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# Parental versus offspring control on food division within the brood: the role of hatching asynchrony

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Using an individual-based simulation model we study how different mechanisms of food division among multiple offspring influence nestling number and quality, as well as parental effort. We consider the combination of different scenarios of food availability (feeding conditions), hatching asynchrony and food division. If parents have full control on how to divide food among offspring, asynchronous broods have higher breeding performance than synchronous ones in a wide range of feeding conditions, giving theoretical support to empirically proved benefits of hatching asynchrony. If parents accept the outcome of sibling competition there is a threshold in feeding conditions below which asynchronous broods produced more fledglings and the reverse was true above the threshold. Interestingly, parents relying on the outcome of nestling competition do not necessarily differ in breeding performance from those which have full control over food allocation. Our study combines hatching asynchrony, provisioning behaviour of parents, jostling behaviour of nestlings and feeding conditions as a network of interacting processes of enormous interest to fully understand the parent–offspring conflict.

How to divide resources among multiple offspring constitutes one of the most important challenges of evolutionary ecology, economy and behavioural sciences (Becker 1991, Davis and Todd 1999, Wells 2003, Whittingham et al. 2003). In the evolutionary context, parents should maximize their lifetime reproductive success (i.e. the number and quality of the offspring along their reproductive life; Newton 1989). This implies the optimization of each breeding attempt without negative consequences on both adult survival, and next breeding episodes (Mock and Forbes 1994). On the other hand, each descendent will try to get the maximum investment from the parents on its own, and this is achieved by different behaviours that could be accommodated to the terminology used by Parker et al. (1989), namely hierarchical cases when stronger sibs have first access to the food (single-straw models according to Haig and Wilkins 2000) or scrambling cases when stronger sibs are more effective at gaining food (multi-straw models: Haig and Wilkins 2000; see also Davis and Todd 1999, Wright and Leonard 2002, Johnstone 2004). Both parents and offspring benefit from parental provisioning of nestlings, but genetic conflicts occur between offspring and parents, and also among offspring, over the amount and duration of care (Trivers 1974, Cotton et al. 1999). This parent–offspring conflict constitutes one of the most interesting topics in studies on the evolution of life history traits (McGinley et al. 1987, Kacelnik et al. 1995, Strohm and Linsenmair 2000, Forbes 2007). Both theoretical and experimental approaches have contributed to our understanding on the parent–offspring conflict in an evolutionary context (Trivers 1974, Davis and Todd 1999). Many of them have focused on birds, because data on food allocation among chicks, reproductive outputs, and behaviour of both parents and offspring are easier to obtain in this taxon.

Although many previous empirical work have concluded or assumed that parents primarily control resource allocation decisions (reviewed by Royle et al. 2004), many others have highlighted the important role of competition among nestlings in resource allocation. This includes different forms of competition ranging from lethal, direct and aggressive competition to non-lethal, indirect, and non-aggressive competition (Bonabeau et al. 1998). Both ideas are supported by empirical works: coot *Fulica atra* parents proved to be able to control food allocation among nestlings despite having semi-altricial and mobile offspring (Horsfall 1984), while other studies showed older or heavier nestlings monopolizing food resources by intimidating, fighting and even killing its sibs without the intervention of parents (Mock 1987, Parker et al. 1989, Forbes 1993, McRae et al. 1993).

Because of the parent–offspring conflict, it is difficult to assess whether parents or offspring are in control of food distribution by observation alone (Clutton-Brock 1991), but there are scenarios where parental control is more plausible (cup-shape, open nests, non-aggressive nestlings; Davis et al. 1999) while other are more susceptible to offspring control (very mobile, aggressive nestlings and tube-like nests; Ploger and Mock 1986, Kacelnik et al. 1995, Whittingham et al. 2003, Ploger and Medeiros 2004). A good example for the latter is the lesser kestrel *Falco naumanni*, a small migratory falcon that breeds in the western Palaearctic, inhabiting open and cultivated landscapes. Urban colonies are typically located in castles and churches (Negro 1997) with tube-like nests (Negro and Hiraldo 1993). This species lays a relatively constant clutch of 4–5 eggs (Negro 1997, Serrano et al. 2005, Rodríguez et al. 2006), and has a high hatching success (above 80%; Negro 1997, Liven-Schulman et al. 2004, Serrano et al. 2005). Nestling starvation is common (up to 90% of observed mortality; Negro et al. 1993) leading to frequent brood reduction. In this scenario, evolutionary pressures might have resulted in the selection of those provisioning rules that allow parents to minimize the 'wasted' parental investment. However both the tube-like nest structure and competing behaviour of nestlings prevent parents from having free access to all nestlings in the brood, and they could accept the outcome of sibling competition as found in other species (Kacelnik et al. 1995, Ostreiher 1997, Whittingham et al. 2003, Ploger and Medeiros 2004). Thus parents may use alternative strategies to influence how food is allocated among nestlings. Hatching asynchrony could be this mechanism, creating a hierarchy among the nestlings that allows parents to improve their breeding output. This modest early bias produces asymmetries in the sibs' abilities to compete for limited food deliveries (Lack 1947, reviewed by Pijanowski 1992, Mock and Parker 1997). The resulting phenotypic variation among nestlings, and its evolutionary causes and consequences have been object of study for decades and different hypotheses have been proposed and reformulated to explain why parents create more offspring than they can normally rear and why they start incubation before laying has been completed (Lack 1947; see also Amundsen and Slagsvold 1996, Forbes et al. 2002, Laaksonen 2004). In this paper we focus on how hatching asynchrony influences breeding performance under different scenarios of feeding conditions, and food allocation rules played by parents, also considering that nestling competition influences how food is finally distributed among them.

