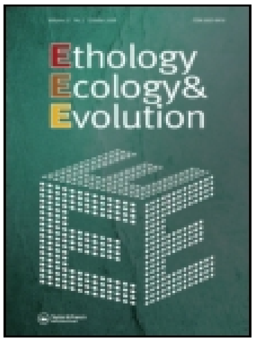

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V. Morandini & M. Ferrer

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Sibling aggression and brood reduction: a review

V. Morandini and M. Ferrer[1]

Department of Ethology and Biodiversity Conservation, Estación Biológica de Doñana (EBD-CSIC), c/Americo Vespucio s/n, 41092 Sevilla, Spain

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Siblicide may be "facultative" or "obligate". When food resources provided by the parents are insufficient to rear a whole litter successfully, dominants may kill their subordinate siblings, either directly by physical damage, or indirectly through enforced starvation. This phenomenon is termed "facultative siblicide" and occurs in a wide range of bird species and at least one mammalian species. In contrast, when the lowest ranking sibling is routinely killed by its dominant brood mate or littermate this is called "obligate siblicide", and seems to affect in particular large, long-lived species characterized by intense competition for breeding sites. This "obligate siblicide" has intrigued researchers for decades, trying to find an evolutionarily satisfactory explanation for this extreme behaviour. We review all scientific literature concerning sibling aggression published in the last 66 years. A bibliography search resulted in 104 references during the last 66 years, where birds represented 88% of the total published papers. Eleven hypotheses have been formulated for explaining these results, finding that siblicide is a complicated behaviour not controlled only for parents or chicks or environmental changes, but for a whole range of factors. These hypotheses have been identified and discussed according to actual supporting data. The relationship between food resources and brood reduction was widely documented; a sustained increase in food availability led to a highly significant decrease in both frequency and intensity of aggressiveness of the older chick towards its younger sibling in facultative species, also finding similar results in obligate siblicidal species. These results would suggest siblicide is an adaptive behaviour. This review tends to show that there is probably more than a single cause behind this behaviour. We conclude that more aspects must be considered in the design of future studies in order to understand the potential evolutionary sense of aggressive behaviour among siblings, especially those concerning food allocation decisions by parents.

KEY WORDS: siblicide, hatchling asynchrony, brood reduction, evolutionary hypotheses, obligate siblicide, facultative siblicide, resource allocation.

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[1] Corresponding author: Miguel Ferrer, Department of Ethology and Biodiversity Conservation, Estación Biológica de Doñana (EBD-CSIC), c/Americo Vespucio s/n, 41092 Sevilla, Spain (E-mail: mferrer@ebd.csic.es).

INTRODUCTION

Sibling rivalry is broadly defined as "any features of animals or plants that have the effect of promoting individual survival and/or reproduction at the expense of siblings" (Mock & Parker 1997). When Darwin wrote that "the instincts of lower animals are never so perverted as to lead them regularly to destroy their own offspring", he was wistfully mistaken (Darwin 1871). This kind of dominant relationship within litters and its effects have been reported in several bird species, including some Ciconiformes species such as the great blue heron (*Ardea herodias;* Mock 1985) and the cattle egret (*Bubulcus ibis*; Mock & Parker 1986, 1997), sea birds like the western gull (*Larus occidentalis*; Pierotti & Bellrose 1986; Spear & Nur 1994) and the blue-footed booby (*Sula nebouxi*; Drummond & Chavelas 1989; Guerra & Drummond 1995; Osorno & Drummond 1995), several species of Falconiformes (Simmons 1988) and also in some mammalian species, like the spotted hyena (*Crocuta crocuta*; Hofer & East 2008). Consequently, it seems to be a widespread behaviour.

When sibling rivalry is intense it can eventually lead to the death of the subordinate member(s) of a brood or litter through enforced starvation, physical damage or eviction from the nest (Stinson 1979; Mock & Parker 1997). If sibs dispute, the smallest concedes, reducing overall energy consumption (Mock & Ploger 1987). This fatal sibling competition is termed siblicide (or brood reduction) and is well documented in birds, where this phenomenon is common, particularly among raptors such as the osprey (*Pandion haliaetus*; Machmer & Ydenberg 1998), or in colonially nesting birds such as blue-footed boobies (*Sula nebouxii;* Drummond & Chavelas 1989), brown boobies (*Sula leucogaster*; Drummond et al. 2003), great blue herons or kittiwakes (*Rissa tridactyla*; reviewed by Drummond 2006). Lack (1966) suggested that siblicide may be advantageous to both parents and surviving offspring in years when environmental conditions make it difficult to successfully rear a complete brood.

