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# THE EVOLUTION OF SIBLICIDE

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NOVEMBER 27, 2016

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Essay MSc Ecology and Evolution

Images:

On the left: Frans Floris (1516 - 1570). '*Cain and Abel*' [[www.the-saleroom.com](http://www.the-saleroom.com)]

On the right: kookaburra, *Halcyonidae*, attacking its younger sibling.  
[<http://dragonflyissuesinevolution13.wikia.com/wiki/Siblicide>]



## Abstract

Since the development of Hamilton's inclusive fitness framework, the study of the evolution of kin aggression has been facilitated, since it provides an adequate basis for it and does not require a deep knowledge of the genetic nature of the studied trait. Sibling aggression, which arises as a consequence of limiting resources and that can lead to the death of the attacked individual through physical attack or socially enforced starvation, has been the focus of numerous inclusive fitness studies. In particular, birds have been the center of most of the studies on siblicide since this behavior is especially common in this taxa. Several hypotheses have been proposed to explain siblicide; however, there is not a universal answer to the question of how this behavior evolved. Here, I review and discuss some of hypotheses with greater impact in this field, focusing my attention of avian taxa. Although each of them give different explanations to the same behavior, they somehow overlap in ideas that seem to be key in the evolution of siblicide. Food is one of those common factors, although it alone cannot provide a definitive explanation. I point out a few erroneous assumptions that have previously been made in the study of siblicide as well as some limitations of the inclusive fitness framework, and I suggest some considerations for future studies.

**Key words:** siblicide, cainism, brood reduction, sibling conflict, evolution.

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## INTRODUCTION

As strange as it can sound, family conflicts are quite frequent, spread not only among animals but also in plants, and they often have fatal consequences such as the killing of an infant by its progenitor, or *infanticide*; the killing of an infant by a sibling, which is referred to as *siblicide*, or *cainism* in the case of older chicks that kill the younger; and even the consumption of one family member by another one, a form of cannibalism (1). For example, in the burying beetles, *Nicrophorus*, it is frequent that the parents feed on their offspring since there is usually a mismatch between the number of progeny and the available resources. In such a case, the strategy followed by the parents is to eliminate the excess of offspring to ensure a small well-fed progeny rather than a larger undernourished progeny (1). In some other species like the tiger salamander, *Ambystoma tigrinum*, it is not the parents who kill and consume the offspring but other siblings, among which there are ‘cannibal morphs’ that develop special weaponry used for that purpose (2). These are examples of infanticide and siblicide, respectively, in which cannibalism happens; however, killing a family member not always involves their consumption and this is actually a rather risky behavior since it increases the chances of injury and parasitic disease acquisition (3-5). Siblicide is especially common among birds and in many species the younger sibling usually dies within a few hours after its hatching, either by starvation or by direct aggression from its older sibling(s) (6). In particular, sibling competition is likely to occur in species in which the offspring is confined to a limited space where the available resources are not sufficient to rear the usually large size of progeny (7). The common factor of these extreme behaviors seems to be the lack of availability of resources.

In nature, individuals make use of the available resources - such as food, space or mating partners- that are invested in fitness, that is, their success in transmitting their genes to the following generations (8). However, resources are often scarce and to be shared, mainly with conspecifics, creating a competitive scenario in which aggressive behaviors can be favored when the number of competitors is large relative to the amount of available resources and if an individual can obtain an increase in fitness at the expense of the others (9). Despite that it clashes with the idea of caring relations among kin, this competition also applies to family members. How is it possible that the killing of a sibling receives positive selection?

