Etología, 3:187-198 (1993)

Have avian parents lost control of offspring aggression?

H. Drummond

Centro de Ecología, Universidad Nacional Autónoma de México,
A.P. 70-275, 04510 D.F., México

ABSTRACT. *Have avian parents lost control of offspring aggression?-* Avian siblicide has been interpreted as a manifestation of underlying parent-offspring conflict. Recent theoretical models support this interpretation, although a model by Forbes (1993) shows that behavioral conflict is not necessarily expected. Descriptive and experimental studies of several species have failed to provide convincing support for the conflict interpretation of sibling aggression, partly because data are frequently vulnerable to alternative interpretations. Experimental thwarting of siblicide is now needed to establish whether siblicide prejudices parental lifetime fitness.

KEY WORDS. Avian siblicide, Parent-offspring conflict, Offspring aggression.

Introduction

In colonies of egrets, boobies and pelicans one often sees nestlings beating up on their siblings, striking them with their beaks, tugging and twisting at the head and nape, and even thrusting them out of the nest. Death frequently results, through starvation, lesions or expulsion from the nest. This siblicide also occurs in numerous species of raptors and diverse avian species including the black-legged kittiwake (*Rissa tridactyla*, Braun & Hunt, 1983) and the blue-throated bee-eater (*Merops viridis*, Bryant & Tatner, 1990). It compels us to ask why parents create the conditions for it to occur and why they do not stop it. In addressing these issues I provide a personal perspective on the most widely distributed forms of avian siblicide. I shall not deal with non-violent brood reduction through begging competition. More comprehensive accounts of avian siblicide are in Mock (1984), Drummond (1987), Mock et al. (1990) and Mock & Forbes (1992).

Lack (1947; 1966) and Dorward (1962) recognized that extra, disposable chicks might be created to insure against failure of other brood members (as eggs or chicks) or to contribute an extra fledgling if feeding conditions turn out especially favorable. If an extra chick becomes surplus to parental requirements, it must be removed. But then the selection thinking of the Seventies suggested a quite different explanation. In a seminal paper, O'Connor (1978) explained avian siblicide as an outcome of genetical parent-offspring conflict (POC). In his view, parents lay the last egg in their clutch in order to raise an extra offspring to independence; then elder chicks kill it off to get a greater share of parentally provided food for themselves.

As in Triver's (1974) formulation of general POC theory, O'Connor's reasoning is based on the fundamental genetical inequality between diploid parents and their progeny. When available food is insufficient for the whole brood, both elder chicks and parents can benefit from discarding a supernumery chick and concentrating family resources to produce a few, high quality fledglings. But the food shortage thresholds of parents and elder chicks should be different. Senior chicks should favor siblicide when the benefit to self exceeds half the cost to the victim; parents should favor siblicide when the benefit to the senior chick exceeds the cost to the victim.

Since O'Connor's original formulation, more models have been published and numerous field studies have been carried out on a variety of species. Consequently, we know a great deal about siblicide now, but we have not answered the big question: Does siblicide represent POC? This problem is soluble, but we have not solved it yet.

Theory

In general, theoreticians agree that in some circumstances birds should reduce their brood size by siblicide. And POC over siblicide is predicted by both fitness models and genetical models for the situation where there is a brood hierarchy and thus a designated victim (O'Connor, 1978; Stinson, 1979; Dickins & Clark, 1987; Godfray & Harper, 1990). In fact, there usually is a hierarchy, since eggs are hatched at intervals of one or more days and the most junior chick can seldom escape the role of potential victim. Furthermore, the cited models show that conflict is especially likely in small broods. For example, in broods of two chicks, where S is the probability of survival of a singleton chick and D is the probability of survival of a doubleton chick, when $S/D > 3/2$, siblicide invades; but parents should oppose siblicide unless $S/D > 2$ (O'Connor, 1978; Dickins & Clark, 1987; see also Stinson, 1979).

How will the genetical conflict be resolved or played out in the field? In principle one party could possess overwhelming advantages that would make it useless for the other to contend, or the parties could be evenly matched and locked into phenotypic struggles. Such scenarios have been explored for less drastic sibling conflict through begging competition (e.g., Parker, 1985; Parker et al., 1989).