Siblicide may either be "facultative" or "obligate" (Tables 1 and 2). When food resources provided by the parents are insufficient to rear a whole litter successfully, dominants may kill their subordinate siblings, either directly by physical damage, or indirectly through enforced starvation. This phenomenon is termed "facultative siblicide" and occurs in a wide range of bird species and at least one mammalian species: the spotted hyena (*Crocuta crocuta*). In contrast, when the lowest ranking sibling is routinely killed by its dominant broodmate or littermate, this is called "obligate siblicide", and seems to affect in particular large, long-lived species characterized by extreme subadult mortality and intense competition for breeding sites (Simmons 1988). This "obligate siblicide" has intrigued researchers for decades, trying to find an evolutionarily satisfactory explanation for this extreme behaviour (Simmons 1988).

Here, we make a review of the current hypotheses trying to explain the evolutionary meaning of sibling aggression, especially the particular case of obligate siblicide, and the data supporting them.

METHODS

For this review, we conducted a search of references using ScienceDirect, browsing by the subject "enviromental science" and looking for the words "siblicide", "hatchling asynchrony" and "brood reduction". We used in addition "Jostor.com", "Google Scholar", "Scirus" and "freefullpdf".

We considered it 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.

Table 1.

Obligate siblicide.

Sulidae:	
Brown booby (*Sula leucogaster*)	Woodward (1972); Nelson (1978); Drummond et al. (2003)
Masked booby (*Sula dactylatra*)	Dorward (1962); Kepler (1969); Woodward (1972); Nelson (1978); Anderson (1990)
Sphenescidae:	
Rockhopper penguin (*Eudyptes chrysocome*)	Williams (1980)
Balaenicipitidae:	
Shoebill (*Balaeniceps rex*)	Brown et al. (1982)
Pelecanidae:	
American white pelican (*Pelecanus erythrorhynchos*)	Cash & Evans (1986)
White pelican (*P. onocrotalus*)	Brown et al. (1982)
Pink-backed pelican (*Pelecanus rufescens*)	Burke & Brown (1970); Brown et al. (1982)
Brown Pelican (*Pelecanus occidentalis*)	Ploger (1997)
Accipitridae:	
Bearded vulture *(Gypaetus barbatus*)	Simmons (1988); Margalida et al. (2004)
Egyptian vulture (*Neophron percnopterus*)	Brown et al. (1982)
Augur buzzard (*Buteo augur*)	Simmons (1988)
Lesser spotted eagle (*Aquila pomarina*)	Simmons (1988)
Tawny eagle (*A. rapax*)	Simmons (1988)
Black eagle (*A. verreauxii*)	Brown et al. (1977); Simmons (1988); Gargett (1993)
Wahlberg's eagle (*A. wahlbergi*)	Simmons (1988)
Harpy eagle (*Harpia harpyja*)	Simmons (1988)
African hawk eagle (*Hieraaetus fasciatus*)	Steyn (1983); Simmons (1988)
Crowned eagle (*Stepanoaetus coronatus*)	Simmons (1988)
Swallow-tailed kite (*Elanoides forficatus*)	Gerhardt et al. (1997)
Booted eagle (*Hieraaetus pennatus*)	Casado et al. (2008)
Lesser spotted eagle (*Aquila pomarina)*	Meyburg (2001)
Augur buzzard (*Buteo augur*)	Gargett (1970)
Gruidae:	
Wattled crane (*Bugeranus carunculatuis*)	Benson & Pitman (1964)
Whooping crane (*Grus americana*)	Novakowski (1966)
Strigidae:	
Giant eagle owl (*Bubo lacteuis*)	Steyn (1983)
Pel's fishing owl (*Scotopelia peli*)	Steyn (1983)
Bucerotidae:	
Southern ground hornbill (*Bucorvus leadbeateri*)	Kemp & Kemp (1980)

Table 2.

Facultative siblicide.