To investigate this topic, we modified and extended an individual-based simulation model for the lesser kestrel to compare breeding performance of parent versus offspring control of food allocation among the nestlings in different scenarios of hatching asynchrony. The model simulates the body mass gain of lesser kestrel broods depending on daily food intake (Rodríguez et al. 2006). This model was built on the basis of experimental and field studies and was satisfactorily validated against empirical data (Rodríguez et al. 2006). It is able to quantify both the influence of different feeding conditions (prey availability and quality around the colony) and the influence of different nestling and parental behaviours. We considered three classical provisioning rules under parents' control: feeding preferentially the largest, feeding preferentially the hungriest and feeding at random, and compared the breeding performance under these three alternatives with a hierarchy-based feeding in which differences in weight among sibs determine a more despotic or equal (sensu Forbes 1993) allocation of food. Different scenarios of hatching asynchrony were also considered because of its important role in creating competitive asymmetries among siblings.

# Methods

## The model

The individual-based model considers the daily growth in body mass of each nestling during the 37 day nestling period (Bustamante and Negro 1994) as a function of food supply. The basic event for the model is a feeding trip, which is repeated throughout daylight hours. Different feeding conditions are simulated by means of two parameters that are considered to be the main drivers of lesser kestrel hunting performance: prey weight and prey availability (Rodríguez et al. 2006). These two parameters determine the frequency of food provisioning and its quality. When a parent arrives to the nest (kestrels feed on big insects and deliver a single non-shared prey per trip), it provides the prey item to one nestling. Nestlings that receive insufficient food will lose weight and eventually die if they fall below a threshold. This was set in accordance with the minimum weights for each age recorded in the field from more than 3800 living chicks of different ages (Rodríguez and Bustamante 2003). Daily food supply is the cumulated prey biomass delivered to the nest each day. Throughout the day, the model records the number of provisioning events, and the amount of food consumed by each chick. It also considers the metabolic requirement of chicks, and their maximum food intake, which were calculated as a function of individual nestling body mass on the basis of experimental studies that provided data on a daily basis (Rodríguez et al. 2006). Because nestlings' body masses change along the growing period, these values were updated daily. When the chick receives the maximum daily intake, it is set as 'full' and is not considered for further feeds until the next day. If all chicks are 'full' parents stop feeding chicks (the model assumes that parents intend to fledge all chicks in the brood). At the end of the nestling period, the model records the number of surviving fledglings, their weight (as a measure of their quality and posterior survival probability, Magrath et al. 1991, Wright et al. 1998), and the total number of provisioning flights performed by adults as a measure of parental effort (Stauss et al. 2005). Each simulation run starts with an initial random brood size selected from the frequency distribution of brood sizes recorded in the authors' long-term lesser kestrel monitoring programme (Rodríguez and Bustamante 2003).

## Food division among nestlings

We considered two different scenarios of food division. In the first one (hereafter parents' control) parents have full control and select the nestling to be fed by using different provisioning strategies already observed in nature (reviewed by Davis and Todd 1999). In the second one (hereafter offspring's control), parents accept the outcome of sibling competition for food (Cotton et al. 1999).

### *Parents' control*

Three feeding strategies used:

1) Feeding the largest (hereafter 'Largest'), is a hierarchical strategy similar to the 'despotic allocation' described by Forbes (1993), or 'single-straw' models described by Haig and Wilkins (2000). The chick showing the highest body mass is considered to be the largest and it is fed preferentially. If it is full, food is offered to the next largest, and so on.

2) Feeding the hungriest (hereafter 'Hungriest'). Before each provisioning event, the chick showing the higher unbalance between maximum food intake and current intake (Rodríguez et al. 2006) is considered to be the hungriest (we also assume that begging constitutes an honest signal on which parents rely; Godfray 1991).

3) Feeding at random (hereafter 'Random'). This is a null model that could mirror the situation of no parental feeding strategy, and stochasticity of provisioning frequency and relative position of chicks in the nest at adult arrival.

