



FORUM

Siblicide provides food benefits for raptor chicks: re-evaluating brood manipulation studies

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Implicit in most ideas explaining the siblicidal behaviour of nestlings that kill related siblings is that, by eliminating a competitor, surviving nestlings increase their share of food resources from the parents (e.g. O'Connor 1978; Stinson 1979; Simmons 1988; Mock et al. 1990; Mock & Parker 1997). However, in a detailed paper assessing the food benefits to pelicans (*Pelicanus* spp.), Ploger (1997) found that senior (surviving) nestlings did not receive more food once their nest mate had been eliminated. The same result has been reported for egrets (*Bubulcus* spp.) by Mock & Lamey (1991). This arose from the behaviour of the parents reducing their provisioning rate to broods reduced through siblicide. Ploger went on to argue that the now well-known decreased provisioning rates to experimentally reduced broods 'provides evidence against the assumption that parents feed similar (food biomass) amounts to broods before and after brood reduction' (Ploger 1997, page 1071). Hence some senior chicks may not gain any food bonuses following brood reduction. She further noted that because the high-ranking individuals she studied received more food anyway regardless of other siblings, the amount of food received after brood reduction for these birds differed very little to that prior to brood reduction.

Her results are valuable because they highlight an untested assumption pivotal to most models explaining siblicidal behaviour (i.e. remaining chicks receive a food bonus). Since raptors (Falconiformes) do not feed their chicks in the same manner as pelicans or egrets, but show siblicidal brood reduction (Meyburg 1974; Simmons 1988; Gargett 1990) and have been subject to several brood manipulation studies, it is timely to ask: do raptor

chicks in broods reduced by experimental manipulation or siblicide also enjoy no benefit in increased food resources from their parents? This is important because a 'no benefit' result would undermine most models of siblicidal brood reduction, which assume there is a food and subsequent survival benefit. I also assess the idea that senior raptor chicks gain no advantage because they already receive the majority of the food even in competition with their siblings. The results provide the second review of raptor brood manipulations, updating and extending the first such review (Simmons 2000).

Methods

Data on raptor brood manipulations was reviewed in the literature and augmented by my own studies of parental provisioning responses in raptors in the northern and southern hemisphere (Simmons 1986, 1997, 2000). Individual authors were also approached for unpublished information. I ascertained both the overall ('bulk') rate of food provisioning for raptor broods that had been manipulated, and then ascertained the rate to individual members of the reduced brood. The latter figure was determined using the mean food intake (bulk food/number of nestlings). This is possible because of the even allocation of food to nestling raptors by their parents (see Discussion). The increased or decreased rate is expressed as a proportion of the biomass provisioned to broods in the unmanipulated state.

It is also of interest to determine the response of adults provisioning experimentally enlarged broods because it helps us understand (1) whether parents actually recognize changes in brood sizes and (2) whether they then compensate for increased demand. Therefore, I have included brood enlargements too since most studies

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report both. Broods of 11 raptor species have been manipulated in 15 published studies (some species were studied in different areas). Samples are sometimes small because of the length of time needed to collect provisioning data, so I compare the trends from studies with large samples to those with smaller samples.

Results

Theoretical considerations

In most experimentally reduced broods bulk food deliveries from the parents indeed decrease (see Table 1) as found by Ploger (1997). However, food per individual nestling can increase despite the bulk food decrease for the following reasons. In many actively brood-reducing raptors (Falconiformes), especially eagles (Accipitridae), broods are reduced from two to one (Steyn 1982; Simmons 1988; Gargett 1990). Theoretically, the senior chick will still receive a food bonus despite a drop in food provisioning down to a level of 50% of original food-provisioning rates. Only below 50% would a food bonus no longer accrue. Similarly, in species in which broods are reduced from three to two (e.g. egrets, some pelicans, raptorial birds, swifts), food supplies would have to drop by 33% for no benefit to accrue to the remaining chicks. Clearly, the level at which 'benefit' switches to 'no benefit' is brood-size dependent and in the case of small broods, which are common in actively siblicidal species, food delivery rates need to drop disproportionately for there to be no benefit to remaining chicks.

Exceptions to this brood-size dependency can occur when older nestlings dominate their siblings to the extent that they receive the majority of the food regardless of any competition (Ploger 1997), or the allocation of food changes to reduced broods. These possibilities are considered below.