Pandiodidae:	
Osprey (*Pandion haliaetus*)	Poole (1982); Machmer & Ydenberg (1998)
Sulidae:	
Blue-footed booby (*Sula nebouxii*)	Drummond & Chavelas (1989); Guerra & Drummond (1995); Osorno & Drummond (1995)
Sphenescidae:	
Chinstrap penguin (*Pygoscelis antarctica*)	Moreno et al. (1994); Belliure et al. (1999)
Gentoo penguin (*Pygoscelis papua*)	Williams & Croxal (1991)
Laridae:	
Black-legged kittiwake (*Rissa tridactyla*)	Braun & Hunt (1983); Dickins & Clark (1987)
Western gull (*Larus occidentalis*)	Pierotti & Bellrose (1986); Spear & Nur (1994)
Apodidae:	
Whitebellied swiftlet (*Collocalia esculenta*)	Bryant & Tatner (1990)
Meropidae:	
Blue-throated bee-eater (*Merops viridis*)	Bryant & Tatner (1990)
Ardeidae:	
Great egret (*Casmerodius albus*)	Mock (1985)
Great blue heron (*Ardea herodias*)	Mock (1985)
Cattle egret (*Bubulcus ibis*)	Fujikoa (1985); Mock & Parker (1986, 1997)
Accipitridae:	
Spanish Imperial eagle (*Aquila adalberti*)	Meyburg (1987); Ferrer & Penteriani (2007)
Hyaenidae:	
Spotted hyenas (*Crocuta crocuta*)	Golla et al. (1999); Watcher et al. (2002); Hofer & East (2008)

RESULTS

The bibliography search resulted in 104 references from the last 66 years. The most common study species on this topic were birds, representing 88% of the total published papers.

Pre-requisites for the evolution of sibling aggression

The begging of brood mates that use aggression to compete for food has seldom been studied. Eight traits have been proposed (Gonzalez-Voyer et al. 2007) as necessary to facilitate the evolution of aggressive competition: feeding method (monopolization of food), effective weaponry (pointed or sharp beaks), limited escape possibilities (altricial behaviour, nest site topography) and differences in age, sex and size of brood mates (hatching asynchrony; Edwards & Collopy 1983; Mock et al. 1990); in addition, Drummond (2002) suggested spatial and temporal concentration of food, small brood size, aggressive potential (maturity and body size) and slow food transfer. All or some of these traits must be present to facilitate sibling aggression.

Both incidence and intensity of aggression increased with length of nestling period; however, length of nestling period may not influence the evolution of brood mate aggression in the very small minority of species with obligate siblicide (prompt unconditional elimination of the brood mate), because the period of brood mate cohabitation is very short and the payoff for aggression is guaranteed (Gonzalez-Voyer et al. 2007).

Phylogenetic comparative analysis of morphometric, life history and behavioural hypotheses of sibling aggression in any vertebrate showed that indirect feeding, small broods and long nestling periods (nestling period hypothesis) are significantly correlated with brood mate aggressive competition (Gonzalez-Voyer et al. 2007). Aggression was both more common and more intense among species with indirect feeding and long nestling periods, and more intense in species with small brood (Gonzalez-Voyer et al. 2007)

In the last 66 years, 11 hypotheses have been formulated to explain these results, finding that siblicide is a complicated behaviour not controlled only for parents or chicks or environmental changes, but for a whole range of factors; in addition, if we look for the evolutionary sense of siblicide, differences between species would probably be expected.

Current hypotheses and supporting data

Many hypotheses to explain siblicide have been proposed; we focused this review on the more common hypotheses, trying to aggregate them according to whether they concern obligate or facultative siblicide, and if they support that is an adaptive behaviour or not.

Overproduction. The first step necessary for siblicide is the overproduction, in the avian case, of eggs. Why do parents incur the costs of a second egg and, for a short period, a second nestling, if second nestlings have no reproductive value?

As Malthus explained two centuries ago, “Through the animal and vegetable kingdoms, nature has scattered the seeds of life abroad with the most profuse and liberal hand. She has been comparatively sparing in the room and the nourishment necessary to rear them” (Malthus 1798: 6).

Since then, a great number of cases have come to light where the procreative excesses of parents generate disastrous mismatches between the investment they can (or will) supply and what the brood actually needs, which lead routinely to acute sibling competition. In such squeezes, the most expedient solution is usually to trim offspring demand, and parents of many animal and plant taxa abort, abandon, abscise, bludgeon, cannibalize, cull, eject, impale and/or recycle some or all of their offspring (Mock & Forbes 1995).