### *Offspring's control*

If parents accept the outcome of sibling competition, body weight of nestlings could be used as an indicator of brood hierarchy. Because nestlings may fight for food, and jostle for position in the nest (Kacelnik et al. 1995), high differences in body size within the brood could determine a more despotic or hierarchical distribution of food, while low differences in body size among nestlings are expected to render a more equalized (random) distribution of food resources. We fitted a logistic function based on the difference in body mass among nestlings that calculates the probability of the largest getting the food ($p_{rank}$).

$$p_{rank} = \frac{1}{1 + e^{(8 - 0.13 \times \Delta W)}}$$

where $\Delta W$ is the difference in body mass between the heaviest and the lightest nestling. This function was fitted on the basis of our data and experience on lesser kestrels, which defined the two extremes of this equation: at small $\Delta W$, which could approach zero in real data, all nestlings have similar probabilities of getting the food, and it was distributed randomly. At the other extreme the maximum $\Delta W$ found in our data is 100 g, which correspond to a very particular situation where the heaviest nestling approached the maximum weight and the lightest approached the minimum weight to be alive. In this extreme, the function is getting a value of 1, which means that the largest will monopolize food until it is full, then the next largest will monopolize remaining food until full and so on (in the same way as Largest). In between of these extremes (which is the most common situation), there is a continuous where the function gives intermediate values that were translated into the model as a probability of feeding at random, and the complementary probability of feeding in the same way than Largest. For instance, if $\Delta W = 70$ g, feeds are 75% hierarchical and 25% random, which promotes the smallest chick to be singled out for death, but also allows changes in hierarchy due to random feedings when differences among heavier nestlings small. $\Delta W$ was calculated daily, which allows to update allocation rules depending on current brood size and hierarchy. We used a sigmoid function because it makes it possible to deal with threshold $\Delta W$. In this case, we set a threshold $\Delta W$ of 30 g from which differences among chicks start to play a role in accordance with our observations of lesser kestrel broods. Although this function was thought to fit lesser kestrel brood reduction, thus facilitating that the smallest chick is singled out for death, the average difference in weight among sibs could also be used to calculate how hierarchical food distribution should be. This alternative was also considered in the simulations.

## Hatching asynchrony

We considered three different scenarios of hatching asynchrony for both parent and offspring control: 1) no hatching asynchrony (hereafter synchronous broods): all nestlings hatch at the same time; 2) high hatching asynchrony (hereafter asynchronous broods): a time-lag of two days between consecutive hatched chicks was set, and 3) context-dependent (hereafter adaptive) hatching asynchrony: hatching span depended on feeding conditions; at very poor environments, a high hatching asynchrony is used because it demonstrated to be more efficient in single out a chick for death (Wiebe and Bortolotti 1995). The improvement of foraging conditions is progressively reducing hatching asynchrony. This is simulated by means of a logistic function:

$$\text{Hatching\_asynchrony} = 3 - \frac{2.99}{1 + e^{4 - 60 \times \text{FeedCond}}}$$

where FeedCond $= 0.7 \times$ mean prey weight $\times$ probability per minute of finding prey. This value was then rounded to the next integer and multiplied by the hatching interval (1 between the first and the second chick, 2 between the second and third, and so on). This means that under a hatching asynchrony of 0.4 the first and the second chicks hatched at the same time ($0.4 \times 1 = 0.4$), the third and fourth chicks hatched a day after ($0.4 \times 2 = 0.8$, and $0.4 \times 3 = 1.2$), and the last chick hatched two days after the first ($0.4 \times 4 = 1.6$). Nestling weight at hatching was set in 10.5 g with standard deviation of 1.5 g to account for natural variability within broods.

## Input parameter ranges and sensitivity analyses

In accordance with natural variability found in our study area (Rodríguez et al. 2006), the mean prey weight ranged from 0.4 to 3 g (in step units of 0.1 g), and the range of prey availability (introduced in the model as a probability per minute of finding prey) varied from 0.06 to 0.27 (in step units of 0.01). We simulated 100 runs for each combination of mean prey weights, probabilities of finding prey, strategies of food division, and scenarios of hatching asynchrony. Simulations were run on Delphi Professional ver. 5.0.

## Results

### Feeding conditions

Feeding conditions are determined by the mean prey weight and the probability of finding prey in the field. They had a strong influence on the breeding performance (Fig. 1), especially at intermediate feeding conditions (Table 1). The number of fledged chicks and their mean body mass increased when feeding conditions improved, although the latter showed slight declines when the improvement of feeding conditions allowed an additional chick to be fledged. The pattern showed by the parental effort per offspring was less clear, showing a marked increase at the beginning, and declining afterwards (Fig. 1). Because this parameter was calculated on the basis of the number of fledglings, it was very dependent on the fact that fledglings were discrete units. Once the improvement of feeding conditions allowed an additional chick to be reared, this significantly decreased the number of provisioning flights per fledgling, especially in strategies with step-like increases in the number of fledglings. Parental effort per parent (total number of provisioning flights) increased in a sigmoid way when feeding conditions improved. Pilot work suggested that this pattern was true for the whole simulation range. Because this is too vast to be shown here, and results are quite redundant once the maximum number of fledglings has been reached (Rodríguez et al. 2006), we focused on the conditions defined by the lowest probability of finding prey in the field and increasing mean prey weights from 1 g to 2.6 g. (Table 1, Fig. 1). The alternative option of fixing the mean prey weight, and running simulations for the range of probabilities of finding prey, rendered very similar results to those shown here (Appendix 1).