An answer to this question was found when Hamilton (10, 12) developed a mathematical evolutionary framework, usually simplified to what is known as Hamilton's rule (10, 12) (for a more detailed description, see the section '*Inclusive fitness and Hamilton's rule*' below). Aggression towards family member can be selected if the benefit to the actor, in terms of fitness, is higher than the cost to the victim, weighted by the relatedness between the aggressor and the victim. Hence, sometimes it is not enough to be a family member to escape aggression and siblicide can be selected when the cost of being altruistic is higher than that of being selfish. Despite the existence of apparent altruistic behaviors, the vision of individuals as 'selfish machines' or 'vehicles' whose mere function is to transport genes (11) is still valid. It is only a matter of the strategy followed, either hiding selfishness behind the mask of altruism by promoting inclusive fitness or being openly selfish and choose to promote one's own fitness alone. Although the benefit-cost balance solution provided by Hamilton's rule seems like a feasible explanation for the occurrence of siblicide in nature, it is intriguing under which conditions it can be favored over cooperation. Here, I will discuss some of the questions that emerge from the study of this peculiar behavior: why is sibling aggression present in some species while it is not observable in other closely related species? Does its frequency vary among populations? What are the advantages of killing a family member and when is it favored? I will first introduce Hamilton's inclusive fitness framework and the concepts of family conflict and siblicide before analyzing the scenario under which the latter evolves.

### ***Inclusive fitness and Hamilton's rule***

The concept of inclusive fitness was first developed by Hamilton (10, 12). In his own words, 'a gene might receive positive selection even though disadvantageous to its bearer if it causes them to confer sufficiently large advantages on relatives [...] because relatives tend to carry copies of his own genes'. This means that an altruistic individual would be indirectly benefited from helping to increase its relatives' fitness even if it is at the cost of its individual fitness, since it would be contributing to its *inclusive fitness*. From the inclusive fitness theory derives Hamilton's inequality, which can be expressed as  $Br - C > 0$ , where  $B$  is the benefit received by the helped family member,  $C$  is the cost to the actor, and  $r$  is the coefficient of relatedness, this is, roughly speaking, the chance that two individuals share an allele due to common ancestry (in the absence of inbreeding,  $1/2$  for parent and child and for full siblings,  $1/4$  for half siblings, and so on) (10). It is key for

understanding the operating mode of kin selection and allows to predict the extent to which altruistic behaviors are favored by selection over selfishness and the other way round (10, 12, 13). Self-interested behaviors will be expected whenever the inequality is not met. In the case of full siblings, altruistic behaviors will be selected only if the benefited individual receives an increase in fitness which is at least twice the cost to the benefactor since there is a 50% ( $r = 1/2$ ) probability that the altruistic allele is present in the sibling.

The rule is a helpful tool for the study of the evolution of selfish behavior among family members. Indeed, the inclusive fitness approach has been useful in the development of theoretical models to explain siblicide (15-22, and more recently e.g.23).

For a more extended discussion of Hamilton's rule (e.g. how to calculate the different parameters of the equation, how to adequately use it and its validity) see 24.

### ***Family conflict: an overview***

Conflict within families is a consequence of the different evolutionary interests of the members over Darwinian fitness, and can be classified into three categories or 'social dimensions' (parents' sexual conflict, parents-offspring conflict and sibling conflict) (7, 13). From a genetic point of view, it arises when the expression of genes at different loci in the interacting individuals causes them to have different optimal strategies for the spread of such genes (7). The three categories mentioned above interact with one another, meaning that the mechanisms employed to solve the conflict in each of them have an impact over the other two and that for a resolution strategy to be evolutionary stable they must be solved together (7). In this regard, parental investment (PI) is of special importance since it links the three kinds of conflict. Defined as the actions of the parents toward their offspring that increase the offspring's fitness, in terms of survival, while decreasing the parents' fitness, with respect to their prospective reproductive output (14), it starts with the production of the sex cells and continues after reproduction with parental care (in the taxa in which this have evolved), such as feeding of the young and protection from predators (25).