Two hypotheses can explain the overproduction of zygotes. Bet-hedging assumes that optimal brood size varies unpredictably among breeding attempts. Excess zygotes are produced so that the number of independent offspring can be flexibly adjusted downward to the optimum number for that attempt. Selective abortion in mammals suggests that parents overproduce zygotes, identify those with the highest fitness expectations, then kill or abandon those with lower fitness in order to concentrate investment in those with the best prospects. Both hypotheses for the overproduction of zygotes work in principle, alone or together, and can lead to impressive levels of zygote overproduction (Kozlowski & Stearns 1989).

Thus, although clutches of two eggs are frequently laid, obligate siblicide eliminates the younger hatchling before it reaches the age of independence. The phenomenon presents a challenge to evolutionary theory because parents produce chicks that are virtually certain to be killed and because surviving offspring actively sacrifice the inclusive-fitness increment represented by the victim.

Parental favouritism hypothesis. There is evidence for the role of parents in siblicide species, the parental favouritism hypothesis proposes that parents, in particular mothers, customize the competitive playing field on which their offspring will compete (Mock & Parker; Muller et al. 2007) to maximize their own reproductive output. Mothers may be able to achieve this by differentially provisioning their eggs, hatching them asynchronously or transferring hormones, providing competitive advantages and handicaps on different individuals of their broods to create competitive hierarchies (Howe 1978). As in many other taxa, avian mothers expose their embryos to substantial amounts of maternal androgens by depositing testosterone in their eggs, affecting behaviour and physiology of the chicks (Von Engelhardt & Groothuis 2011), and this maternal testosterone compensation to last-hatching eggs is stronger when size differences among siblings become smaller (Muller & Groothuis 2013).

Food amount hypothesis. Rowe (1947: 606) suggested that the significance of cainism is “that the hatchling of two chicks provide one with the stimulus which causes it to take more food than it strictly needs and so produces a more robust fledgling at the expense of the other chick” which is killed.

Mock (1987) formalized this idea with the “food amount hypothesis” (FAH) according to which sibling aggression is negatively correlated with the quantity of food the aggressor ingests (Mock et al. 1987). This hypothesis is largely supported by field studies (osprey, *Pandion haliaetus*, western grebe, *Aechmophorus occidentalis*, cattle egret, *Bubulcus ibis*; reviewed in Mock & Parker 1998) and has now been experimentally confirmed for several species that show facultative siblicidal brood reduction (osprey: Machmer & Ydernberg 1998; blue-footed booby, *Sula nebouxii*: Drummond & Chavelas 1989; black-legged kittiwake, *Rissa tridactyla*: Irons 1992; reviewed in Drummond 2001b).

The food amount hypothesis holds that a chick’s tendency to attack its brood mates increases with food deprivation. It has been supported by studies of several avian species in which aggression of dominant brood mates increased when their food ingestion was experimentally restricted (review in Drummond 2001a), and by comparative observations of spotted hyena *Crocuta crocuta* litters suggesting that siblicidal aggression is greater when food availability is poorer (Golla et al. 1999; review in Drummond 2006).

A sustained increase in food availability led to a highly significant decrease in both frequency and intensity of aggressiveness of the A-chick towards its younger sibling; these results provide experimental support for the notion that siblicidal aggression is adaptive, as they relate food supply levels to brood mate aggression levels (Braun & Hunt 1983; Irons 1992) Thus, increased aggression under conditions of food shortage would provide a mechanism by which brood sizes are adjusted to food resources during the nestling period; if food becomes short, the smallest chicks are sacrificed to benefit the remainder (Ricklefs 1965).

Observation of a siblicide event in a Northern goshawk (*Accipiter gentilis*) indicates a relationship between food resources and brood reduction. These observations are consistent with the idea that goshawks exhibit facultative siblicide, and that resource levels as predicted by the food amount hypothesis directly influence it (Estes et al. 1999). The same results were found in the Swainson's hawk (*Buteo swainsoni*), again supporting the hypothesis (Bechard 1983). Elder blue-footed booby chicks increase their attacks on brood mates when they receive less food, and this mechanism may be sufficient to tailor brood size to food availability (Drummond & Rodriguez 2009).

However, in obligate siblicidal species, there is no relationship between food abundance and sibling aggression (Simmons 1988; Mock et al. 1990). Obligate siblicide, known as "cainism" in large raptors, is a taxonomically widespread avian phenomenon that remains inexplicable as a simple consequence of food stress: two young can be raised to independence in experimentally manipulated nests, and food supplements do not decrease sibling aggression (Simmons 1988).

