name suggests, they are almost always found in the company of grazing cattle or other large mammals, riding on their backs and feeding on grasshoppers stirred up by the movement of the animals. Despite their differences in habitat, great egrets and cattle egrets have a number of behaviors in common. Typically, three or four egret nestlings hatch at one- to two-day intervals, and fighting starts almost as

Figure 2. Aggression in black eagle nestlings almost always results in the death of the younger sibling. Here a six-day-old black eagle chick tears at a wound it has opened on the back of its day-old sibling.

Peter Steyn

soon as the second sibling has hatched. Aggressive attacks lead to a "pecking order" that translates into feeding advantages for the elder siblings (Fujioka 1985a, 1985b; Mock 1985; Ploger and Mock 1986). In about a third of the nests, the attacks culminate in siblicide through socially enforced starvation and injury or eviction from the nest.

Obligate and Facultative Siblicide

It is useful to distinguish those species in which one chick almost always kills its sibling from those in which the incidence of siblicide varies with environmental circumstances. Species that practice obligate siblicide typically lay two eggs, and it is usually the older, more powerful chick that kills its nestmate. The black eagle is a good example of an obligate siblicide species. In 200 records from black eagle nests in which both chicks hatched, only one case exists where two chicks fledged (Simmons 1988). Similar patterns of obligate siblicide have been reported for other species that lay two eggs, including certain boobies, pelicans and other eagles (Kepler 1969; Woodward 1972; Stinson 1979; Edwards and Collopy 1983; Cash and Evans 1986; Evans and McMahon 1987; Drummond 1987; Simmons 1988; Anderson 1989, 1990).

A far greater number of birds are facultatively siblicidal. Fighting is frequent among siblings in these species, but it does not always lead to the death of the younger nestling. There are various patterns of facultative siblicide. For example, in species such as the osprey, aggression is entirely absent in some populations, and yet present in others (Stinson 1977; Poole 1979, 1982; Jamieson et al. 1983). In other species aggression occurs at all nests but differs in form and effect. In the case of the blue-footed booby a chick may hit its sibling only a few times per day for several weeks, and then rapidly escalate to a lethal rate of attack (Drummond, Gonzalez and Osorno 1986). Egret broods tend to have frequent sibling fights—there are usually several multiple-blow exchanges per day—but the birds do not always kill each other (Mock 1985, Ploger and Mock 1986).

Traits of Siblicidal Species

Five characteristics are common to virtually all siblicidal birds: resource competition, the provision of food to the nestlings in small units, weaponry, spatial confinement and competitive disparities between siblings. The first four traits are considered essential preconditions for the evolution of sibling aggression; the study of their occurrence may shed some light on the origin of siblicidal behavior. The fifth trait—competitive disparities among nestmates resulting from differences in size and age—is also ubiquitous and important, but it is probably not essential for the evolution of siblicide. In fact, competitive disparities may be a consequence rather than a cause of siblicidal behavior; having one bird appreciably stronger than the other reduces the cost of fighting, since asymmetrical fights tend to be brief and it is less likely that both siblings will be hurt during combat (Hahn 1981, Fujioka 1985b, Mock and Ploger 1987).

Of the five traits common to siblicidal species, the competition for resources is probably the most fundamental. Among birds, the competition is primarily for food. Experiments have shown that the provision of additional food often diminishes nestling mortality (Mock, Lamey and Ploger 1987a; Magrath 1989). But "brood reduc-

Figure 3. Blue-footed booby nestlings maintain dominance over their younger siblings through a combination of aggression and threats *(upper photograph)*. The assaults do not escalate to the point of eviction unless the food supply is inadequate. An evicted chick has little chance of survival in the face of attacks from neighboring adults *(lower photograph)*. (Photographs courtesy of the authors.)

tion"—the general term for nestling deaths brought about by the competition for food—does not necessarily entail direct aggression. Nestlings die even in nonsiblicidal species, but the usual cause of death is starvation; weaker chicks continually lose to their more robust siblings in the scramble for food. What distinguishes siblicidal species is that the competition for food is intensified to the point of overt attack. (In nonavian species, the competition may be over reproductive opportunity. For example, male fig wasps and female "proto-queen" honeybees kill all of their same-sex siblings immediately after hatching in order to gain the breeding unit's single mating slot. In certain species of mammalian social carnivores, one female dominates her sisters, rendering them effectively sterile.)