There is a general disagreement regarding the amount and duration of the PI the parents are selected to give and that demanded by the offspring, and this is referred to as parent-offspring conflict (POC): while the parents tend to adjust their PI so that it maximizes the survival of all their offspring without that being a high cost to them, the offspring tend to



demand more than the parents are willing to offer (14). This high demand arises as a consequence of the early start of the individuals to enhance their reproductive success, achieved by maximizing the resources input they receive. However, parents are a limited source of PI (in long-lived organisms, intense PI can decrease the survival of the adults and affect lifetime reproductive success (26, 27, in 28) and the resources provided to the progeny have to be shared. This generates sibling competition, of which intensity can often be diminished by an increased PI in a negative feedback mechanism. Mock and Parker (7, 13) emphasized the importance of ‘nurseries’ - restricted spaces in which close genetic relatives are confined and face resource shortages (e.g.: a nest or uterine horns in mammals) as promoters of competition among the offspring. In these nurseries, the extent to which selfishness evolves in the progeny is limited, as it can be predicted using the logic of Hamilton’s rule, and a high-demanding offspring that causes an important negative effect over the parents’ fitness will not be selected. Within these limits, it can be said that sibling competition influences the POC, which is at the same time influenced by sexual conflict (Fig. 1 (taken from Mock and Parker (7))).

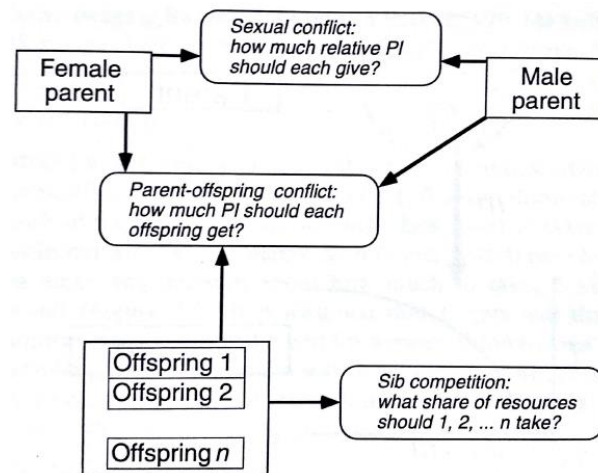


Figure 1. General schema for family conflict over resources provided by parents (7). When there is biparental care, sexual conflict arises from the different interests concerning the amount of PI supplied by each parent. The same way, the offspring also have different interests regarding the PI that each one should obtain (sibling conflict). Both dimensions are connected by the POC over the amount of PI provided.

We have seen that POC and sibling competition are inevitably related and that the actions taken by the parents to counterbalance the harmful effects of sibling competition generate a response in the offspring which can in turn further stimulate parents’ measures, as in an ‘arms race’ (14). This evolutionary game between the parents and their progeny can be solved if one of the ‘players’, parents or offspring in this case, adopts a strategy

that becomes fixed in the population so that it cannot be replaced by any other mutant strategy, also called evolutionary stable strategy (ESS) (29, 30). For example, the begging behavior of some bird species has been seen as an ‘evolutionary blackmail’ used by the offspring to exploit the parents’ investment (31). As the loud sounds of begging attract predators and endanger the parents’ fitness, they are forced to respond by increasing the PI (e.g.: food provisioning). When the parents can control the distribution of the resources over each of the offspring, honest signaling has been proposed as an ESS to solve POC. According to this idea, begging is costly and thus, it would reliably be reflecting an individual’s quality (32, 33). Contrariwise, if the parents have no control over the allocation of resources, scramble models, according to which the begging is compensated by PI in proportion to the effort made by the begging individuals, are more adequate (34, 35). These begging behaviors might result in the death of one or more individuals through enforced starvation and represent a way in which POC affects sibling competition (for a detailed discussion of the POC resolution models see 7). There are other strategies that involve direct aggression that are especially important when resources are scarce. Before examining those, it might be useful to first give a more detailed definition of siblicide, including the ways in which it is observable in nature, the commonalities of siblicidal species and some documented cases up to date.