Brood reductions

Quantitative examples from all experimental raptor brood manipulation studies known to me (Table 1) illustrate that while parentally provisioned food sometimes decreases to reduced broods, food amounts per remaining individual frequently increases. Eight of the following nine studies showed the same tendency, five of which were reported as significant. The three studies that did not report a significance level all showed very high increases (260, 278 and 313%) in biomass received by individual chicks following brood reductions. In the first study to quantify food biomass to experimentally reduced broods (from five to two chicks), Snyder & Snyder (1973) showed provisioning effort by parents at two Cooper's hawk, *Accipiter cooperii*, nests remained constant following brood reductions. Thus, biomass per chick increased following the reductions from 29 to 90 g in one nest, and 127 to 263 g in the second nests (Table 1). Similar results are found in brood size manipulations for three African species. For African redbreasted sparrowhawks, *A. rufiventri*, parental provisioning did not differ as brood size was altered between one and three chicks, thus singletons received the most biomass. This was

reflected in their increased growth rates relative to chicks in enlarged broods (Simmons 1986). In a more thorough study of African marsh harriers, *Circus ranivorus* (Simmons 2000), four broods were manipulated to contain two young above and two below natural brood size. Over 163 h of food-provisioning assessment, parents attempted to increase their provisioning rate only twice to enlarged broods and deliveries remained constant or decreased at other times. Overall no consistent trend in parental response was found. However, a clear trend was apparent with the biomass received per chick. Each nestling in a reduced brood received on average between 105 and 122 g more than it received in an unmanipulated state, a significant increase of 30–35% over typical rates (Table 1). For common kestrels, *Falco tinnunculus*, in South Africa, van Zyl (2000) noted no change in delivery rates to broods decreased by two nestlings, resulting in an increase in biomass delivered from 31 to 87 g per chick per day, a 2.8-fold increase. For European kestrels, when natural broods were reduced by two in two studies, bulk provisioning rate per brood decreased in one study and stayed constant in the other (Dijkstra 1988; Tolonen & Korpimäki 1996). Among American kestrels, *F. sparverius*, bulk food to broods reduced by three or one nestlings stayed constant in the first and surprisingly increased in the second study (Gard & Bird 1990; Dawson 1999). For both species in all studies, however, the critical measure, biomass per individual, was significantly higher for the reduced broods relative to control broods (Table 1). In a study of gyrfalcons, *F. Rusticolus*, Poole (1988) determined that prey biomass per nestling was also significantly greater in nests with the fewest number of chicks (Table 1).

In naturally reduced Eurasian sparrowhawk, *Accipiter nisus*, broods, Newton (1978) observed no decrease in delivery rates to three nests, although Geer's (1981) study of prey deliveries to one experimentally reduced brood indicated a nonsignificant drop from 0.31 to 0.26 prey per h per chick (biomass not given). This was the only species to show no increase in prey biomass for individual nestlings, but like several others, requires greater brood samples and hours of observation.

Brood enlargements

I simultaneously assessed parental responses to brood enlargements because it allows us to determine whether parents are indeed assessing changes in brood size (some of the above results can be explained by a lack of response by the parents). It also gives insight into individual optimization of brood planning and the (in)ability of parents to rear larger than normal broods. For common kestrels and African marsh harriers in South Africa, van Zyl (2000) and Simmons (2000) noted an increase in delivery rates to broods increased by two nestlings, but as with many other examples given below, this did not result in more food for individual nestlings (Table 1). For both European and American kestrels, when natural broods were increased by two nestlings, bulk provisioning rate to the enlarged broods increased in both species. For each individual nestling, however, there was a (nonsignificant) decrease in food biomass for European

Table 1. Summary of all known brood manipulation experiments conducted on birds of prey