Recently, Osorno & Drummond (2003) in their study with Brown boobies show that aggression of senior Brown-booby brood mates may be flexible and food sensitive in order to optimize the timing of siblicide or to make siblicide weakly facultative. Upholding these conclusions, studies of video-monitoring show similar results; in *Gypaetus barbatus*, sibling aggression generally began on day 1 after hatching; in nests supplemented with food, aggression was delayed until the 2nd and 3rd day after hatching and the second chick survived for 9 days. This suggests that food supplied indirectly could delay aggressiveness between broods, allowing the second chick to have a better physical condition and possibilities of accessing food (Margalida et al. 2010).

Prey size hypothesis. According to the "prey size hypothesis" (Mock 1985), selection favors brood mate aggression in species in which food passes directly from the adult's beak to the chick's beak (direct feeding), allowing dominants to violently exclude competitors. When food is deposited on the nest floor (indirect feeding) and is accessible to all brood mates, aggression is less effective for monopolizing it than seizing mouthfuls and ingesting them quickly (Mock 1985; Mock & Parker 1997).

Many species show a transition in feeding method as sensory and motor capabilities of chicks develop, for example, from indirect to direct feeding in herons and pelicans, and from direct to indirect feeding in raptors. The feeding method hypothesis predicts greater use of aggression in species in which direct feeding predominates throughout the nestling period. The feeding method hypothesis is supported by descriptive and experimental field studies (Mock 1984, 1985; Mock et al. 1987; but see Drummond 2001a).

Thus, rather than being restricted to species with direct feeding, aggressive competition is increasingly common and intense as species engage in more indirect feeding during the nestling period. Finally, the first empirical test of the feeding method hypothesis' assumption that aggression is more efficient for securing a large share of food during direct than indirect feeds (Mock & Parker 1997: 106) found no support for it in cattle egrets (*Bubulcus ibis*: Gonzalez-Voyer & Drummond 2007) where aggression may be especially effective with indirect feeding because in this location food tends to be simultaneously accessible to all brood mates.

Insurance egg hypothesis. Theoretical (Forbes 1990; Forbes & Lamey 1996) and empirical evidence (Cash & Evans 1986; Anderson 1990; Clifford & Anderson 2001) indicates that second eggs act as insurance, providing a chick for the parents to raise when the first egg fails to hatch or when the first chick dies shortly after hatching. The insurance egg hypothesis predicts that if a second egg sometimes produces a fledgling after a first egg fails, then the evolution of insurance egg production in single-chick species is governed by the ratio of the benefit of the increased probability of producing a hatchling to the relatively low cost of egg production (Dorward 1962; Meyburg 1974). A field study of the obligate siblicidal Masked booby (*Sula dactylatra*) demonstrated that second eggs contribute a surviving hatchling after the first egg's failure in 19.2% of two-egg clutches. The primary source of hatching failure was exceptionally high infertility or early embryonic death (Anderson 1990). Alternatively, the insurance hypothesis predicts that extra eggs should occur where hatch failure is not trivial and second eggs are inexpensive (Forbes 1990).

Egg quality hypothesis. Simmons (1997) suggested an alternative, adaptive explanation for the insurance egg hypothesis in single-egg species that do not lay insurance eggs, the clutch size variation within obligate siblicidal taxa: one- and two-egg clutches represent alternative strategies, with some individuals laying one large, high-quality egg and others laying two small, lower-quality eggs. In this view, large, single eggs have high hatchability and produce more robust chicks, and two-egg clutches trade off size-related disadvantages with the insurance value of the second egg. Thus, the higher hatchability of a single, large egg decreases the need for an insurance egg and simultaneously enhances viability of resultant chicks in siblicidal eagles and possibly sulids.

However, the egg quality hypothesis was rejected as an explanation for clutch size variation in the Nazca booby. Instead, two-egg clutches appear to be favoured because of the insurance value of the second-laid egg, while one-egg clutches result from food limitation (Clifford & Anderson 2002).

Challenge hypothesis. Most recently, the challenge hypothesis has been proposed; it attempts to link siblicidal tendencies to the prevalence of certain hormones, namely testosterone, in the blood (Nazca boobies: Ferree et al. 2004). The challenge hypothesis postulates that male vertebrates can respond to social challenges, such as simulated territorial intrusions, by rapidly increasing their concentrations of plasma androgens, such as testosterone (T). This increase may facilitate the expression of aggressive behaviour and lead to persistence of this behaviour even after withdrawal of the challenge, thus potentially promoting territoriality and the probability of winning future challenges.