### ***Understanding siblicide***

Siblicide (= fratricide, brood reduction) is a form of extreme sibling competition that results in the killing of one individual by a close relative - half or full sibling (36). It is a widespread behavior that has been reported in different animal taxa, with special incidence in birds (in the last bibliographic review (28), birds were the focus of 88% of the papers from the last 66 years) and particularly in raptors, such as the osprey, *Pandion haliaetus*, the lesser spotted eagle, *Aquila pomarina*, and the black eagle, *A. verreauxi*, and in colonially nesting birds such as blue-footed boobies, *Sula nebouxii*, brown boobies, *S. leucogaster*, or great blue herons, *Rissa tridactyla*, (reviewed in 28). It has also been reported in many non-avian taxa, especially in insects (37-42 reviewed in 13), and more recently (43) and (44); mammals, such as the spotted hyena, *Crocuta crocuta*, (45); amphibians, like the tiger salamander, *A. tigrinum*, (2); reptiles, such as spiny lizards, *Sceloporus*, in which siblicide has been recently reported for the first time (46); or the well-known case of intrauterine siblicide in the sand tiger shark, *Carcharias taurus*, (47). The behavioral patterns differ between groups and, in general, birds and mammals do not

consume their relatives unlike most of the siblicidal insects or amphibians (6). For that reason, and because of the especially high incidence of siblicide in bird species, I will mainly refer here to avian siblicide, unless otherwise specified.

Birds are particularly interesting in this field because they tend to be monogamous, easy to observe, highly competitive for food during the breeding period, and because most of the times the parents seem not to be fully committed to ensure the survivorship of all the offspring (6). Natural observations and field experiments have shown that there is a major incidence of siblicide under certain environmental conditions, food stress being the main driver (48). However, some species practice siblicide even when there is no shortage of food (see 49 for a review on experimental evidence) for which an explanation has not yet been found (49, 50). In the first case, siblicide occurs or not depending on the environmental conditions and is termed *facultative siblicide*. In facultative siblicidal species, populations set in different environments can differ in their siblicidal tendencies (e.g.: siblicide is present in some osprey populations while absent in others) (6). In the second case, siblicide almost routinely occurs and it is named *obligate siblicide*. Obligated siblicidal species usually lay two eggs that hatch asynchronously, which allows the older chick to gain advantage over the younger one (6). This reproductive pattern is also called *cainism*, and it is very common in large raptors (49). Despite that all the siblicidal species have a common denominator, the killing of siblings, there are interspecific differences in the way it is performed. So what makes a species siblicidal? How are they different from the non-siblicidal species?

A total of eight traits have been pointed out to be a condition for a particular specie to be siblicidal, as they are frequently present in most of them. Mock et al. (6) mentioned competition for resources, provision of food in small quantities, the presence of weaponry, limited space and differences in the competitive ability between siblings as common characteristics in these species, the first one being the most important (e.g. mainly food in birds while it is reproductive opportunities in insects or mammals) (6). Drummond (51) added spatial and temporal concentration of food, slow food transfer and small brood size to the list (52).

As the food supply decreases, selection favors brood reduction by means of siblicide in the first place, then siblicide and infanticide and finally, suicide, as defined by O'Connor thresholds (20). Siblicide has been proposed to be an effective evolutionary strategy to solve POC over brood size (21) and models have been developed from both the inclusive fitness framework (16, 20, 53) and the population genetics approach (15) to

determine the conditions under which brood reduction through siblicide is selected. That is only one of the several hypotheses that have been proposed, and even though it is clear now that food supply plays a role in the evolution of siblicide, it cannot be exclusively explained by food stress (28).

The meaning of siblicide is still puzzling to evolutionary biologists, that have extensively studied its possible adaptive value. Here, I review and discuss some of the most important hypotheses of siblicide.

## EVOLUTIONARY HYPOTHESES

All the hypotheses mentioned here as well as the supporting evidence and rejecting arguments are summarized in Table 1.

### ***Overproduction***

The overproduction of offspring generates a mismatch between the amount of resources that the parents can provide to the young and the actual needs of the latter, creating a competitive situation in which sibling competition and its fatal consequences, are likely to occur (54, in 7). That is, readjustments in the brood size are promoted by the overproduction of zygotes. Even though the production of offspring that are certain to be killed seems to be a constraint to the parents' fitness, it can actually be beneficial under certain circumstances (7, 13). Specifically, the excess of offspring has been proposed to be beneficial in three different ways: when it is used as an insurance against sudden changes in the environmental conditions, and/or resources availability, (e.g.: if the environmental conditions allow the parents to rear all the offspring, they will do it; if not, the excess or 'marginal' offspring will die); when some offspring serve as helpers or meals for the others ('sibling facilitation'); or, lastly, when they can be used as replacement offspring in case others die. The idea of overproduction being beneficial to the parents because it serves as an insurance against premature death of other offspring is the basis for the insurance egg hypothesis.