In avian species, if the source of food cannot be defended, aggression does not appear to be advantageous. The food must come in morsels small enough to be monopolized through combat. In all known species of siblicidal birds, food is presented to the young in small units through direct transfer from parent to chick (Mock 1985). For example, very young raptor chicks take small morsels held in the mother's bill, whereas boobies either reach inside the parent's throat or use their own bills to form a tube with the parent's bill, and egrets scissor the parent's bill crosswise so as to intercept the food as it emerges.

Figure 4. Great egret chicks fight frequently, regardless of food levels. Siblicide occurs in about a third of the nests, through socially enforced starvation and injury or as a result of eviction. As in other species of siblicidal birds, the parents do not interfere with the fights and evictions among their offspring. (Photograph courtesy of the authors.)

The link between the size of the food and sibling aggression lies in the relation between intimidation and monopolization. From the chick's perspective, food descends from the inaccessible heights of its parent's bill, becoming potentially available only at the moment it arrives within reach. A sibling's share depends primarily on its position relative to its competitors; that position can be enhanced through physical aggression or threat (much as the use of elbows can enhance a basketball player's chance of catching a rebound). For food items that can be taken directly from the parent's bill, the sibling's share should rise in relation to the degree of intimidation achieved. Thus, small food items create incremental rewards for aggression.

A diet of large, cumbersome items that cannot be intercepted by the chicks generally does not give rise to sibling aggression. Although killing all of its siblings would enable a chick to monopolize large items, the rewards for mild forms of aggression are sharply reduced. Thus, when food units are large, sublethal fighting may be less effective than simply eating as fast as possible. The great blue heron (*Ardea herodias*) is developmentally flexible with respect to prey size and aggression. These birds express siblicidal aggression only when the food is small enough to be taken directly from the parent. Great blue heron nestlings in Quebec fight vigorously over small units of food that can be intercepted by aggressive actions (Mock et al. 1987). In contrast, nestlings of the same species in Texas typically receive very large morsels and seldom fight (Mock 1985). Moreover, if the normally nonaggressive Texas herons are raised by great egrets, which feed their young small morsels of food, the herons quickly adopt the direct feeding method and exhibit siblicidal aggression (Mock 1984).

Figure 5. Five characteristics are common to virtually all siblicidal birds (*from top left to bottom right*): competition for food, provision of food to the nestlings in small units, weaponry, competitive disparities between siblings and spatial confinement. Four of the traits are considered essential preconditions for the evolution of sibling aggression, whereas competitive disparities between siblings may be a consequence rather than a cause of siblicidal behavior.

A shortage of food, and the ability to defend each unit of food, set the stage for siblicide, but the nestling must also possess some means of carrying out a lethal attack. In this regard it is notable that most siblicidal birds are predatory and have hooked or pointed beaks capable of inflicting serious damage on nestmates. Even so, where obvious weaponry is lacking, other means of siblicide may be possible—such as simply rolling eggs out of the nest cup.

Weaponry aside, effective aggression among nestling birds is also correlated with small nests or nesting territories. Chicks assaulted by their senior siblings do not necessarily have the option of escaping the nest. In tree-nesting species, a chick that leaves its nest risks falling from a narrow limb. Dominant chicks of the cliff-nesting kittiwake (*Rissa tridactyla*) simply drive their siblings off the nest ledge (Braun and Hunt 1983). In the dense colonies of the blue-footed booby, young chicks oppressed at home by their siblings may face even greater persecution from adult neighbors if they leave their natal territory. In a tunnel-nesting bee-eater species, the nestlings have a special hook on their beaks with which they defend the opening to the nest (and the source of the food) against their younger siblings (Bryant and Tatner 1990). In each of these cases, the lack of suitable space (either for escape or as an alternative route to food) contributes directly to the victim's death.

