

ECOLOGY LETTERS

Volume 16 Number 3 | March 2013



WILEY
Blackwell



ISSN 1461-023X www.ecologyletters.com

LETTER

Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism

Daizaburo Shizuka^{1,2*} and
Bruce E. Lyon³

Abstract

Parental food allocation in birds has long been a focal point for life history and parent–offspring conflict theories. In asynchronously hatching species, parents are thought to either adjust brood size through death of marginal offspring (brood reduction), or feed the disadvantaged chicks to reduce the competitive hierarchy (parental compensation). Here, we show that parent American coots (*Fulica americana*) practice both strategies by switching from brood reduction to compensation across time. Late-hatching chicks suffer higher mortality only for the first few days after hatching. Later, parents begin to exhibit parental aggression towards older chicks and each parent favours a single chick, both of which are typically the youngest of the surviving offspring. The late-hatched survivors can equal or exceed their older siblings in size prior to independence. A mixed allocation strategy allows parents to compensate for the costs of competitive hierarchies while gaining the benefits of hatching asynchrony.

Keywords

Brood division, brood reduction, compensation, hatching asynchrony, life history, parental aggression, parent–offspring conflict, sibling rivalry, survival analysis.

Ecology Letters (2013) 16: 315–322

INTRODUCTION

Clutch size has long been recognised as a fundamental life history trait (Lack 1947). It is now clear that the amount of resources invested in individual offspring (i.e. offspring quality) is equally critical, and some have argued persuasively that investment patterns rather than number of offspring is the more important target of selection (Lloyd 1987). The optimal allocation of resources in offspring depends not only on the trade-off between size and number of offspring (Smith & Fretwell 1974) but also on unpredictable external factors such as resource availability and intra-specific competition (Lack 1947). Further complicating the task for parents is parent–offspring conflict, whereby parents and offspring may have different optima for investment patterns (Trivers 1974). The degree to which parents are able to optimise resource allocation to their offspring in the face of these challenges, and the mechanisms used to achieve this allocation, are central issues for understanding both the evolution of family conflict and the evolution of life history strategies generally (Mock & Parker 1997; Parker *et al.* 2002).

Competitive hierarchies among offspring in a brood have particularly strong influence on patterns of juvenile mortality in taxa where parents feed their offspring. These hierarchies may be part of an adaptive parental strategy in some contexts, but they may negatively impact parental fitness in others (Mock & Parker 1997). In birds, a widespread cause of competitive asymmetries is hatching asynchrony, whereby early-hatching chicks gain a significant advantage over later-hatched siblings simply due to age and size (Clark & Wilson 1981; Magrath 1990; Mock & Parker 1997). Lack (1947, 1954) first proposed that hatching asynchrony comprises an adaptive parental strategy to facultatively reduce brood size to align with resource availability. Although adaptive brood reduction is unlikely

to be a universal explanation for the existence of hatching asynchrony (Clark & Wilson 1981; Magrath 1990; Stenning 1996; Stoleson & Beissinger 1997), it remains clear that competitive asymmetries set up by parents often have repercussions for nestling mortality, and thus reproductive success (Mock & Parker 1997).

The distribution of food among the brood is the outcome of both parental and offspring decisions. Parents can mediate the effect of hatching asynchrony on offspring mortality by controlling food distribution to offspring (hereafter ‘parental allocation’). Some theoretical models of parental allocation from a parent–offspring conflict perspective show that parents should feed the ‘neediest’ chicks, though defining an empirical metric for need is the source of some debate (Godfray 1991; Price *et al.* 1996; Mock *et al.* 2011). However, in asynchronously hatching broods, sibling competition may supersede parental control for optimal distribution of resources regardless of the specific needs of each offspring. Early-hatching chicks are generally larger than their later-hatching siblings, and can often receive more parental provisioning simply by outcompeting or even killing their younger siblings (Mock 1984; Drummond *et al.* 1986; Ploger & Mock 1986; Cotton *et al.* 1999). Life history theory confirms that the demise of junior chicks can, on average, benefit parental fitness – that is, sibling rivalry can be a mechanism of adaptive brood reduction (Mock & Parker 1986). However, hatching asynchrony and sibling rivalry also come with costs, such as too much brood reduction when conditions are good (Forbes 1994). When brood reduction is costly parents are expected to compensate for hatching asynchrony by investing more in later-hatching chicks (Slagsvold *et al.* 1984; Budden & Beissinger 2009). Despite such expectation, parental compensation is apparently uncommon except in a few taxa; for example, parrots (Stamps *et al.* 1985; Krebs *et al.* 1999; Budden & Beissinger 2009) and some waterbirds (Horsfall 1984; Leonard *et al.* 1988).