### ***Insurance Egg Hypothesis***

According to the insurance egg hypothesis, the overproduction of zygotes serves as insurance against the loss of offspring (due to infertility, predation, parasitism, congenital defect...) before their independence (59, 60). In two-egg species that are unable to

maintain two chicks, if both chicks hatch successfully the second to do it is killed by the older one (cainism). Stinson (53) discussed the adaptive value of the second egg and demonstrated how it can be selected despite that it decreases the parents' reproductive productivity. A condition for extra eggs to be produced is that hatch failure is important and that second eggs are inexpensive (61). This hypothesis has received extensive support (Table 1). However, its validity has been discussed by Simmons (49), who reviewed a number of cases that do not support the hypothesis and proposed that siblicide is a product of selection for offspring quality and competitive ability, the egg-quality hypothesis.

### ***Egg-Quality Hypothesis***

Arguing that the insurance egg hypothesis is not valid for single-egg species, Simmons (62) suggested that these species, which lay a large high-quality egg, do not need an insurance egg since they produce more robust chicks. In some of these species, such as the obligate siblicidal Wahlberg's eagle, *Aquila wahlbergi*, the tendency of laying one egg can be substituted by laying two eggs, and this varies between populations. Laying one or two eggs would represent alternative population density-based reproductive strategies (at low density populations it can be beneficial to lay two poor quality eggs while laying a single egg would be favored at high densities). This author provided evidence that supports the hypothesis for *A. wahlbergi*, in which the hatchability and viability of its large single egg is higher than that of two-egg species of the same body size. However, it was not accepted as an explanation for the clutch size variation in the Nazca booby, *Sula granti*, in which one-egg clutches has been proposed to be consequence of food limitation (63, in 28).

Although this hypothesis provides an explanation to siblicidal species that trade the two-egg clutch for one egg in some populations, it does not explain siblicide. Instead, it presents one-egg clutches as an adaptation and for this reason it will not be further discussed.

### ***Prey Size Hypothesis, PSH (=‘Feeding Method’)***

Proposed by Mock (50), it states that under certain conditions (limited food provisioning by the parents, delivery of food to the nestlings in small units that are easily monopolizable and offspring as a potential threat to one another) aggression in order to access the food and hence increase survival would be favored. Siblicide will be selected

in species with direct feeding, in which the food passes directly from the adult's beak to the chick's beak, allowing dominants to exclude competitors through aggression. In contrast, when food is deposited on the nest floor so that it is accessible to all the brood mates, aggression is less effective. This hypothesis has received descriptive and experimental field support (36, 48, 50, 51, 55, 56).

However, there are some species that feed small food parcels to their young but these do not fight, as it has been observed in little egrets, *E. garzetta* (6). Moreover, phylogenetic comparative analysis carried out by Gonzalez-Voyer et al. (52) revealed that siblicide is common in species with indirect feeding and provide evidence that does not support the prey-size hypothesis. Mock (50) already pointed out that the provisioning of food in small amounts is a necessary condition but not sufficient for avian sibling aggression.

### ***Food Amount Hypothesis, FAH***

Two years after the development of the PSH, Mock (57) formulated the FAH, according to which the intensity of sibling aggression is inversely related to the amount of food delivered by the parents to the chicks. It has received support by field and experimental studies in several siblicidal bird species (e.g.: osprey, western grebe, cattle egret, blue-footed bobby) and by comparative observations of spotted hyena (reviewed in 28). In these species, incidence and intensity of brood mate aggression were correlated to the food supply levels. However, these are facultative siblicidal species and in obligate siblicidal species food amount has a poor direct influence on the fighting behavior (6, 49, 57). Hence, although it influences chick survival, food amount is not a sufficiently stable parameter on which to base sibling aggression strategies. Drummond (48, 64) argued that there is a lack of consistent evidence that supports the hypothesis and proposed an alternative for both the FAH and the PSH, the food parcel hypothesis.