The competitive disparities commonly observed among nestlings of siblicidal birds may hold an important clue to the evolution of sibling aggression. Parents usually create such disparities by starting to incubate one egg at some point prior to laying the final egg in the clutch. Because eggs are produced at intervals of one or more days, the chick hatched from the egg laid first has an important head start. (Parents may also initiate competitive asymmetries by laying different-sized eggs within a clutch or by feeding certain young preferentially, but these mechanisms are less common than asynchronous hatching.)

The Oxford ornithologist David Lack proposed that asynchronous hatching is a behavioral adaptation that allows for a secondary adjustment in brood size to match resource levels

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Figure 6. Food is presented directly to the chick in small units in all known species of siblicidal birds. This direct method of feeding means that a chick may increase its share of food by physically intimidating, and not just by killing, its competing siblings. The young black eagle (*top*) is fed a piece of hyrax meat by the direct-transfer method, even though the bird is well into the fledgling stage. In the blue-footed booby (*lower left*), the parent transfers small pieces of fish from its mouth directly into the mouth of a chick. An osprey chick (*lower right*) receives a piece of meat from its parent while its sibling waits. Osprey chicks take turns feeding, and will fight only if food becomes scarce.

(Lack 1954). Parents must commit themselves to a fixed number of eggs early in the nesting cycle, before the season's bounty or shortcomings can be assessed. Thus, it is often advantageous for parents to produce an additional egg or two, in case later conditions are beneficent, while reserving the small-brood option by making the "bonus" offspring competitively inferior, in case the season's resources are poor. The production of an inferior sibling may be advantageous, since the senior sibling can then eliminate its younger nestmate with greater ease. In fact, experimentally synchronizing the hatchings of cattle egrets results in an increase in fighting, which reduces the reproductive efficiency of the parents (Fujioka 1985b, Mock and Ploger 1987).

Siblicide as an Adaptation

To understand siblicide, we must understand how the killing of a close relative can be favored by natural selection. At first this may seem a simple matter. Eliminating a competitor improves one's own chance of survival, and thereby increases the likelihood that genes promoting such behavior will be represented in the next generation. According to this simple analysis, natural selection should always reward the most selfish act, and siblicide is arguably the epitome of selfishness.

The trouble with this formulation is that it implies that all organisms should be as selfish as possible, which is contrary to observation. (Siblicide is fairly common, but certainly not universal.) A more sophisticated analysis was provided in the 1960s by the British theoretical biologist William D. Hamilton. In Hamilton's view, the fitness of a gene is more than its contribution to the reproduction of the individual. A gene's fitness also depends on the way it influences the reproductive prospects of close genetic relatives.

This expanded definition of evolutionary success, called inclusive fitness, is a property of individual organisms. An organism's inclusive fitness is a measure of its own reproductive success plus the incremental or decremental influences it has on the reproductive success of its kin, multiplied by the degree of relatedness to those kin (Hamilton 1964). Hamilton's theory is generally invoked to explain apparently altruistic behavior, but the theory also specifies the evolutionary limits of selfishness.

An example will help to clarify Hamilton's idea. Suppose a particular gene predisposes its bearer, *X*, to help a sibling. Since the laws of Mendelian inheritance state that X and its sibling share, on average, half of their genes, *X*'s sibling has a one-half probability of carrying the gene. From the gene's point of view, it is useful for *X* to promote the reproductive success of a sibling because such an action contributes to the gene's numerical increase. Therefore, helping a sibling should be of selective advantage. It is in this light that we must understand and explain siblicide. Since selection favors genes that promote their own numerical increase, what advantage might there be in destroying a sibling—an organism with a high probability of carrying one's own genes? The solution to the problem lies in the role played by the "marginal" offspring, which may be the victim of siblicide.