However, in a study of Brown booby juniors and Blue-footed booby juniors, mothers of each species may steer their broods toward parentally optimal patterns of social interaction mainly by manipulating not androgens but the variables over which they ultimately have most control: relative age and size (Drummond et al. 2008).

Food parcel size hypothesis. The size of food parcels fed to chicks could affect the profitability of aggressive competition. According to the food parcel size hypothesis, because aggression is likely to be costlier than mere begging and scrambling, for it to yield a net benefit the food reward for the aggressor has to be high (Drummond 2002). In aggressive species, parental food parcels appear to be large and infrequent, and clustered in bouts or meals, resulting in a sizeable payoff for the aggression of dominant chicks (whether they receive food directly or indirectly).

Brood size. The brood size hypothesis holds that chicks respond to the number of accompanying brood mates per se: aggressiveness increases with brood size and declines when the number of brood mates falls.

In several avian species, aggression appears to be more intense in large broods than in small broods (Mock et al. 1987), but this could be because per capita ingestion is lower in larger broods (Ploger 1997). The results of Drummond & Rodriguez (2009) suggest that Elder blue-footed booby chicks increase their attacks on brood mates when they receive less food, and the dominant chicks do not become less aggressive to each other after disappearance of their youngest brood mate, showing that this species does not show brood size-dependent aggression.

Interestingly, the results of Ferrer (1994) suggest that the correlation between brood size and nutritional level is positive, so the largest clutch size would be the one with better nourished nestlings because it would tend to be associated with the best parents and/or territories.

Hatching asynchrony. Hatching intervals between successive eggs can be large, up to 5 or 6 days between the first and second chick in the two-chick broods of the brown booby and the Nazca booby (*Sula granti*: Mock & Parker 1997). The resulting age and size disparities confer significant growth and survival advantages to the larger siblings.

The parental manipulation (Alexander 1974) of asynchronous hatching has been interpreted as a reproductive strategy for dealing with ecological unpredictability: when resources turn out to be abundant, brood redirection is unnecessary and all nestlings may survive to independence (Lack 1947, 1968). For example, Pijanowski (1992) considers brood reduction as a result of hatching asynchrony to be adaptive in varying environments, depending on the relative frequency of good and bad years for food.

Some studies appear to refute Lack's explanation for asynchrony and favour other alternatives (Clark & Wilson 1981; Hillstrom & Olsson 1994). In some marine species, it is usual for the second or third chick to survive. In these species, the explanation for asynchrony is often a reduction in sibling rivalry, as in the Jackass penguin (*Spheniscus demersus:* Seddon & Heezick 1991). It seems that chicks of unequal size fight less because the smallest chick consistently concedes, rather than meets, the challenge of its older sib. If chicks are not expending energy on fighting, they can grow more efficiently. This also benefits the adults as less food needs to be collected.

Recent studies with Chinstrap penguins (*Pygoscelis antarctica*), however, showed another alternative: hatching asynchrony was not correlated with asymmetries inside the brood (Moreno et al. 1994; Viñuela et al. 1996). Other studies (Ferrer et al. 2013) demonstrate that lighter broods were more asymmetric and associated with lower values of adult nutritional condition (plasma urea, uric acid and creatine kinase), and authors interpret these findings as evidence that the adult birds allocate fewer resources to their chicks in these broods than do adults with more symmetric broods. Thus, asymmetries inside the brood seem to be related to total parental investment; those parents investing less obtained young that are more asymmetric.

Tasty chick hypothesis. There is evidence for a relationship between body condition, nestling mortality and immunocompetence in nestlings of *Parus major*: food brought by parents to their nestlings is more unequally distributed among chicks in broods infested by ectoparasites compared with broods reared in parasite-free nests, suggesting more intense intra-nest competition for access to food provoked by the presence of parasites (Christie et al. 1996).

In the Barn swallow (*Hirundo rustica*), parasites are not equally distributed among chicks within a brood but aggregated on chicks of poor quality. Detection of parasites by parent birds before laying could induce hatchling asynchrony. In this case, the adaptive significance of weight hierarchies is unrelated to an unpredictable environmental factor like weather, but to a much more predictable factor since the presence of ectoparasites in nest sites is detectable before start of laying. Thus, the tasty chick hypothesis, which takes into account the important ecological factor of parasitism, provides another way to explain why parents of obligate siblicide species lay a second egg where hatchling asynchrony establishing weight hierarchies within broods may provide a way to partially circumvent the detrimental consequences of parasites (Christie et al. 1998).