Forbes (1993) recently explored POC over siblicide with a model that incorporates some novel and realistic assumptions. For instance, it models the trade-off between investment in the current brood and in future offspring, and it recognizes that parents may reduce provisioning after a death. Reduced provisioning after a death has actually been demonstrated for cattle egrets (*Bubulcus ibis*) and brown pelicans (*Pelecanus occidentalis*) (Mock & Lamey, 1991; Ploger, in prep.). The model shows that fundamental genetical conflict does not necessarily lead to behavioral conflict. Behavioral cooperation is actually a more likely evolutionarily stable strategy, and this is because it is the parents that initially set the brood size and the parents that set and adjust the provisioning level. Second, when food allocation is despotic or hierarchical, as we usually see in the field, the risk of conflict over brood size is diminished. Finally, when conflict occurs, the magnitude of the fitness terms at issue should be small. Given the small discrepancy, Forbes (1993) predicts parent-offspring "quibbles" rather than conflict.

In summary, theory teaches that genetical conflict is present in siblicidal systems, but likely phenotypic manifestations have been little explored and one model shows that phenotypic conflict is likely to be trivial or inexistent, at least when broods are small. What do we see in the field?

Does behavioral conflict occur?

O'Connor (1978) predicted overt behavioral conflict, such as elder chicks attacking sibs and parents struggling to defend them. With hindsight this may seem simplistic, since O'Connor did not ask how conflict is likely to be resolved; he simply assumed that underlying genetical conflict would translate into phenotypic conflict. However, Parker's (1985) game-theoretical analysis of conflict over parental investment in members of a brood showed that three solutions could evolve: "parent wins", "offspring wins" and, most likely, "pro rata compromise". In a pro rata compromise underlying conflict continues to be expressed through aggressive food solicitation. By analogy, genetical conflict over sacrifice of a chick might result in one party winning and no conspicuous behavioral conflict or, alternatively, in a compromise mediated by behavioral skirmishes or negotiation of some kind.

Yet the first fieldworkers who looked for patent discord and strife over siblicide were disappointed; parents and senior chicks are not obviously at cross purposes over killing. Consequently, to detect the more subtle strife that may be going on, careful and probing assessments of behavior are needed. Let us consider first what senior chicks typically do, then take a look at what parents do.

Senior chicks

One or more chicks in a brood are always older and aggressively dominant over nestmates; even if ages are experimentally equalized, one chick becomes aggressively dominant (e.g., Meyburg, 1977; Mock & Ploger, 1987; Osorno, 1991). These senior chicks show at least three types of strategy or role, according to species.

First, in the so-called obligate brood reducers like the brown booby (*Sula leucogaster*), the lesser spotted eagle (*Aquila pomarina*) and the black eagle (*A. verreauxii*) there is typically a brood of two chicks and *all-out aggression* that is apparently unconditional. The senior chick pecks, bites, tugs and twists relentlessly, and its sibling dies in a few days (e.g., Meyburg, 1974; Cohen Fernandez, 1988). Senior chicks have to rest and sleep, but apart from these activities there is no evidence of any restraint. In some raptors, abundant food at the nest seems to have no influence on aggressiveness (e.g., Gargett, 1978). Strangely, no formal tests of the influence of food have been made.

great egret (*Casmerodius albus*) and probably the cattle egret and great blue heron (*Ardea herodias*), show *restrained aggression*. Although very violent, this aggression is less constant than the all-out type and frequently is not fatal (Mock & Ploger, 1987). Surprisingly, aggression does not vary with food amount; descriptive and experimental studies show that the two eldest great egret chicks in a brood of three do not intensify their pecking when food decreases or even slacken off when the normal ration is artificially doubled (Mock et al., 1987). So the survival of the extra chick simply depends on whether it is getting enough food to withstand the batterings and attempted expulsions. Yet ardeids clearly show flexibility in response to other variables. For example, aggression in cattle egrets intensifies if sibling ages are equalized and declines abruptly when one chick is removed from a brood of three (Mock & Ploger, 1987; Mock & Lamey, 1991).