¹School of Biological Sciences, University of Nebraska, Lincoln, NE, 68588, USA

²Department of Ecology and Evolution, University of Chicago, IL, 60637, USA

³Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, 95064, USA

*Correspondence: E-mail: dshizuka2@unl.edu

These theoretical and empirical patterns of parental allocation beg the question: when should parents favour the strong, advantaged chicks, and when should they favour the disadvantaged chicks? The particular conditions that favour one strategy over the other (e.g. resource abundance, brood size, offspring condition) may change rapidly. One potential way to track such changes is to use different allocation rules during different stages of the parental cycle, allowing advantaged chicks to outcompete their siblings at one point and favouring disadvantaged chicks at another (Mock *et al.* 2011). Theoretical models do not yet account for such potential shifts in parental allocation strategies (Mock *et al.* 2011), and we currently lack empirical data to suggest whether, and how, such shifts in allocation play a systematic role in parental strategies. The lack of empirical tests for shifts in parental allocation rules is at least in part due to the difficulty of observing parental provisioning after the offspring leave the nest. However, such changes in allocation strategies should be observable in species where offspring can be followed throughout the parental care period.

In this study, we investigate how patterns of parental allocation patterns change across time in asynchronously hatching broods of American coots (*Fulica americana*), and we explore how parents can control allocation patterns through aggression and favouritism. We further connect these flexible allocation patterns to two important life history traits: offspring number and size. We suggest that flexibility in parental allocation patterns with respect to brood reduction and compensation may be an important component of avian life history and parent–offspring dynamics.

MATERIALS AND METHODS

Study species

American coots lay relatively large and highly variable clutch of eggs (median = 9 eggs, range 4–15 eggs, $n = 279$ clutches) in nests built in vegetation over water. Incubation begins during egg-laying (Arnold 2011), and hatching asynchrony can be extreme (range 2–11 days from first to last egg to hatch; median = 6 days $n = 98$ nests). Coot chicks are able to leave the nest soon after hatching but require parental provisioning of at least 10 days or until they are able to feed independently, although some chicks are fed for 30–40 days (Ryan & Dinsmore 1979; Lyon 1993). There is no overt sibling aggression, but chicks compete for parental provisioning by following parents during foraging forays within the breeding territory. Death by starvation is common: in broods that successfully hatched chicks, half of the offspring died before independence, on average (proportion of eggs lead to fledglings: 52% of 1289 eggs, Lyon 1993; 51% of 601 eggs, this study). Most broods fail to fledge all of the chicks that hatch (97% of 156 nests, Lyon 1993; 93% of 61 nests, this study), and chicks hatching later in the sequence have disproportionately high rates of mortality (Lyon 1993).

American coots and other close relatives commonly display parental aggression in the form of ‘tousling’, whereby the parent grabs and shakes the chick by the head or nape (Horsfall 1984; Leonard *et al.* 1988). Extreme aggression is used by American coots to reject brood parasitic chicks, but the form of aggression differs qualitatively from the typical level of aggression shown to their own offspring (Shizuka & Lyon 2010). Previous studies in other species showed that tousled chicks subsequently spend less time near the adult, and thus, tousling is used to regulate the amount time each

chick spends following the parent and encourage them to begin feeding independently (Horsfall 1984; Leonard *et al.* 1988).

Another salient feature of coot parental care is brood division, whereby each parent selectively favours a subset of the brood – although this is only known previously from a study of three broods of Eurasian coots (*Fulica atra*) (Horsfall 1984), and is apparently absent in moorhens (*Gallinula chloropus*) (Leonard *et al.* 1988). Brood division has been observed widely in altricial species in the period after fledging (reviewed in Lessells 2002). In this study, we focus additionally on within-parent skew in feedings towards a preferred chick – hereafter ‘single-chick favouritism’.