### Parents' control

In the worst feeding conditions of the range, Largest was the best strategy in terms of number of fledglings, it showed intermediate values of nestling body mass, and it was among the best in parental effort per offspring and per parent (left part of Fig. 1a and Table A1). When feeding conditions improved, Largest remained to be the best in terms of offspring quality and parental effort, but resulted in fewer fledglings and double to triple parental effort per surviving offspring (Fig. 1a). In general (details in Table A2), asynchronous broods performed better than synchronous ones when using this strategy.

Random and Hungriest strategies performed best under intermediate and good conditions where they produced the highest number of fledglings and lower parental cost per offspring. Differences between these strategies were small (Fig. 1a) and varied depending on the feeding conditions: in terms of number of fledglings, Random performed slightly better than Hungriest under poor feeding conditions while the opposite was true at intermediate conditions. They performed almost alike under good conditions. In terms of parental effort per offspring and total parental effort, Hungriest performed slightly better than Random (Table A1). These differences were higher in scenarios of hatching synchrony and more subtle in asynchronous broods. In general (Fig. 1a, Table A2) asynchronous broods produced a similar or higher number of nestlings, of higher quality, but with higher parental cost.

### Offspring's control

When parents accepted the outcome of sibling competition, a different pattern in the influence of hatching asynchrony appeared. When calculating $\Delta W$ as the difference between the heaviest and lightest nestling (option 1 in Methods): the number of chicks produced by asynchronous broods was higher than in synchronous ones under the worst feeding conditions throughout the range but above a certain threshold, asynchronous broods produced fewer fledglings with higher parental costs per offspring. On the other hand, fledglings had a better body condition connected with a lower parental cost per parent. The adaptive hatching asynchrony produced a close to maximum number of fledglings, with intermediate body conditions, parental costs per offspring, and parental cost per parent (Fig. 1b). The second alternative of calculating $\Delta W$ performed similarly to Random strategy (results not shown).

When comparing parents versus offspring control in the range of feeding conditions (Fig. 1, Table A1), the latter approached the maximum values reached by the best parent strategy in terms of number of fledglings and parental effort per offspring, especially in synchronous broods.

## Discussion

Previous studies have concentrated either on food distribution determined by the provisioning behaviour of parents (parents' control, Davis et al. 1999), or on the importance of nestling competition on how food is finally distributed (Ploger and Mock 1986, Parker et al. 1989, Forbes 1993, Bonabeau et al. 1998, Cotton et al. 1999). However, the combined effect of parent or offspring control with hatching asynchrony has received little attention. We fill this gap using an individual-based simulation model on the example of the lesser kestrel. Our results showed high variations in breeding performance depending on how food is divided among nestlings, which stresses the importance of this process. In addition, results highlight the role played by hatching asynchrony in food division within the brood.

Model outputs are evaluated concerning the number of offspring per breeding pair, their quality, or the parental effort. Lifetime reproductive success of individuals can depend on these three parameters in a context-dependent way (Caley et al. 2001). For instance some situations may favour a low frequency of provisioning flights because of high predation risk (Eggers et al. 2005), others may favour a higher number of chicks (Tella 1996, Wiehn et al. 2000), and others may favour chicks flying from the nest in a better body condition and having higher survival probabilities (Monros et al. 2002). For lesser kestrels, previous studies have documented that colonies with fewer daily provisioning flights produced fledglings in a lower body condition, but not a lower number of fledglings, nor lower survival rates of these fledglings (Tella 1996, see also Wiehn et al. 2000 for similar