In all siblicidal species studied to date there is a striking tendency for the victim to be the youngest member of the brood (Mock and Parker 1986). The youngest sibling is marginal in the sense that its reproductive value can be assessed in terms of what it adds to or subtracts from the success of other family members. Specifically, the marginal individual can embody two kinds of reproductive value. First, if the marginal individual survives in addition to all its siblings, it represents an extra unit of parental success, or extra reproductive value. Such an event is most likely during an especially favorable season, when the needs of the entire brood can be satisfied. Alternatively, the marginal offspring may serve as a replacement for an elder sibling that dies prematurely. In such instances the marginal individual represents a form of insurance against the loss of a senior sibling. The magnitude of this insurance value depends on the probability that the senior sibling will die.

Among species that practice obligate siblicide, the marginal individual offers no extra reproductive value; marginal chicks serve only as insurance against the early loss or infirmity of the senior chick. In these species, if the senior chick is alive but weakened and inca-

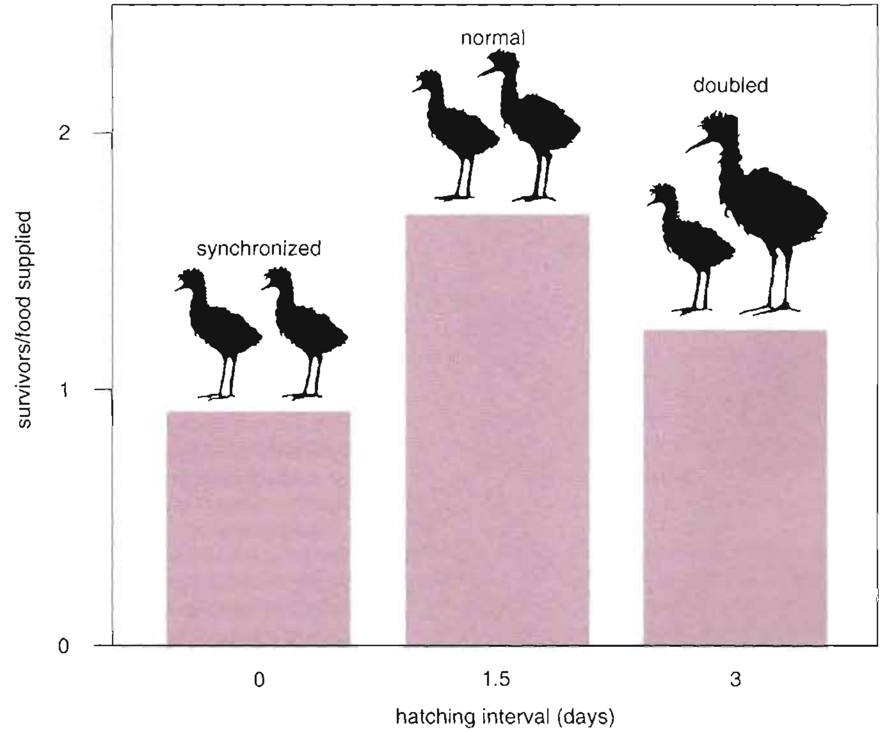

Figure 7. Effect of hatching asynchrony on avian domestic violence was investigated by switching eggs in the nests of cattle egrets. Reproductive efficiency is maximal when chicks hatch at an interval of one and one-half days (as they do under normal conditions). Synchronized hatching (an interval of zero days) increases the amount of fighting between chicks, which results in greater chick mortality. The normal one-and-a-half day interval reduces the amount of fighting since the older chick is able to intimidate the younger chick. Doubling the asynchrony, so that the eggs hatch three days apart, greatly reduces the amount of fighting but exaggerates the competitive asymmetries, so that the youngest nestmates receive little food. The experiments were performed by Douglas Mock and Bonnie Ploger at the University of Oklahoma.

pable of killing the younger chick, the latter may be able to reverse the dominance and kill the senior chick. Such scenarios appear to be played out regularly: In a sample of 22 black eagle nests in which both chicks hatched, the junior chick alone fledged in five of the nests, and the senior chick alone fledged in the remaining 17 cases (Gargett 1977). Similarly, in a sample of 59 nests of the masked booby, the junior chick was the sole fledgling in 13 nests, and the senior chick the sole fledgling in the other 46 nests (Kepler 1969). In both of these species, the junior chick's chance of being the sole survivor—its insurance reproductive value to the parents—is about 22 percent. Removing the "insurance" eggs results in a reduction in the mean number of fledglings per nest (Cash and Evans 1986). Consequently, the insurance value of the marginal offspring should improve parental fitness if the cost of producing that offspring is reasonable. (In fact, the cost of producing one additional egg seems fairly modest: approximately 2.5 percent of the body weight of the black eagle female.)