Third, other facultative brood reducers such as the blue-footed booby (*S. nebouxii*), and possibly the South Polar skua (*Catharacta maccormicki*), the black-legged kittiwake (*Rissa tridactyla*) and the osprey (*Pandion haliaetus*) show *restrained food-sensitive aggression* (Procter, 1975; Poole, 1987; 1982; Drummond & García Chavelas, 1989). The senior blue-footed booby chick invariably pecks its sibling about 1-15 times each day and often maintains this rate throughout the three-month nestling period (Drummond et al., 1986). But when food goes short such that the senior chick's own weight falls to roughly 20-25% below potential, its aggression intensifies and precipitates the death of the junior chick. The effect of food was demonstrated by taping the necks of pairs of chicks to prevent them swallowing parentally-provided food. Under this deprivation the weight of both chicks declined, then seniors pecked their sibs at several times the baseline level; when tapes were removed pecking declined (Drummond & García Chavelas, 1987).

Evidently senior blue-footed booby chicks have the means to eliminate their sibs at will, and probably could routinely insist on an even greater share of parental food for themselves, but they do not. A telling observation is that when both chicks are begging, the senior chick often allows junior to receive feeds, when clearly senior could aggressively prevent food transfer (personal observation). Watching these birds, I get the impression that the senior blue-foot chick is husbanding its sib as a valuable, but dispensable asset

Potential victims

Little attention is generally paid to the behavioral roles of the most junior chicks, the designated victims, except to note that, *contra* O'Connnor's (1978) prediction, they never appear to commit suicide. In species with *all-out aggression*, juniors are too immature to do much and they are constantly overwhelmed by the batterings of their nestmates (e.g., Meyburg, 1974; Cohen Fernandez, 1988). These juniors generally seem to be limited to cowering, hiding and fleeing. This behavior has been characterized as "acceptance of intimidation" (Meyburg, 1974; 1977), although I suspect that acceptance is tactical and, given the chance, juniors would be very aggressive. In the species with *restrained aggression* and *restrained food-sensitive aggression*, some fighting back occurs. For example, junior skuas occasionally fight back and junior great egrets and bald eagles (*Haliaeetus leucocephalus*) frequently fight back and even initiate fights, although they usually lose them (Procter, 1975, Mock, 1985, Bortolotti, 1986). By contrast, in the western grebe (*Aechmophorus occidentalis*) and the blue-footed booby, junior chicks are seldom aggressive (Nuechterlein, 1981; Drummond et al., 1986). Instead, they habitually adopt a submissive posture, and this evidently inhibits aggression by seniors. However, junior blue-footed boobies monitor the correlation of sibling forces and will become aggressive if they detect a personal advantage (Drummond & Osorno, 1992).

Parents

The behavior of parents of siblicidal species is more difficult to interpret. In general parents do not cross swords with senior chicks in any obvious way, and it is tempting to conclude that they simply cooperate with the senior chick. But there are elements in their behavior that can be construed as attempts to raise the extra chick in the teeth of siblicidal opposition, and other acts, or rather omissions, that look like "hands off" complicity with the potential killer. I shall briefly scan across these elements, as they have been reported and quantified in diverse species, to provide a global appreciation of parental roles. My theme is that what we know of parental behavior does not allow us to confirm or reject the POC hypothesis because that behavior is usually vulnerable to alternative interpretations. First, what do parents do to promote survival of the extra chick?

Attempts to raise the extra chick. Laying an extra egg in the first place suggests an attempt to produce an additional fledgling, but we can satisfactorily explain the extra egg as an insurance policy against failure of first-laid eggs during or after incubation (Dorward, 1962) or as bet-hedging by parents who cannot predict food availability during the nestling stage at the time of laying (Lack, 1947; 1966). Populations that practice obligate siblicide derive only the insurance benefit, but those practicing facultative siblicide can derive both benefits. There is solid descriptive, experimental and comparative evidence showing that extra eggs serve these two functions (e.g., Cash & Evans, 1986; Mock & Parker, 1986; Anderson, 1990a; Mock et al., 1990), and no convincing evidence that siblicidal removal of the extra chick prejudices parental fitness in any species.

In obligately siblicidal species like the brown booby and the masked booby (*S. dactylatra*), parents nurture the extra chick until it dies or is expelled from the nest. Dorward (1962) noted that booby parents even care for an expelled chick that is returned by a human to the nest, and Cohen Fernandez (1988) observed that brown booby parents occasionally attend and accommodate dried grass around juniors expelled by their sibs. For O'Connor (1978) such phenomena evidence a parental attempt to fledge both chicks, but equally they could reflect a policy of nurturing both chicks while the chicks themselves sort out which one will be the survivor. If parents were to interfere, they might kill a vigorous chick and end up investing in a sickly one; whereas a duel between two well nurtured chicks is unlikely to be won by an invalid (Drummond, 1989).