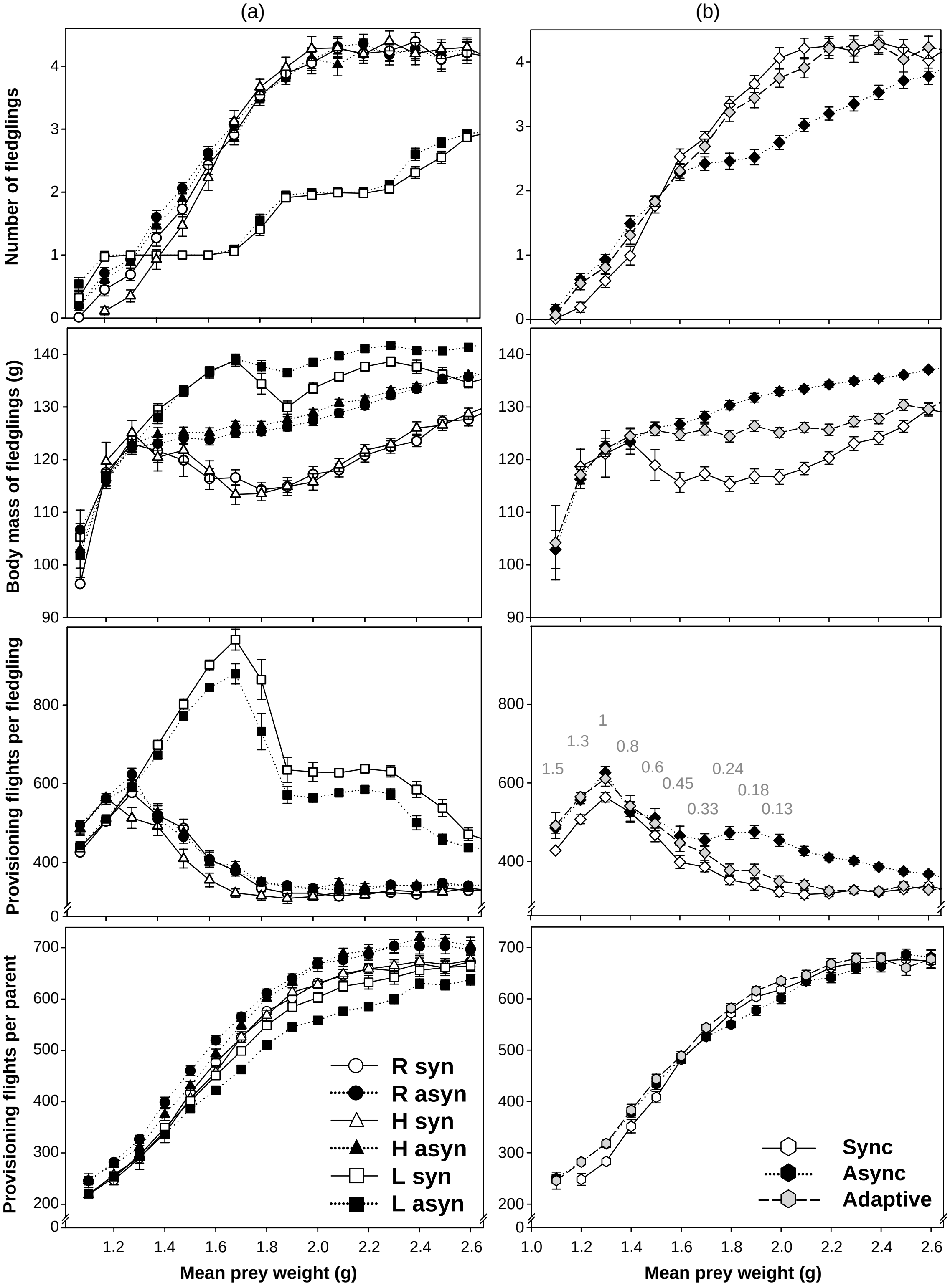

Fig. 1. Mean breeding performance (±95% CI) at a low probability of finding prey (0.06) and variable mean prey weight in different scenarios of food division among nestlings according to (a) parents' control: Random (R), Hungriest (H), and Largest (L) and (b) offspring control. Empty symbols are used for synchronous broods, black symbols for asynchronous, and grey symbols in (b) for adaptive hatching asynchrony. Numbers above symbols in (b) indicate the value (if $>0$) of the adaptive hatching asynchrony. Note that plots of body mass start in 90 g, which is approximately the minimum body mass to be alive.

Table 1. Results of a GLM fitted to the four parameters of breeding success investigated under four different feeding conditions: low (1–1.4 g of mean prey weight), low-medium (1.5–1.8), medium-high (1.9–2.2), and high (2.3–2.6). Normal errors and identity link were used. Explanatory ability (as % of explained deviance) of feeding strategies (Hungriest, Largest, Random and offspring control), and hatching asynchrony is shown. Whether the interaction between these factors is significant is also shown ns = non significant.

| | Feeding conditions | Strategy % | Asynchrony % | Interaction |
|---|---|---|---|---|
| Log (fledglings + 1) | low | 10 | 8 | <0.01 |
| | low–medium | 37 | 0.4 | <0.01 |
| | medium–high | 65 | 2 | <0.01 |
| | high | 48 | ns | – |
| Body mass | low | ns | 0.5 | <0.01 |
| | low–medium | 39 | 10 | <0.01 |
| | medium–high | 33 | 32 | <0.01 |
| | high | 25 | 27 | |
| Effort per offspring | low | 6 | 0.1 | <0.01 |
| | low–medium | 73 | ns | – |
| | medium–high | 71 | 0.9 | <0.01 |
| | high | 60 | ns | – |
| Effort per parent | low | 12 | 2 | <0.01 |
| | low–medium | 10 | 0.4 | <0.01 |
| | medium–high | 19 | ns | – |
| | high | 8 | 0.8 | <0.01 |

results in the Eurasian kestrel). Food supplementation experiments conducted with the similar-sized American kestrel, also pointed in the same direction, since nestlings in supplemented nests did not fledge in a better condition or had higher survival rates than control nestlings (Dawson and Bortolotti 2002). Thus, the number of fledglings seems to be a particularly adequate measure to evaluate different food division strategies for these species.