Species	Number of broods manipulated	Brood size change	Adult bulk provisioning effort			Biomass provisioned per individual nestling			Source
			Brood enlarged	Brood reduced	Brood enlarged	Brood enlarged	Brood reduced		
European kestrel (Netherlands)	50	+2, -2	Increase**	Decrease**	Decrease (NS)	Increase (33%)†**	Dijkstra 1988		
European kestrel (Finland)	29	+2, -2	No change (NS)	No change (NS)	Not reported	Not reported	Tolonen & Korpimäki 1996		
Common kestrel (S. Africa)	5	+2, -2	Increase*	No change (NS)	No change (NS)	Increase (278%)§	van Zyl 2000		
American kestrel	12	5-7; 5-2	Increase (NS)	No change (NS)	Decrease/increase‡	Increase (313%)§	Gard & Bird 1990		
American kestrel	38	-1		Increase*		Increase (36%)**	Dawson 1999		
African marsh harrier	4	+2, -2	Increase**	Decrease (NS)	Decrease*	Increase (33%)*	Simmons 2000		
Cooper's hawk	2	2-5-2	No change§	No change§	Decrease§	Increase (260%)§	Snyder & Snyder 1973		
Eurasian sparrowhawk	2	2-4; 4-3	Increase (NS)	Decrease (NS)	Decrease (NS)	Decrease (NS)	Geer 1981		
Redbreasted sparrowhawk	1	1-2-3-2-1	No change (NS)	No change (NS)	Decrease (NS)	Increase (172%)*	Simmons 1986		
Gyrfalcon	2	+3, -3	Decrease**	Decrease*	Decrease*	Increase (39%)*	Pooler 1988		
Snail kite	28	+1, +2	Increase (NS)		Decrease§		Beissinger 1990		
Savanna hawk	10	+1	No change§		Decrease§		Mader 1982		
Wahlberg's eagle	8	+1	No change§		Decrease§		Simmons 1993, 1997		
Osprey	6	+2	Increase§		Decrease§		Pooler 1989		
Osprey	16	+1, -1	Increase (NS)	Not reported	Decrease*	Not reported	Green & Ydenberg 1994		

Sparrowhawks to eagles were assessed for the parents' ability to increase and decrease provisioning effort when brood size was varied. Remaining nestlings in all but one species experienced increased food intake when broods were reduced (penultimate column).

†The percentage increase in biomass provisioned (g/chick) relative to biomass provisioned in unmanipulated (control) broods.

‡In one exceptional prey-rich year, prey deliveries per chick increased to enlarged broods.

§Significance level not reported. NS ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$ (as reported by the authors).

kestrels (Dijkstra 1988), and for American kestrels (Gard & Bird 1990), there was a decrease in food biomass in one year and an increase in another year. This latter result was the only increase reported in 13 studies (Table 1) and arose during a particularly prey-rich year (Gard & Bird 1990). In his study of gyrfalcons, Poole (1988) found that parents did respond to enlarged brood size with significantly more food deliveries, but biomass per individual once again decreased (Table 1). In two studies of the osprey, *Pandion haliaetus*, bulk food supply increased 20% in Green & Ydenberg's (1994) study but this was not significant, and in Poole's (1989) study, significance was not reported. In both cases, however, chicks in enlarged broods suffered decreased food supply, about 20% and significantly so in the former study (Table 1). These studies confirm that parents are sensitive to changing brood sizes. In six other species in which broods were enlarged (Cooper's hawk, Eurasian sparrowhawk, redbreasted sparrowhawk, snail kite, *Rostrhamus sociabilis*, savanna hawk, *Buteogallus meridionalis*, Wahlberg's eagle, *Aquila wahlbergi*), there was no increase in bulk food supply during brood enlargement and, consequently, individual nestlings of these species suffered decreased food supply. For savanna hawks brood mortality was common (Mader 1982), for snail kites no broods of four were ever reared and only 40% of three-chick nests were (Beissinger 1990), and in siblicidal Wahlberg's eagle broods that had been doubled (and siblicide experimentally bypassed), most young died (Simmons 1997). For young ospreys in enlarged broods, growth was slower and fighting more frequent (Poole 1989; Green & Ydenberg 1994), despite adult females sacrificing their own intake. Since body growth was also significantly impaired in enlarged broods of African marsh harriers (Simmons 2000) and European kestrels (Dijkstra 1988), larger than planned broods are demonstrably detrimental to chicks of large and small species (although mortality was more apparent in the subtropical species) and this may set an upper limit to optimal brood size.

Discussion

This analysis has shown that the remaining nestlings in experimentally reduced raptor broods enjoyed a net benefit in food intake, despite a drop in bulk food deliveries by their parents. In 15 raptor brood manipulation studies involving 11 species from small kestrels to large eagles, there were no species in which food supply to individual nestlings significantly decreased following the reduction of brood size. In all (eight) cases in which it was accurately measured, the biomass received per individual increased by 33–313% over unmanipulated controls. Five studies reported significant results ($P < 0.05$), and the remaining three did not report significance but showed biomass increases ($\bar{X} = 284\%$) much higher than that found in the studies reporting significant results ($\bar{X} = 63\%$). Only one study (of sparrowhawks) showed a decrease (Geer 1981): the result was nonsignificant and biomass was not measured. The results were unaffected by sample size: kestrel broods with 50 nests manipulated showed exactly the same trends as redbreasted sparrow-