Observers of several species have noted that parents occasionally diminish sibling aggression by brooding chicks or by their mere presence at the nest (e.g., Cash & Evans, 1986; Mock, 1987), but none has interpreted this as anything but an incidental consequence of behavior serving other functions.

The exception is the reports of South Polar skuas dividing their broods and one parent attending each chick, with several meters of distance preventing aggression between chicks (Spellerberg, 1971; Young, 1963). These parents even intercept attacks and emit apparently deceptive alarm calls that temporarily distract chicks from assaulting each other. Probably we should suspend judgement in this case until appropriate quantification confirms the anecdotal reports. My caution derives in part from frequently observing brood division in blue-footed boobies that appeared to result not from adult shepherding but from junior chicks escaping to a safe remove from their sibs, followed by one adult approaching and attending each chick.

Finally, in the course of observing hundreds of blue-footed booby broods over 13 years, including dozens that were experimentally manipulated to provoke increased aggression, I have twice seen an adult repeatedly peck an intensely aggressive senior chick on the cranium, thereby quelling it briefly. In no other context do blue-foot parents peck their own young nestlings. Also, during bouts of sibling aggression blue-foot parents sometimes shift about jerkily, suggesting agitation or nervousness (personal observation). These behaviors could imply parental inconformity with siblicide, but they are rare and ill-defined, tantalizing but not persuasive. (Although I cannot resist the temptation to suggest that they might be vestiges from a time when parents did struggle against siblicide).

Hands-off complicity. Many things that parents presumably could do to shield and succour young victims they simply do not do. Numerous reports state that parents do not interfere in sib fighting (e.g., Fujioka, 1985; Drummond et al., 1986; Ploger & Mock, 1986; Mock, 1987; Pinson & Drummond, 1993), even when severe fighting has been experimentally elicited (e.g., Drummond & García Chavelas, 1989, Drummond & Osorno, 1992) or when food is plentiful (e.g. Gargett, 1978). Nor do parents attempt to retrieve expelled chicks that are visible near the nest (e.g., Braun & Hunt, 1983; Cohen Fernandez, 1988). This passivity at first appears the most damning evidence of complicity, but in reality it is unpersuasive. As chicks get older and larger they surely become more difficult to control, and parents of many species are obliged progressively to diminish nest attendance in order to forage more. Under these circumstances it seems unlikely that parents can permanently prevent siblicide. If not, then they should probably permit and even connive at siblicide early on, since persisting in opposition will only incur greater costs while gaining little benefit (Drummond, 1989).

Parents also do not preferentially feed victims (e.g. Drummond et al., 1986; Mock, 1987; Pinzon & Drummond, 1993). In fact, under conditions of artificially induced food shortage and elevated aggression, blue-footed booby parents did the opposite: they increased preferential feeding of the senior chick (Drummond & García Chavelas, 1989). Again, this behavior is open to counterintuitive interpretations. For instance, we cannot be sure how much parents actually control food allocation, since sibling aggression can inhibit a junior chick's begging and deny it access to the parents. If this can be done during feeding bouts then parental attempts to succour the victim may be hampered. Furthermore, in species with food-dependent aggression, parents attempting to save a junior chick under intense attack may paradoxically be obliged to increase differential feeding of the attacker, in order to appease it (Drummond & García Chavelas, 1989). Food-dependent aggression could be an effective strategy for seniors partly because it serves an armtwisting function.

Conclusion

There is no compelling evidence for behavioral conflict between parents and senior offspring, and in most species parental behavior more closely resembles cooperation with senior chicks (Drummond et al., 1986; Drummond, 1989). That is, parents set up a brood with competitive asymmetries, through the laying and incubation regime and by differential feeding of seniors, then more or less stand by while those asymmetries run their course. However, much apparent favoritism by parents toward seniors could simply represent tactics to diminish or manage sibling aggression. For example, hatching chicks several days apart may facilitate formation of a dominance relationship and thereby mitigate agonism among them (Hahn, 1981).