Among species that practice facultative siblicide, the marginal offspring may be a source of insurance but may also provide extra reproductive value. The relative contribution of the marginal offspring to the reproductive success of the parents appears to vary considerably within and between species. For example, among great egrets the proportion of nests in which all nestlings survive—the extra reproductive value—varies from 15 to 23 percent, whereas the proportion of the nests in which at least one senior sibling dies and the youngest sibling lives—the insurance reproductive value—may vary from 0 to 48 percent (Mock and Parker 1986). The blue-footed booby shows great variation in the extra reproductive value provided by the marginal offspring (5 to 67 percent), whereas the insurance reproductive value is generally quite low (5 to 6 percent). In both of these species the magnitudes of the total reproductive values depend on the size of the brood. In general, the marginal offspring provides a greater total reproductive value to the parents when the brood size is smaller.

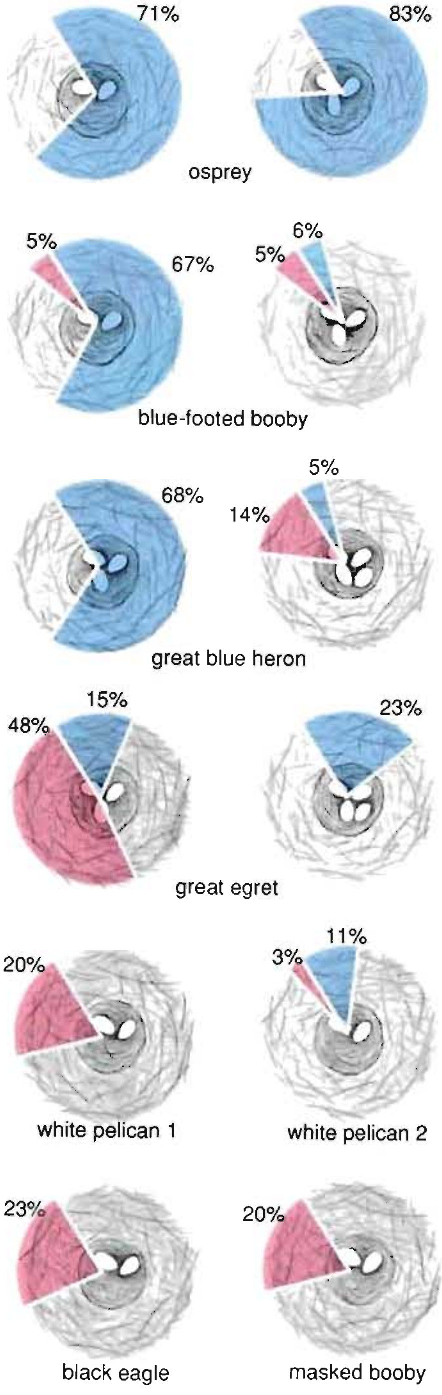

Figure 8. Reproductive value of the youngest member of a brood (the usual victim of siblicide) varies across species and brood size. The reproductive value is represented as the proportion of nests (in broods of two, three or four eggs) in which the youngest chick survives. If the youngest chick survives in addition to its elder siblings, it contributes "extra reproductive value" (*blue sections*); when the youngest chick survives as a replacement for an elder sibling that dies early, the junior bird provides "insurance reproductive value" (*red sections*). Among birds that almost always commit siblicide, such as the black eagle and the masked booby, the youngest chick's reproductive value is entirely due to its role as an "insurance policy." In species where siblicide is more occasional, such as the great egret, the youngest chick may provide either form of reproductive value. These estimates of reproductive value are maxima, since they represent survival only part way through the prefledgling period and not recruitment into the breeding population. These data are derived from studies by: Gargett 1977 (black eagle), Stinson 1977 (osprey), Cash and Evans 1986 (white pelican 1), Evans and McMahon 1987 (white pelican 2), Mock and Parker 1986 (great egret and great blue heron), and Drummond (unpublished data on the blue-footed booby). The data on the masked booby are combined from studies by Kepler 1969 and Anderson 1989.