hawks with one brood manipulated. This confirms the central assumption of a food benefit for surviving raptor chicks in siblicide models, and also confirms that the behaviour of raptor parents differs from that of egrets and pelicans (Mock & Lamey 1991; Ploger 1997). Equally important, growth and survival of chicks was negatively affected in eight species in which broods were enlarged (Mader 1982; Newton 1986; Simmons 1986, 1993, 2000; Dijkstra 1988; Poole 1989; Beissinger 1990; Green & Ydenberg 1994). Whether growth and survival of chicks in reduced broods, receiving increased food amounts, are improved is poorly understood. However, in three of five such studies, enhanced growth was not found compared to controls (Korpimäki 1988; Dawson 1999; Simmons 2000) but in European kestrels and Canadian ospreys, increased body mass was found (Dijkstra 1988; Green & Ydenberg 1994). However, neither kestrel study found enhanced survival in such broods (Dijkstra 1988; Dawson 1999). This suggests, as with passerines (Pettifor et al. 2001), that a lower threshold brood size exists, below which no further increase in chick quality is achieved. This may set a limit to the amount of siblicidal brood reduction that is adaptive for parents and surviving siblings.

Results of experimental studies of raptors thus differ from conclusions reached by Ploger (1997) for other species. Why is this? One reason has already been explored: determining bulk biomass provisioning to reduced broods is inappropriate to assess effects on remaining individuals within these broods. Food rate per individual is more appropriate, as measured by Ploger (1997) and Mock & Lamey (1991).

A second important question raised is: do senior chicks accrue few benefits from siblicide because they dominate other siblings and secure most food, regardless of competitors (Ploger 1997)? This possibility is unlikely among raptors for two reasons. First, for those species (like black eagles, *Aquila verreauxii*) laying two eggs, obligate siblicide is typical (Simmons 1988) and death of the second chick occurs within a few days of hatching (Steyn 1982; Gargett 1990); thus the dominance question no longer applies (only one chick remains). Second, when final brood size is two or more, dominance appears to play a surprisingly little role in access to food. For two species detailed data exist on individual food ingestion in relation to hatching order and sex. In Eurasian sparrowhawks, Newton (1978) found equal consumption of food by nestlings throughout the nestling period in three nests, regardless of the hatching order and despite the fact that females grow to be twice the size of males in this species. In the slightly less sexually dimorphic northern harrier, *Circus hudsonius*, MacWhirter (1994) found that hatching order also made no difference to food intake for individual nestlings ($N = 18$). First-hatched nestlings consumed as much biomass ($\pm 1\%$) as later-hatched individuals. Only following first flight did any differences become apparent. The equal ingestion by nestlings arose because adult females in both species stripped meat off carcasses held in their feet, and offered strips one by one to the chicks in front of them. This is common to all raptorial birds (Newton 1979). Females also changed position in many

cases and when chicks got older and attempted to dominate prey by pulling it from the parent, it was retrieved and distributed evenly, long after chicks could self-feed (Newton 1978; Simmons 1986; MacWhirter 1994). For ospreys, when food supply is low, nestlings begin fighting at about 12 days old (Poole 1989). In these nests, dominant chicks are fed first, but when they are sated, subordinate chicks are able to feed unmolested. Individual food intake was not measured in these circumstances (Poole 1989). This differs from feeding styles used by egrets and pelicans in which prey are dumped onto the nest or into the gullets of the dominant chicks and consumed by them (Mock 1984; Ploger 1997). The different feeding styles may explain the dichotomy between raptors on the one hand and pelicans and egrets on the other following siblicide. It is also unlikely that food allocation to individuals would change with a reduction in brood size given that in all the raptors mentioned, female chicks slowly become larger than their brothers, yet still no differences in food allocation were measured by Newton (1978) or MacWhirter (1994). Body growth also does not vary among individuals of reduced kestrel broods (Dijkstra 1988).

To conclude, I applaud Ploger's (1997) experiments, her measurement of food intake in relation to chick rank and her questioning of the assumption that senior chicks receive a food bonus by killing their nestmates (also see Mock & Lamey 1991). However, eight examples from experimental studies of raptors indicate that while bulk food deliveries to broods often do decrease with brood reduction, food biomass per nestling significantly increases in all but one species in which it was accurately measured. This occurs because brood size decreases proportionately faster than does the food provisioning rate, resulting in a net increase of food for remaining chicks. The equal allocation of food to raptor nestlings ensures all chicks receive this benefit. Thus a central assumption of siblicide models pertaining to raptors (and other species in which chick feeding is relatively even) is supported. Improved survival through enhanced growth or physiology of remaining chicks has yet to be shown and this may set a limit to the amount of brood reduction that is adaptive for parents and remaining chicks.

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