Although our results draw a more general picture on the process of food division among nestlings than previous modelling efforts (Beauchamp et al. 1991, Davis et al. 1999) our basement on lesser kestrel data and simplifying assumptions impose limitations to generalize our findings to other species. For instance, we assume a quite constant clutch size, which is empirically true of the kestrel, but high variable clutch sizes are found in other species. Likewise, we assume that parents intend to fledge chicks from every egg they lay, which is not always the case (Forbes and Mock 2000).

Previous studies assuming full control of parents on food division found that the strategy of feeding preferentially the largest is the best in very poor environments, where feeding the hungriest is the worst (Davis et al. 1999). Above this threshold, feeding the hungriest or in a random way produce a higher number of fledglings than feeding the largest. Nonetheless, differences between strategies are smaller with increasing food resources (Davis et al. 1999). Our results matched these previous findings. However, considering hatching asynchrony in the scenario of parents, control reduced the range of conditions where feeding the Largest produced more nestlings, and it also reduced the difference between Random and Hungriest strategies. Note that the pure Largest strategy is probably unrealistic, so it should be interpreted as a theoretical extreme to which some species approach (Price and Ydenberg 1995). Accordingly, a pure random strategy could also be seen as a theoretical extreme to which some species may also approach (Reed 1981, Leonard and Horn 1996). Nonetheless, it should be noted that in birds that forage away from the nest site, there will always be some travel time for foraging that make a genuinely random schedule impossible.

In terms of number and quality of fledglings, asynchronous broods had atleast similar higher on breeding performance than synchronous ones. This highlights the potential benefit of hatching asynchrony for species with full parental control on food division among nestlings, also giving theoretical support for empirical evidences in favour of hatching asynchrony in nature (Mock and Forbes 1994, Hebert and McNeil 1999, Krebs 1999). Nonetheless, other factors such as predation risks (Dewey and Kennedy 2001), high seasonality of food resources, and viability of first-laid eggs (Arnold et al. 1987, Veiga 1992, reviewed by Viñuela 2000) may contribute to limit hatching asynchrony. On the other hand, synchronous broods performed generally better in terms of parental effort per offspring and total parental effort (Table A2). This could be the cost assumed by parents which decide to hatch asynchronously, as suggested by Amundsen and Stokland (1988). The Largest strategy did not seem to pay this penalty and the parental effort per surviving offspring was lower in asynchronous than in synchronous broods.

The findings discussed so far consider full control of parents on how to divide food among nestlings, which is plausible in species where provisioning parents could access all nestlings in the brood, and their behaviour does not prevent parents to select any of them. In other scenarios, however, parents lack full control on food division and accept the outcome of sibling competition for food. We investigated these two possibilities by using simulation models where we set a priori whether parents or offspring are in control of food distribution, which is normally difficult to assess in field studies (Clutton-Brock 1991). Whether the hierarchical distribution of food could be considered as offspring control is tricky because parents may give them that control by designing their nests or hatching their young so asynchronously that offspring control is inevitable. Thus, it should be noted that the use of ‘offspring control’ in this paper simply refers to the situation in which parents do not actively follow any provisioning rule but they accept the result of sibling competition (Ploger and Mock 1986, Forbes 1993, Kacelnik et al. 1995, Cotton et al. 1999). Because similar competitive abilities among nestlings cannot be assumed to be universal (Cotton et al. 1999), it is important to consider this "offspring control" in combination with hatching asynchrony, a common process in nature creating siblings with different competitive abilities.

In this simulated scenario (parents lack full control on food division and accept the outcome of nestling competition for food; Fig. 1b) a tradeoff appears between body condition of nestlings and parental effort, two factors significantly influencing lifetime reproductive success of parents. Asynchronous broods maximized body conditions of fledglings (potentially increasing their survival probabilities), but synchronous broods minimized parental effort per offspring (potentially increasing survival probabilities of adults). Nonetheless, even when nestlings govern division of food within the brood, parents may be less sensitive to begging when fledgling dates approaches (Bustamante and Negro 1994), stopping feeding before fledglings reach the relatively high body mass showed for asynchronous broods (Fig. 1b). This would diminish differences in body mass between synchronous and asynchronous broods, also making similar or even smaller the parental cost associated to asynchronous broods as documented in previous empirical studies (reviewed by Mock and Parker 1997). In terms of number of fledglings, we found a clear threshold below which asynchronous broods performed slightly better than synchronous ones, while above the threshold synchronous broods performed better than asynchronous ones (Fig. 1b). Thus, parents could potentially benefit from a context-dependent (adaptive) manipulation of hatching span producing asynchronous broods in poor environments, and synchronous broods in intermediate ones (Fig. 1b). Nonetheless, it should be noted that the adaptive hatching asynchrony function was parameterized on the basis of our experience with lesser kestrels, but no empirical data was available for that. In addition, an important limitation for this adaptive hatching asynchrony is that it requires that laying females predict, at the beginning of incubation, how feeding conditions will be during the nestling period, and only some evidence of this has been reported for the American kestrel (Wiebe and Bortolotti 1995). Thus, further research is necessary to quantify how frequent the manipulation of hatching span is in nature and how sensitive is to environmental conditions.