The Timing of the Deed

A senior sibling should kill its younger sibling as soon as two conditions are met: (1) the senior sibling's own viability seems secure; and (2) the resources are inadequate for the survival of both siblings. Killing the junior sibling before these conditions are met would waste the potential fitness the junior sibling could offer in the form of extra reproductive value or insurance reproductive value. Delaying much beyond the point at which the conditions are met also has a cost. First, the food eaten by the victim is a loss of resources, and, second, the cost of execution may increase as the victim gains strength and is more likely to defeat the senior sibling.

In obligate siblicide species, the average food supply is presumably inadequate for supporting two chicks at reasonable levels of parental effort, and as a result the second chick is dispatched as soon as possible after it hatches. For example, the mean longevity of the victim in the case of the masked booby is 3.3 days (Kepler 1969), and only 1.75 days for brown boobies (Cohen et al. in preparation).

Among facultative siblicide species, the mean longevity of the victim is usually greater; in the blue-footed booby it is 18 days (Drummond, Gonzalez and Osorno 1986). Although the senior blue-footed booby chick may peck at the head or wrench the skin of its nestmate, the younger sibling is seldom killed by these direct physical assaults. Instead, death typically results from starvation or violent pecking by adult neighbors when the junior chick is routed from the home nest (Drummond and Garcia Chavelas 1989).

The Causes of Siblicide

The evolutionary difference between the obligate and the facultative forms of siblicide may be a function of the risk that a junior chick poses to the welfare of its senior sibling. That risk can be defined both in terms of resource consumption and in terms of the potential for bodily harm. If the resources are adequate only for the survival of a single chick, or if a young chick poses a significant physical threat to an older chick, then the senior sibling might be expected to destroy the younger one. On the other hand, if there is enough food for both chicks, and if the younger sibling can be subjugated so that it does not present a threat, then the survival of the younger sibling is beneficial because it increases the inclusive fitness of the senior sibling. In such circumstances, natural selection should favor a measure of clemency on the part of the senior sibling. Accordingly, we would expect obligate siblicide to evolve in circumstances in which resources are routinely limited and siblings tend to pose a physical threat to one another. In contrast, facultative siblicide should arise in circumstances in which resources are not always limited.

The analysis offered above concerns the inheritance of a long-term predisposition to siblicide. Recent studies suggest that food shortages also act as an immediate stimulus to, or proximal cause of, sibling fighting. A link between the food supply and siblicide was suggested by the finding that brood reductions in the blue-footed booby tend to occur soon after the weight of the senior chick drops about 20 percent below the weight expected at its current age in a good year (Drummond, Gonzalez and Osorno 1986). The relationship between food deprivation and aggression was confirmed by experiments in which the senior chick's neck was taped to prevent it from swallowing food. The experimentally deprived senior chicks pecked their nestmates about three to four times more frequently with the tape in place than without the tape, and they subsequently received a greater share of the food (Drummond and Garcia Chavelas 1989).