Nest monitoring and observations

We monitored 75 non-experimental nests across five different wetlands in the Williams Lake, British Columbia, Canada area in 1988 and 2005–2008. We monitored nests every 1–4 days during egg-laying. In 1988, chicks were captured at the nest upon hatching. In 2005–2008, we hatched chicks in captivity to ensure that all chicks could be captured and accurately identified to individual at each nest. We took eggs from nests at first sign of pipping, typically one or 2 days before the chicks hatched. Eggs were uniquely labelled and hatched in an incubator (Hovabator model 1602N, GQF Manufacturing, Savannah, GA, USA), with each egg inside its own individual mesh pouch. We returned chicks to nests within 24 h of hatching. For all chicks, we attached colour-coded nape tags that were individually unique within each brood so we could follow individual chicks throughout the parental care period (Arnold *et al.* 2011).

In all years, we conducted censuses and feeding observations periodically throughout the parental care period (median = 9 observations per brood; median last day of observation = 25 days after hatching completion). Brood censuses and behavioural observations were conducted at close range (10–40 m) from floating mobile blinds equipped with camouflage coverings. The sex of each parent was determined by the unique vocalisations of each sex (Guillon 1950). Once birds were sexed by call we then noted plumage and frontal shield characteristics that enabled reliable visual identification of each of the two parents on each territory.

Measuring chick size in the wild

To obtain body size measurements of the highly mobile chicks, we used a digital Nikon D70 camera with a 400 mm manual-focus lens calibrated to accurately indicate the distance of an object in focus up to a distance of 15 m. We took photos of swimming chicks ($n = 186$ photographs of 115 chicks from 23 broods) from floating blinds and then estimated sizes of chicks (body length at waterline) using calculation methods previously described for this species (Lyon 1994). To ensure accuracy in our size estimates (Lyon 1994), we used only photographs that fit all of the following criteria: (1) chick was in sharp focus, (2) chick photographed in profile and (3) chick’s length at waterline could be accurately assessed. Body length at waterline was strongly correlated with body mass in the previous study (Pearson $r = 0.97$, Lyon 1994), indicating that the method is accurate. To compare relative chick sizes within a brood, we photographed multiple chicks from a brood on the same day and calculated relative chick size as the deviance from the mean body length of the brood on a given day.

Survival analysis and identifying the timing of brood reduction

We used survival analysis ($n = 435$ chicks at 57 nests in 2005–2008 for which we had survival data up to at least 16 days) to determine whether patterns of chick mortality were related to hatching order. We binned the census data into 5-day ‘census periods’ beginning with the day after all chicks in a nest had hatched (1–5 days, 6–10 days, 11–15 days, 16–20 days, 21–25 days and 26 + days after all chicks hatched). Not all broods were observed at every time period. A chick was assessed as dead on the first census period in which it was not observed, given that it was never seen again. The data were right-censored. Each chick was assigned a position in the hatching sequence (hereafter ‘hatch order’) based on the day it hatched relative to all others in the nest (hatch order of chicks hatched on first day = 1). When multiple chicks hatched on the same day at the same nest, they were classified with the same hatch order.

Our goal was to use survival analysis to determine the period during which hatch order has a predominant effect on offspring mortality above and beyond background rates of mortality – that is, the period of brood reduction (Mock 1994). We used a series of Cox regressions with change point (Liang *et al.* 1990; Pons 2003). Briefly, these models divide the data into two discrete time steps, and we analyse the effect of hatch order on survival at both time steps. If brood reduction is restricted to the early period of parental care, then there will be a time step that divides the brood reduction period (i.e. where hatch order is a significant factor) from the non-brood reduction period (i.e. hatch order is not a significant factor). If brood reduction were continuous across the parental care stage, then hatch order would be a significant factor in the model before *and* after every time step. We conducted a Cox regression with a change point set at 5, 10, 15 and 20 days to determine whether there were any time steps that distinguished between a brood reduction vs. non-brood reduction period. All Cox regressions included nest as a random effect.

Analysis of relative body size

After determining the timing of brood reduction, we investigated the effects of feeding rates and hatch order on the relative body size of chicks during and after the brood reduction period. We constructed separate linear mixed-models for the time period during brood reduction (days 1–10) and after brood reduction (post day 10) with hatch order and proportion of feedings received during that time period as fixed effects and nest as the random effect. The response variable was relative body size, measured as deviance from the mean body size in the brood. Members of the same brood were photographed on the same day.