Disregarding adaptive hatching asynchrony, our results suggest that highly asynchronous broods are advantageous in poor environments, probably because they single out more efficiently a particular chick to die (Wiebe and Bortolotti 1995). On the other hand, asynchronous broods are producing a lower number of chicks than synchronous ones at intermediate conditions. For unpredictable environments, where the average frequency of good years is expected to determine laying behaviour of females (Pijanowski 1992), low asynchrony should prevail because the highest differences in breeding performance between synchronous and asynchronous broods are at intermediate feeding conditions, where synchronous broods are advantageous (Fig. 1b). Intermediate conditions are expected to be more frequent in nature than extremely good or extremely bad conditions. Supporting this, 567 lesser kestrel broods with three or more fledglings monitored between 1988 and 2005 showed a median hatching span of 1.7 days for the entire brood (i.e. 0.4 days between consecutively hatched eggs). However, good reproductive years are probably contributing more than poor years to these values, and further experimental studies are needed to investigate this potential relationship between food availability and hatching asynchrony, its influence on the distribution of food among nestlings, as well as the role played by both parents and nestlings under these controlled circumstances.

To conclude, by contrasting parent versus offspring control on food division under different scenarios of hatching asynchrony, our modelling approach disentangles the relative importance of these processes on breeding performance for different bird species in different environments. Remarkably, breeding performance of parents accepting the outcome of sibling competition may approach the maximum values reached by strategies under parents' control, which allow them to maximize breeding investment by creating higher or lower competing asymmetries among nestlings via hatching asynchrony and accepting the outcome of nestling competition for the distribution of food. This key role played by hatching asynchrony seemed to be more important in species lacking access to the entire brood during provisioning, where asynchronous and synchronous broods performed differently depending on feeding conditions. Further studies should investigate in detail this promising field of interacting processes between feeding conditions, hatching asynchrony and food allocation rules, which also consider the influence of competing nestlings on food distribution.

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# Appendix 1

Table A1. Results of the Wilcoxon rank sum test on the differences in breeding performance between feeding strategies for each value of mean prey weight shown in Fig. 1. Comparisons were made within the same situation of hatching asynchrony (either synchronous or asynchronous broods). We show which strategy is statistically significantly better that the rest ($p < 0.05$, twotailed test): R = Random; L = Largest; H = Hungriest; O = offspring control. When two strategies performed alike, but both significantly better than the other, two initials are shown. A dash is shown for no significant differences.

| Prey weight | 1.1 | 1.2 | 1.3 | 1.4 | 1.5 | 1.6 | 1.7 | 1.8 | 1.9 | 2.0 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nestlings | | | | | | | | | | | | | | | | |
| synchronous | L | L | L | R | RO | – | H | H | RH | H | – | – | – | – | – | – |
| asynchronous | L | L | – | – | R | RH | R | RH | RH | RH | R | RH | RH | RH | RH | RH |
| Mass | | | | | | | | | | | | | | | | |
| synchronous | L | – | – | L | L | L | L | L | L | L | L | L | L | L | L | L |
| asynchronous | – | – | – | L | L | L | L | L | L | L | L | L | L | L | L | L |
| Effort per offspring | | | | | | | | | | | | | | | | |
| synchronous | RL | – | – | – | – | – | H | H | H | H | – | – | – | – | – | RH |
| asynchronous | L | – | LH | – | RH | RH | RH | RH | RH | RH | R | RH | RH | RH | RH | RH |
| Effort per parent | | | | | | | | | | | | | | | | |
| synchronous | L | R | RO | – | L | L | L | L | L | L | L | L | L | L | L | L |
| asynchronous | L | L | – | L | L | L | L | L | L | L | L | L | L | L | L | L |

Table A2. Results of the Wilcoxon rank sum test on the differences in breeding performance between synchronous and asynchronous broods within each feeding strategy and value of mean prey weight shown in Fig. 1. We show which strategy is statistically significantly better that the rest ($p < 0.05$, two-tailed test): S = synchronous broods; A = asynchronous ones. A dash is shown for no significant differences.