### ***Food Parcel Size Hypothesis***

Drummond (51) suggested that sibling aggression is favored when the food parcels delivered by the parents to the offspring are big enough to outbalance the costs of it (direct aggression is more costly than begging and scrambling). The important factor would be the size of the food pieces, regardless of whether it is directly or indirectly supplied. Consistent with this, in aggressive species parental food deliveries are large and

infrequent, which results in a sizeable profit to the aggressor (e.g.: obligate siblicide is mostly observed in predatory species, in which the young are fed large preys rather than small animals or seeds). Conversely, Gonzalez-Voyer et al. (52) found no support to this hypothesis: food parcel size was not correlated with the incidence or intensity of aggression and thus, it is not likely to have a significant influence in the presence of aggressive competition in the seven families of birds studied (*Accipitridae*, *Sulidae*, *Anhingidae*, *Threskiornithidae*, *Ardeidae*, *Pelecanidae* and *Alcedinidae*).

### ***Brood Size Hypothesis***

Mock et al. (55) observed that sibling aggression is more intense in larger than in smaller broods. According to the brood size hypothesis, the level of sibling aggression is positively correlated with brood size and as it diminishes, aggression decreases as well. It has been suggested that this happens because a larger brood size means less food per capita (58) and this idea has been supported by descriptive and experimental studies on cattle egrets. An alternative form of this hypothesis has been proposed by Drummond (64) according to which the predictor of sibling aggression is small brood sizes instead of large sizes, aggression being more frequent when broods are small. Evidence of this is found in accipitrids (*Accipitridae*) and ardeids (*Ardeidae*) (51) and it is further supported by the results obtained by Gonzalez-Voyer et al. (52).

### ***Hatching Asynchrony Hypothesis (=Brood reduction)***

Hatching asynchrony has been interpreted as a reproductive strategy (parental manipulation (25) to facilitate brood reduction when environmental conditions do not allow to successfully rear a whole brood (65). The hatching intervals between eggs generate significant differences in the size of the chicks, which is advantageous for the older ones. This has been supported by some authors, such as Pijanowski (66); however, some other studies refute this idea and propose instead that hatching asynchrony reduces siblicide since the disparities in size reduce the willingness of the chicks to initiate a fight, or that the asynchrony is simply a reflection of the parents' nutritional condition. Furthermore, it has been observed that hatching asynchrony is not always related with asymmetries in the competitive ability within the brood (reviewed in 28)

The hatching hypothesis has been recently tested in non-avian taxa, particularly in the black widow spider, *L. hesperus*, showing that developmental differences due to

hatching asynchrony increase siblicide. In this species, females modify the cannibalistic tendencies within their clutch by manipulating hatching synchrony through differential maternal investment (67).

Apart from these eight hypotheses, there are some others not mentioned here, such as the challenge hypothesis, the tasty chick hypothesis, the parental favoritism hypothesis (28), or the more recently proposed nestling body size (51) and nesting period hypotheses (52).

*Table 1. Summary of the main evolutionary hypotheses to explain siblicide and the supporting and unsupporting evidence on the left and the right of the dashed line respectively.*