DISCUSSION

The relationship between food resources and brood reduction was widely documented; a sustained increase in food availability led to a highly significant decrease in both frequency and intensity of aggressiveness of the older chick towards its younger sibling in facultative species (Braun & Hunt 1983; Golla et al. 1999; Drummond 2006), also finding similar results in obligate siblicidal species *Sula leucogaster* (Osorno & Drummond 2003) and *Gypaetus barbatus* (Margalida et al. 2010); these results would suggest siblicide is an adaptive behaviour.

In addition, we found differences between species, for example *Sula leucogaster* (obligate siblicide) and *Sula nebouxii* (facultative siblicide), but also in the same species appearing to be innate in populations of Swallow-tailed kites (*Elanoides forficatus*), even though the northern subspecies does not exhibit this behaviour (Gerhardt et al. 1997).

From an evolutionary point of view, the main question in brood reduction through sibling aggression is whether there is or is not an adaptive mechanism involved; that is, an adaptive regulatory mechanism that facilitates the death of the chicks in situations of reduced availability of food. We have to distinguish between the trivial idea of one or more chicks in a brood that probably died when there was not enough food from the evolutionarily-based idea of a mechanism generating differences among chicks in the brood, avoiding an unnecessary waste of energy if the available food is not enough (Ferrer & Penteriani 2007).

The reduction of the brood is not by itself a demonstration of an evolutionary mechanism operating. The basic idea is that, after overproduction, some mechanism that facilitates the death of one or more chicks in situations of reduced availability of food must be operating. This mechanism would be regulated by the parents or would be mediated by chick interactions and asymmetries. The first case is an example of asymmetric resource allocation among chicks and the second leads to sibling aggression and, potentially, cainism.

A trade-off between quantity and quality of offspring is generally assumed in sibling aggression studies. Nevertheless, some studies found a significant relationship between brood size and nutritional conditions of the young but in the opposite direction; large broods showing better nutritional conditions (Ferrer 1994; Ferrer & Penteriani 2007). This kind of relationship was a consequence of high differences in quality among territories under a density-dependent regulation by habitat heterogeneity

(Casado et al. 2008). Differences in territory quality are not usually considered in sibling aggression studies. When they have been considered, results showed that sibling aggression is more frequent in low-quality territories and during poor years and probably affecting young parents (Casado et al. 2002).

The cost of reproduction is of fundamental importance in life-history evolution (Harshman & Zera 2007). A core idea is that the differential allocation of limited internal resources (the traditional "Y" model of resource allocation where food input is shown at the base of the "Y", and energy resources are allocated to reproduction versus the rest of the body) has a central role in the cost of reproduction and other life-history trade-offs (Harshman & Zera 2007).

A major trade-off faced by breeding birds is resource allocation to offspring versus to self-maintenance, because strong parental investment may reduce survival of breeding adults, and thus overall lifetime reproductive success in long-lived organisms (Stearns 1976; Noordwijk & De Jong 1986). Regulation of reproductive effort in terms of provisioning offspring is particularly important for those long-lived birds for which foraging and meal delivery are energetically expensive and risky behaviours (Chappell et al. 1993; Ydenberg 1994). Nevertheless, most of the studies in brood reduction and sibling aggression did not take into account potential decisions of resource allocation by the parents, considering that food provisioning merely reflects parental ability to find food. Food provisioning, however, involves two processes: resource acquisition through foraging activity, and resource allocation between self-maintenance and offspring's demands (Boggs 1992; Viñuela et al. 1996; Weimerskirch 1999). Recent studies have highlighted no correlation between the intensity of parental foraging effort and the offspring growth rates in the Adélie penguin (*Pygoscelis adeliae*; Takahashi et al. 2003), suggesting that parental resource allocation rather than the foraging effort would be the most important factor explaining differences in offspring performance. It seems important to clarify the role of parental resource allocation in brood reduction by sibling aggression. Some of the factors affecting resource allocation would be the age of the parents, the nest/territory quality, the quality of the year, etc. These factors should be considered in more detail in future sibling aggression studies.

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