Moreover, no matter how harmonious and cooperative the behavioral relationship between seniors and their parents, we are entitled to suspect that underlying genetical conflict has been won by one of them or that a compromise has been reached. Nor is it unrealistic to think that chicks might win or draw a conflict with their imposing parents. After all, parents are often absent from the nest and may tend to be ill informed regarding the net food intake of each chick; and as chicks grow and develop their motor skills, skirmishes with them probably become increasingly costly to parents.

In conclusion, since behavioral conflict is either absent, difficult to discern or easy to explain away, we are more likely to uncover really convincing evidence of genetical conflict and its effects on reproduction by looking directly at fitness (Drummond, 1987; cf. Stamps & Metcalf, 1980). We must ask the traditional detective's question: Who benefits from siblicide?

Siblicide and Fitness

The clinching evidence for POC over siblicide should be sought in a demonstration that siblicide increases the inclusive fitness of the perpetrators, the senior chicks, while lowering the fitness of parents. This would be strong evidence that genetical POC exists and that senior chicks have won it. If, however, we find that siblicide *benefits* parents, this result could mean that parents have prevailed or that there was no genetical conflict in the first place - and the two explanations are indistinguishable (Stamps & Metcalf, 1980). A critical experiment would be to prevent siblicide in a sample of nests and monitor the effects on parents' and senior chicks' lifetime fitness. (Of course, we might find that siblicide lowers the inclusive fitness of both parents and senior chicks. This result could be consistent with some models showing that it is difficult for a non-siblicidal genotype to invade once a siblicidal genotype has reached fixation (Godfray & Harper, 1990).)

Experiments with very limited samples have shown that some obligately siblicidal species can feed more than a single chick during part of the nestling period, for example the lesser spotted eagle (Meyburg, 1977) and brown and masked boobies (Dorward, 1962). But these observations, based on small samples and brief periods of observation, are merely suggestive. The best data come from studies of the masked booby in the Galapagos Islands.

The masked booby commonly lays a clutch of two eggs, then the first-hatched chick almost invariably kills its sib shortly after hatching. Anderson's (1990a) comparative study of booby clutch sizes shows that the second egg serves an insurance function, and this is a sufficient functional explanation for why parents lay two eggs. But when both eggs happen to hatch, whose interests are served by the prompt slaying of the junior chick? Anderson and Ricklefs (1992) estimated food requirements of masked booby chicks and parental foraging capacity, and concluded that parents could feed two chicks right through to fledging. This result is provocative, but a practical demonstration is required.

Anderson (1990b) also experimentally doubled 15 one-chick broods to size two, prevented siblicide and compared subsequent development of the broods with that of controls (unmanipulated singleton broods). I shall discuss the results of this unique experiment in some detail since it is the type of experiment I advocate, and because my interpretation of the results differs from Anderson's.

Mortality was higher for doubletons than singletons, but even so, parents of doubletons on average fledged 0.35 more chicks per brood than parents of singletons, mainly because they more frequently raised a single chick than did parents of singletons. The existence of POC was not supported since the inclusive fitness of both senior chicks and parents apparently benefitted from suppressing siblicide. Further, in my opinion the data fall short of refuting the existence of food limitation or demonstrating that parents or senior chicks enjoy higher fitness in the absence of siblicide, for two reasons.

First, doubletons grew very poorly; throughout the last 50 d of development, on average they weighed roughly 12-17% less than singletons and their wing chords were roughly 10-23% shorter (Anderson, 1990b, figs. 3 and 4). This suggests their reproductive value may have been lower than that of singletons at the age when fledging success was measured. Doubletons whose nestmates died may have eventually become as big as singletons, but this was not demonstrated. Significantly, in another sulid, the Cape gannet, low weight at fledging predicts high mortality (Jarvis, 1974). This problem was compounded by comparing fledging success of the control and doubled broods at the age of 50 d, when chicks were only about half-way through the nestling period. Mortality of nestlings can occur beyond this age, especially in doubled broods (Anderson, 1990b, fig. 5).

Second, it is not known whether parents that reared doubletons paid a fitness price in the next reproductive seasons. They were monitored, but the sample was too small and the measures were too cursory to detect likely effects. Hence, we cannot rule out the possibility that parental lifetime fitness was unaffected or even prejudiced by thwarting siblicide.