<b>HYPOTHESIS</b>	<b>DESCRIPTION</b>	<b>SUPPORTING / UNSUPPORTING DATA</b>	
<b>Overproduction</b>	Siblicide is favored by the mismatch between a large brood size and the resources parents are able to supply, since it generates competition.	7,65,80	52,64
<b>Insurance egg</b>	The second egg of two-egg species serves as insurance against failure of the first one.	53,59,61,81-83	49,101
<b>Egg quality (Simmons 1997)</b>	Alternative adaptive explanation for the insurance-egg hypothesis. States that one-egg species do not need insurance egg because they produce stronger, more viable chicks than two-egg species.	84-92 (see 62)	63
<b>Prey size (=‘Feeding method’) (Mock 1985)</b>	Sibling aggression is related to the degree to which food can be potentially monopolizable by the nestlings	36,50,51,55,56,64	6,52
<b>Food amount (Mock 1987)</b>	Deprivation of food is positively correlated with the occurrence and intensity of brood mate aggression, mediated by chick hunger.	79, 94-97(in 28). See also 7,64,98,99.	6,48,49,57,64
<b>Food parcel size (Drummond 2002)</b>	Sibling aggression is influenced by the size of the food parcels delivered (directly or indirectly) by the parents. Pieces that are large enough constitute a payoff for the cost of aggression.	51	52
<b>Brood size</b>	Aggression incidence and intensity is dependent on brood size.	58,74,78,79	52,64
<b>Hatching asynchrony</b>	The age and size disparities produced by the hatching asynchrony is explained as an adaptive reproductive strategy (parental manipulation) to cope with environmental unpredictability.	65,66,67,80,93	100



The hypotheses that I have made reference to above constitute different interpretations of the same behavior, some of them giving adaptive explanations while others imply that siblicide arises as a consequence of other factors without being an adaptation. However, after having reviewed each of them it seems obvious that they overlap in some aspects. The most important ecological factor and a seemingly necessary condition for siblicide to occur is food shortage. Food is often in short supply, so being responsive to that cue is probably beneficial (7). Taking this as a starting point, it has been suggested that siblicide could be an adaptation to the environmental unpredictability, allowing the survival of a few well-fed progeny that would be likely to perish if brood reduction was not produced. By reducing the number of demanding individuals, the availability of resources would better match the needs of the remaining offspring (e.g. 68). It is important to clarify that brood reduction itself cannot be considered an adaptation since it alone does not demonstrate any evolutionary mechanisms involved, as Morandini and Ferrer (28) pointed out. The idea of siblicide as an adaptation for food scarcity could always be valid for facultative siblicidal species. Indeed, observational studies have revealed differences in the siblicidal tendencies between populations of the same species depending on the location, resources and other factors, including food (reviewed in 55, see also 6). It has also been documented a link between the food availability and the aggression between siblings in some obligated siblicidal species, although this is not the norm. Why obligated siblicidal species always kill their siblings even when the environmental conditions would allow all the progeny to successfully be reared can be explained looking back to the evolutionary history of this trait. Siblicidal behavior could have evolved over a wide range of conditions and once it has been established it would be difficult to go back to a non-siblicidal behavior even if siblicide is not beneficial anymore (15).

If we are going to assume that food disposal is the main factor influencing the evolution of siblicide, we must, however, take some aspects into consideration. First, in species in which the food is delivered by the parents to the young, the amount of food the offspring get access to does not always correlate with food availability. The parents have to obtain the resources in the first place, through foraging activity; and secondly, distribute the resources between the offspring and their self-maintenance (see 28). This implies that, regardless of the availability of resources, the food obtained by the young and, consequently, sibling aggression are influenced by parental allocation. Second, parental foraging effort is not necessarily correlated with parental resource allocation, which is

influenced by the age of the parents, the quality of the territory, the quality of the year, etc., while it is usually assumed that food provisioning relates to parental effort. Parental decisions over their offspring decisively influence siblicide and thus, this factor should receive more attention when studying siblicide (28).

According to the inclusive fitness theory, parents are expected to act in a way so as to minimize the harmful effects of sibling competition (10,12). For example, the maternal reduction of hatching asynchrony in wolf spiders generates small within clutch variance in offspring size and thus reduces siblicide (69). Nevertheless, parents do not always prevent siblicide and it can in fact be tolerated by them (e.g.: when preventing it has a high cost associated, they seem to ‘play favorites’, giving preferential treatment based on the life expectancies) or even promoted by them (e.g.: asynchronous hatching) (1). These parental manipulations (25) range from differential feeding of the young to other rather cryptic ways, such as the uneven vascularization of uterine walls in the pronghorn or differential maternal allocation of egg components among her offspring (reviewed in 13). For instance, maternal effects (when the maternal phenotype influences the offspring phenotype) have been proved to affect chick’s aggressiveness in the black-legged kittiwake by differential allocation of yolk components (70, 71). This is only an example of manipulation that occurs before the offspring is produced, but it can continue after hatching in more obvious ways, creating a continuous ‘battle of interests’ between the adults and the young.