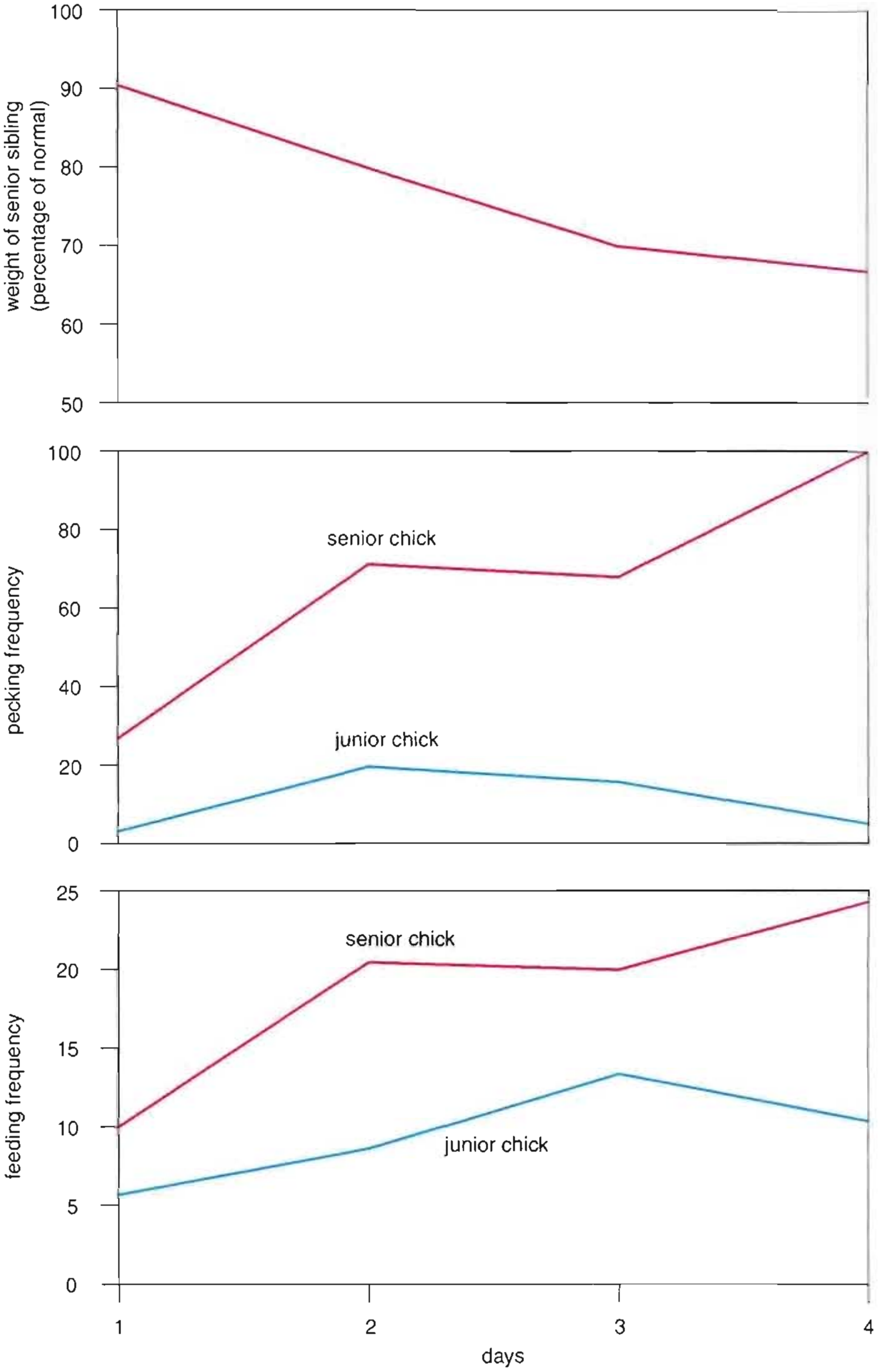

Figure 9. Effect of food deprivation on aggression and food distribution in blue-footed booby nestlings was investigated by taping the senior chick's neck to prevent it from swallowing food. As the weight of the senior chick drops more than 20 percent below normal (*top*), the rate at which it pecks its younger sibling increases more than three-fold (*middle*). The escalating aggression of the elder chick brings it a greater share of food (*bottom*). The experiments were performed by Hugh Drummond and Cecilia Garcia Chavelas at the Universidad Nacional Autònoma de México.

In older booby broods, the increase in the amount of aggressive pecking was delayed by about a day after the chick's neck was taped, suggesting that aggression is controlled by a factor that changes progressively over time, such as hunger or growth status. In fact, the increased pecking rate coincided with a 20 percent weight loss by the senior chick. When the tape was removed, the aggressive pecking rate returned toward the baseline level. These results suggest that nestling aggression among certain facultative species is a reversible response that is sensitive to the weight level of the senior chick.