What *do* the data show? The poor growth of doubletons suggests that most pairs in the focal population could not raise two chicks to a satisfactory fledging size, casting doubt on Anderson & Ricklef's (1992) estimation that parents have enough foraging capacity to raise two chicks. However, only 8 of the 15 experimentally doubled broods were established in nests known to start out with a two-egg clutch, so it is possible that if the experiment were repeated using only two-egg clutches, better growth and survival would be observed. Nonetheless, this experiment is important because the results imply that parents may well be better off if junior chicks survived for a few weeks beyond hatching rather than just a few days. The extra weeks with a brood of two would extend parents' insurance coverage against the very real risk of chick loss through infanticide by neighbours and other external causes.

The way forward is to perform more experiments of the masked booby type, suppressing siblicide and analysing the consequences. This will require ingenuity and dedication because sibling aggression is not easy to control, and large samples and a few years of monitoring are needed to estimate the reproductive value of parents and fledglings into their respective next season's reproduction.

Dominance-subordination

I shall close by mentioning a recently discovered phenomenon with implications for measuring fitness and modelling siblicide. This will not answer the big question, but should add to our appreciation of the complications. Published models assume that all chicks are equal once they fledge, but this does not take into account that growing up as the runt of the brood may somehow make junior chicks less viable fledglings. Oddly, we do not know for any wild vertebrate how status in the brood or litter hierarchy affects survival and reproduction after the end of parental care.

In blue-footed boobies, there is now evidence that brotherly and sisterly thrashings change an infant's agonistic personality during infancy. In two-chick broods one chick, usually the senior one, is aggressively dominant (Nelson, 1978; Drummond et al., 1986). The direction of dominance does not change over time even when the junior chick outgrows the senior one, which is the norm in broods comprising a male with a younger sister (Drummond et al., 1991). By briefly pairing similar-sized chicks from different broods, Drummond & Osorno (1993) showed that each chick's agonistic behavior depends mostly on its own social experience: subordinates (juniors that were habitually submissive in the natal brood) behaved submissively and not aggressively, and dominants (seniors that were habitually aggressive in the natal brood) behaved aggressively and not submissively, whatever the experience of the chick they were paired with. Yet size was of paramount importance when socially inexperienced chicks (singletons) were paired: even when the size difference was very small, the larger chick behaved aggressively and the smaller chick behaved submissively. However, the effects of social experience went beyond mere variation in response tendencies.

To test whether effects of experience can override effects of relative size, dominants were permanently paired with larger subordinates (32% heavier and 3.9 d older, on average) by reciprocally swapping chicks between two nests. As predicted, dominants generally prevailed over larger subordinates, for periods of at least several weeks. Surprisingly, most subordinates became aggressive after pairing, presumably as a result of detecting their new size advantage. More surprising still, aggressive subordinates were apparently unable to overwhelm their smaller opponents, even when hostilities went on for several weeks; they seemed to yield too readily under pressure.

These findings point up the possibility that fledglings of siblicidal species may not all be socially equal. Junior brood members may not only be smaller than their sibs, as occurs in some non-violent species; they may also be less socially competitive. And if inferior size or social prowess diminishes their mean fitness, the scope for POC is less than has been assumed.

Secondly, the findings point up another important and neglected aspect by throwing the spotlight on behavior of juniors. Currently, the most relevant theoretical models for POC over avian siblicide are those that assume there is a brood hierarchy which effectively designates the most junior chick as the potential victim of siblicide. But in at least some species a minority of juniors manage to invert the dominance relationship and even outlive their sibs (e.g., Drummond et al., 1986; Drummond et al., 1991; Pinson & Drummond, 1993). The risk of inversion has surely selected for preventive countermeasures by senior chicks, including the imposition of strict aggressive dominance (Stinson, 1979), and it may have selected for pre-emptive siblicide. Sibs may sometimes be killed or severely suppressed simply because they cannot be controlled, even when this means sacrificing some indirect fitness. This, I suggest, is most likely to occur in populations where (even in the absence of siblicide) juniors have a negligible chance of surviving in addition to their nestmates or of replacing a nestmate after the latter's death through accident, selective predation and so on. In this situation, a junior chick is a "desperado" (Grafen, 1987) that should make an almost suicidal attempt at overthrowing its sibling. This scenario could account for the timing or occurrence of siblicide in some species, like the masked booby, that appear to forego continued insurance cover or the chance of raising an extra chick.