Brood reduction through siblicide has often been seen as a consequence of POC over brood size (e.g. 16, 17, 21, 58). Rodríguez-Gironés (72) showed that the cost the parents pay to provide enough resources to prevent siblicide is smaller than the benefit they obtain from maintaining their preferred brood size, and for this reason it has been discussed in terms of ‘evolutionary blackmail’. This author criticized that the so-called first generation models of resolution of POC through siblicide (15, 20) assume that PI is not altered after siblicide has occurred; however, if parents are expected to reduce their investment after brood reduction (73) and this readjustment of PI is taken into consideration in the models, different results are shown. Hence, adjustments in PI are important in the study of this evolutionary game. Another assumption that has been usually made in studies of brood reduction through siblicide is that there is a trade-off between quantity and quality of the offspring (28). In this sense, siblicide could be advantageous for the parents since it would facilitate the rearing of a small, high quality brood. Nevertheless, some studies have found

a significant positive relationship between brood size and nutritional conditions of the young, larger broods showing better nutritional conditions (74, 75). This is logical, based on the previous arguments: PI is not a constant variable and hence, smaller broods do not necessarily receive a higher amount of food per capita. Instead, nutritional conditions of the chicks could be reflecting the quality of the parents (e.g. high quality parents could afford to successfully rear larger broods with better nutritional conditions) (28).

Researchers have been able to provide several explanations to the possible adaptive value of siblicide; however, there is not a universal answer to it. Hamilton's inclusive fitness framework has been useful in these studies but it must be applied carefully, taking into account that kin selection cannot operate if a 'selfish' trait does not have any kind of damaging effect in its bearer (22). Under extreme competition between relatives, if there is no cost to the selfish individuals, kin selection effects can then be overcome by resource competition (76).

I would like to end the discussion by making a remark about the role of kin recognition in siblicide, a topic that does not seem to have been the focus of many studies but that could open up new perspectives in the evolution of siblicide. Hamilton (10, 12) predicted that an individual should be able to weight its sibling's fitness against its own based on the coefficient of relatedness (this would be done unconsciously). This kin-discrimination has been observed in sibling cannibalistic species, such as the spade foot toad (2, 3), or the tiger salamander (77) that preferentially kill non-full siblings, and it has also been recently reported in the intrauterine cannibalistic sand tiger shark, suggesting that siblicide during the gestation period in this viviparous species could be a form of cryptic post-copulatory process (47). It would be interesting to perform integrative studies that link sexual conflict, POC and siblicide, concepts that are hardly explicable without one another.

## CONCLUSIONS AND FUTURE PERSPECTIVES

- Siblicide hypotheses have frequently been developed and tested for one or a few variables without taking into account the whole range of possible variables that can be affecting its evolution. Also, studies have been mainly restricted to birds, suggesting hypotheses that are not applicable to other animals (or plants). On the other hand, siblicide in other taxa is increasingly being reported. Future studies should include a wider range of factors as well as the interactions among them, and this should be done in different taxa. Later comparative analysis could give a broader view of the evolutionary history of siblicide.
- Inclusive fitness studies are not always easy to carry out and the parameters in the equation might be difficult to estimate. Despite this approach facilitates the study of a certain trait without the need to know its underlying genetic basis, it might soon start to be outdated and, considering the advanced molecular techniques existing nowadays, it could be complemented with more in-depth genetic studies in the future.
- The offspring's point of view has often received most of the attention (e.g. the benefits to the remaining offspring after brood reduction through siblicide has occurred). The parents' point of view is complementary to it and thus, should not be ignored. Since evolution is a dynamic process, both sides of the conflict should be considered together. Looking back to the past and identifying the mistakes or wrongly-made assumptions would be helpful to improve prospective investigations in this field.

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