There is also suggestive evidence in other species that practice facultative siblicide that the amount of food available to the nestlings may affect sibling aggression. For example, junior kittiwake siblings are lost from the nest at higher rates following prolonged periods of bad weather, when parental foraging is reduced (Braun and Hunt 1983). Among osprey populations in which there is a high rate of prey delivery to the offspring, the nestlings are amicable and may even take turns feeding (Stinson 1977). In populations where the food delivery rate is lower, the older nestlings frequently attack their younger siblings, although they do not kill them outright (Henny 1988, Poole 1982).

In contrast, the relative abundance of food does not appear to affect the level of aggression in obligate siblicide species. Black eagle nestlings kill their siblings even in the midst of several kilograms of prey, and even while the mother eagle is offering food to the senior sibling. There does not appear to be the same direct relationship between the immediate availability of food and the level of sibling aggression. Since black eagle nestlings require large amounts of food over a period of many weeks, short-term abundance of food may not be an accurate indicator of long-term food levels. As a consequence, aggression and siblicide might be favored in order to obviate any future competition (Anderson 1990, Stinson 1979).

Perhaps the appropriate "sibling aggression policy" is obtained from simple cues available to the chicks from the outset. Assuming that parents deliver food at some optimal rate, then a chick may be able to estimate in advance whether sufficient levels will be available for its own growth. It is interesting to note that the facultatively siblicidal golden eagle (*Aquila chrysaetos*) provides the same amount of food regardless of the number of chicks in the brood (Collopy 1984). If this is typical, then the senior chick may be able to detect whether the food will be enough to support all nestmates. Eagles that practice obligate siblicide generally deliver less food to the nest than facultative species, and consequently no assessment by the chicks is necessary (Bortolotti 1986). The average amount of food provided by the parents may be consistently low enough for natural selection to favor preemptive killing—a system that benefits both the senior chick and its parents. In other words, the insurance policy is canceled.

Even in species that practice facultative siblicide, aggression is sometimes insensitive to food supply. For example, the level of fighting among heron and egret chicks appears to be independent of the amount of food available (Mock, Lamey and Ploger 1987). It may be that the current food level acts as a proximate cue for sibling aggression only in those species where the current level accurately predicts future food levels. This hypothesis is consistent with the observation that daily food levels are unpredictable and unstable among egrets (Mock, Lamey and Ploger 1987). Interestingly, fighting between egrets ceases when the brood size drops from three to two (thus reducing future food demands) and may be reinstated by restoring the third chick (Mock and Lamey in press). Further studies of other species are necessary to determine whether the degree to which food levels fluctuate is related to aggressive behavior.

Future Directions

The study of siblicide as an adaptive strategy is still in its infancy. Much of the work to date has been devoted to identifying the proximate causes of aggressive behavior and documenting its utility for controlling resources. Less is known about the effects of siblicide on the inclusive fitness of the perpetrators. Although many theoretical models of avian siblicide have been proposed (O'Connor 1978; Stinson 1979; Mock and Parker 1986; Parker, Mock and Lamey 1989, Godfray and Harper 1990), the field data are limited.

Several areas of research need to be explored further. We would like to determine the short-term costs of sibling rivalry, perhaps by comparing the energetics of competitive begging and fighting. Likewise we need to know the long-term costs of temporary food shortages; there is particular interest in the relationship between the development of the chick and the amount of food available. Similarly, what is the relation between the amount of effort parents put into supplying food, the resulting chick survival rate and the long-term costs of reproduction among brood-reducing species? Is there any relation between chick gender, hatching order and siblicide—particularly in siblicidal species that have a large degree of sexual dimorphism? Another area of interest is the role of extra-pair copulations, which reduce the relatedness of nestmates and thereby increase the potential benefits of selfishness; it would be useful to know whether chicks have the ability to discriminate half-siblings from full siblings. Finally, why is it that parents appear not to interfere with the execution process in siblicidal species (O'Connor 1978; Drummond, Gonzalez and Osorno 1986; Mock 1987)? Answers to these questions can give us a better understanding of how siblicidal behavior may have evolved.

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