Acknowledgements

I am grateful to the Spanish organizing committee of the International Ethology Congress for their support, and to Dr. Constantino Macías Garcia for comments on the manuscript.

Resumen

¿Han perdido los padres en aves el control de la agresión de la descendencia?

El siblicido (fratricidio) en las aves se ha interpretado como una manifestación del conflicto padre-hijo subyacente. Los modelos teóricos recientes apoyan esta interpretación, aunque un modelo de Forbes (1993) demuestra que el conflicto conductual no necesariamente debería de ocurrir. Estudios descriptivos y experimentales de varias especies no han aportado evidencias contundentes de la existencia de conflicto, en parte porque los datos frecuentemente son susceptibles a interpretaciones alternativas. Ahora será necesario realizar experimentos para prevenir el siblicidio y determinar si el siblicidio perjudica la adecuación de por vida de los padres.

References

Anderson, D.J., 1990a. Evolution of obligate siblicide in boobies. 1: A test of the insurance-egg hypothesis. *Am. Nat.*, 135(3):334-350.

Anderson, D.J., 1990b. Evolution of obligate siblicide in boobies. 2: Food limitation and parent-offspring conflict. *Evolution*, 44(8):2069-2082.

Anderson, D.J. & Ricklefs, R.E., 1992. Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology*, 73(4):1363-1374.

Bortolotti, G.R., 1886. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.*, 127(4):495-507.

Braun, B.M. & Hunt, G.L.,Jr., 1983. Brood reduction in black-legged kittiwakes. *Auk*, 100:469-476.

Bryant, D.M. & Tatner, P., 1990. Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters. *Anim. Behav.*, 39:657-671.

Cash, K.J. & Evans, R.M., 1986. Brood reduction in the American White Pelican (*Pelicanus erythrorhynchos*). *Behav. Ecol. Sociobiol.*, 18:413-418.

Cohen, E.J., 1988. La reducción de la nidada en el bobo cafe (*Sula leucogaster* nesiotes, Heller and Snodgrass 1901). Universidad Nacional Autónoma de México. Facultad de Ciencias: Tesis de Licenciatura.

Dickins, D.W. & Clark, R.A., 1987. Games Theory and Siblicide in the Kittiwake Gull, *Risa tridactyla*. *J. Theor. Biol.*, 125:301-305.

Dorward, D.F., 1962. Comparative biology of the White Booby and Brown Booby, *Sula* spp. at Ascension. *Ibis*, 103b:147-220.

Drummond, H., 1987. A review of Parent-offspring conflict and brood reduction in the Pelecaniformes. *Colonial Waterbirds*, 10:1-15.

Drummond, H., 1989. Parent-offspring conflict and brood reduction in boobies. In: *Proceedings XIX International Ornithological Congress*: 1244-1253. Ottawa: University of Ottawa Press.

Drummond, H., Gonzalez, E. & Osorno, J.L., 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behav. Ecol. Sociobiolog.*, 19:365-372.

Drummond, H. & García, C., 1989. Food shortage influences sibling aggression in the blue-footed booby. *Anim. Behav.*, 37:806-819.

Drummond, H., Osorno, J.,García, C.,Torres, R. & Merchant, H., 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. *Am. Nat.*, 138(3):623-641.

Drummond, H. & Osorno, J.L., 1992. Training siblings to be submissive losers: dominance between booby nestlings. *Anim. Behav.*, 44:881-893.

Forbes, L.S., 1993. Avian brood reduction and parent-offspring "conflict". *Am. Nat.*, 142(1): in press.

Fujioka, M., 1985. Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret *Bubulcus ibis*. *Anim. Behav.*, 33:1228-1242.

Gargett, V., 1978. Sibling aggression in the black eagle in the Matopos, Rhodesia. *Ostrich*, 49(2):57-63.

Godfray, H.C.J. & Harper, A.B., 1990. The evolution of brood reduction by siblicide in birds. *J. Theor. Biol.* 145:163-175.

Grafen, A., 1987. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.*, 35:462-467.

Hahn, D.C., 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. *Anim. Behav.*, 29:421-427.

Jarvis, M.J.F., 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis*, Lichtenstein). *J. Anim. Ecol.*, 43:1-17.