| Prey weight | 1.1 | 1.2 | 1.3 | 1.4 | 1.5 | 1.6 | 1.7 | 1.8 | 1.9 | 2.0 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nestlings | | | | | | | | | | | | | | | | |
| random | A | A | A | A | A | – | A | – | – | – | – | – | – | – | – | – |
| largest | A | – | – | – | – | – | – | A | – | – | – | – | – | A | A | – |
| hungriest | A | A | A | A | A | – | S | S | – | S | S | – | – | – | – | – |
| offspring | A | A | A | A | – | S | S | S | S | S | S | S | S | S | S | S |
| Mass | | | | | | | | | | | | | | | | |
| random | A | – | – | – | A | A | A | A | A | A | A | A | A | A | A | A |
| largest | – | – | – | – | – | – | – | – | A | A | A | A | A | – | A | A |
| hungriest | A | – | – | A | A | A | A | A | A | A | A | A | A | A | A | A |
| offspring | A | – | – | – | A | A | A | A | A | A | A | A | A | A | A | A |
| Effort per offspring | | | | | | | | | | | | | | | | |
| random | – | S | S | – | – | S | S | S | S | S | S | S | S | S | S | S |
| largest | – | – | – | A | A | A | A | A | A | A | A | A | A | A | A | A |
| hungriest | – | A | A | S | – | S | S | S | S | S | S | S | S | S | S | S |
| offspring | – | S | S | – | S | S | S | S | S | S | S | S | S | S | S | S |
| Effort per parent | | | | | | | | | | | | | | | | |
| random | – | S | S | S | S | S | S | S | S | S | S | S | S | S | S | S |
| largest | – | – | S | S | S | S | S | S | S | S | S | S | S | S | S | S |
| hungriest | – | – | S | S | S | S | S | S | S | S | S | S | S | S | S | S |
| offspring | S | S | S | S | S | S | – | A | A | A | A | A | – | – | – | S |

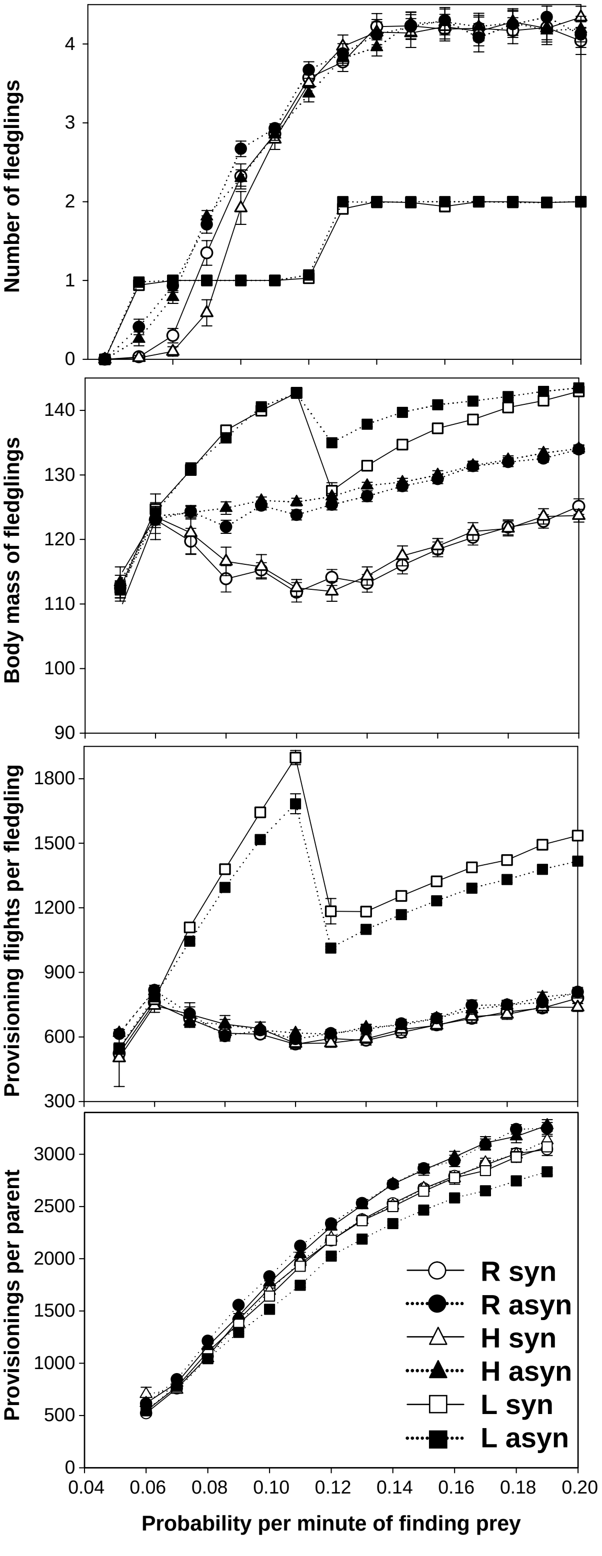

Fig. A1. Mean breeding performance at a low prey weight (1 g) and variable probability per minute of finding prey under different parents' feeding strategies. Empty symbols are used for synchronous broods and black symbols for asynchronous ones. Note that plots of body mass start in 90 g, which is approximately the minimum body mass to be alive.