Lack, D., 1947. The significance of clutch size. *Ibis*, 89:302-352.

Lack, D., 1966. *Population Studies of Birds*. London: Oxford University Press.

Meyburg, B-U., 1974. Sibling aggression and mortality among nestling eagles. *Ibis*, 116:224-228.

Meyburg, B-U., 1977. Sibling aggression and cross-fostering of eagles. In: *Endangered birds*: 195-200. (S.A.Temple, Ed.). Madison: University of Wisconsin Press.

Mock, D.W., 1984. Infaticide, siblicide and avian nestling mortality. In: *Infanticide: Comparative and Evolutionary Perspective*: 3-30. (G. Hausfater & S.B. Hrdy, Eds.) New York, USA: Aldine

Mock, D.W., 1985. Siblicidal brood reduction: the prey-size hypothesis. *Am. Nat.*, 125:327-343.

Mock, D.W., 1987. Siblicide, parent-offspring conflict, and unequal parental investment by egrets and herons. *Behav. Ecol. Sociobiol.*, 20:247-256.

Mock, D.W. & Parker, G.A., 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution*, 40:459-470.

Mock, D.W & Ploger, B.J., 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Anim. Behav.*, 35:150-160.

Mock, D.W., Lamey, T.C. & Ploger, B.J., 1987. Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology*, 68:1760-1772.

Mock, D.W., Drummond, H. & Stinson, C.H., 1990. Avian siblicide. *Am. Sci.*, 78:438-449.

Mock, D.W. & Lamey, T.C., 1991. The role of brood size in regulating egret sibling aggression. *Am. Nat.*, 138: 1015-1026.

Mock, D.W. & Forbes, L.S., 1992. Parent-offspring conflict: Acase of Arrested Development. Tree, 7:409-413.

Nelson, J.B., 1978. *The Sulidae: the Gannets and Boobies*, London, United Kingdom: Oxford University Press.

Nuechterlein, G.L., 1981. Asynchronous hatching and sibling competition in western grebe broods. *Can J. Zool.*, 59:994-998.

O'Connor, R.J., 1978. Brood reduction in birds:selection for fratricide, infanticide, and suicide? *Anim. Behav.*, 26:79-96.

Osorno, J.L., 1991. Análisis experimental del intervalo de eclosión en el bobo de patas azules. Universidad Nacional Autónoma de México, Facultad de Ciencias: Tesis de maestria.

Parker, G.A., 1985. Models of parent-offspring conflict, V. Effect of the behavior of the two parents. *Anim. Behav.*, 33:519-533.

Parker, G.A., Mock, D.W. & Lamey, T.C., 1989. How selfish should stronger sibs be?. *Am. Nat.*, 133(6):846-868.

Pinson, D. & Drummond, H., 1993. Brown pelican siblicide and the prey-size hypothesis. *Behav. Ecol. Sociobiol.*, 32:111-118.

Ploger, B.J. & Mock, D.W., 1986. Role of sibling aggression in distribution of food to nestling cattle egrets, *Bubulcus ibis*. *Auk*, 103:768-776.

Poole, A., 1979. Sibling aggression among nestling ospreys in Florida Bay. *Auk*, 96:415-416.

Poole, A., 1982. Brood reduction in temperate and subtropical ospreys. *Oecologia* (Berl.), 53:111-119.

Procter, D.L.C., 1975. The problem of chick loss in the South Polar skua *Catharacta maccormicki*. *Ibis*, 117:321-331.

Spellerberg, I.F., 1971. Breeding behavior of the McCormick Skua *Catharacta maccormicki* in Antarctica. *Ardea*, 59:189-230.

Stamps, J.A. & Metcalf, R.A., 1980. Parent-offspring conflict. In: *Sociobiology: Beyond Nature/Nature?*: 589-618. (G.W. Barlow & J. Silverberg, Eds.). Boulder, Colorado: Westview.

Stinson, C., 1979. On the selective advantage of fratricide in raptors. *Evolution*, 33:1219-1225.

Trivers, R.L., 1974. Parent-offspring conflict. *Am. Zool.*, 14:249-264.

Young, E.G., 1963. The breeding behavior of the South Polar Skua, *Catharacta maccormicki*. *Ibis*, 105:203-233.

(Recibido: noviembre 1993)