Sequential analysis of parental allocation and aggression

We investigated how parents allocate both feedings and aggression among offspring with respect to relative hatch order, and whether these dynamics changed across time. For each brood, we summed all observations conducted within the same 5-day observation period (same binning as census periods described above), and excluded observation periods in which fewer than 20 total feeds were observed. For each observation, we first classified each chick according to its hatch order relative to all other brood mates that

were alive during that observation. We binned relative hatch order into three classes: ‘first-hatched’, ‘middle-hatched’ or ‘last-hatched’. ‘First-hatched’ chicks were those that had the earliest hatch date among the surviving brood. ‘Last-hatched’ chicks were those that had the two latest hatch dates among the surviving brood – this sometimes included more than two chicks. ‘Middle-hatched’ chicks were those that hatched in between the ‘first-’ and ‘last-hatched’ chicks. Not every brood contained ‘middle-hatched’ chicks at every observation. We use relative hatch order for these analyses rather than absolute hatch order because competitive ranks are affected by the death of brood mates (e.g. if an early hatched chick dies, middle-hatched chicks would then become the earliest-hatched among the survivors).

We used generalised linear mixed-models (GLMM) to determine whether patterns of food allocation changed across time. We first constructed a global model with the number of feedings received as the response variable, brood as a random effect, and hatch order, observation period and their interaction as fixed effects. To compare the specific allocation patterns across time, we then constructed a separate GLMM for each observation period with the number of feedings received as the response variable, brood as a random effect and relative hatch order as the fixed effect. As the response variable showed over-dispersion, we used quasi-Poisson error. We then conducted multiple comparisons to test the effect of hatch order on the proportion of feedings each chick received.

To analyse patterns of parental aggression, we calculated a ‘tousle index’ for each chick for each observation that allowed us to control for the variation in the amount of time each chick spent near parents. The tousle index is $[\# \text{ tousles received}] / [\# \text{ tousles received} + \# \text{ feedings received}]$, which serves as an index of the rate of tousling per interaction with parents. To determine whether patterns of parental aggression changed over time, we constructed a global model with the number of tousles received within each 5-day observation period as the response variable, brood as a random effect, and hatch order, observation period and their interaction as fixed effects. To compare specific patterns of parental aggression within each time period, we then constructed separate GLMM for each 5-day observation period, with the tousling index as the response variable, hatch order class as the fixed effect, brood as the random effect and quasi-Poisson error.

Next, we tested whether tousling during one time period affected the provisioning patterns in the *subsequent* time period. If older chicks reduce their dependence on parental provisioning independently of the amount of tousling they receive, then hatch order but not tousling index will have an effect on the amount of feedings a chick receives in the next time period. Conversely, if parental aggression encourages chicks to feed independently, then aggression should reduce the proportion of feeds that the chick receives in the next observation period, but this effect may be different for older chicks vs. the younger chicks that the parents later favour. We used the same 5-day blocks as observation periods as above, and we included 274 observation blocks from 133 chicks among 21 broods in 1988 and 2005 – the 2 years when we conducted the more intensive observations required for this analysis. We constructed a GLMM with individual nested within brood as the random effect, and hatch order as binary ‘early-’ and ‘late-hatched’ categories, tousling index and their interaction as the fixed effects. The response variable was the number of feedings received in the next observation period with brood total as the offset term.

Skew index

We used the Binomial Skew Index (Nonacs 2000) to quantify the degree to which each parent non-randomly distributed food among the brood:

$$B = \sum_{i=1}^N \left(P_i - \frac{n_i}{N_i} \right)^2 - \frac{(1 - 1/\bar{N})}{K}$$

For a given observation period, N is the total number of chicks in a brood, K is the number of feedings that a parent provisions to the brood and p_i is the proportion of the K feedings that individual i received. Within a given 5-day observation period, n_i is the number of observation bouts in which individual i was seen and N_i is the total sum of n_i for all individuals. \bar{N} is the average number of chicks during an observation bout, for example, N_i divided by the number of bouts. Thus, this index accounts for instances in which an individual offspring was present for only some of the observations because they died during the observation period. Nonacs (2000) showed that

$$B_{\text{equal}} = \frac{(1/\bar{N} - 1)}{K}$$

$$B_{\text{monopoly}} = 1 - \frac{2n_1}{N_i} + \sum_{i=1}^N \frac{n_i^2}{N_i^2} + \frac{(1/\bar{N} - 1)}{K}$$

where B_{equal} is the expected skew index under equal distribution of food, and B_{monopoly} when chick $i = 1$ monopolises all provisioning from a given parent during an observation period. Using these equations, we scaled the skew index:

$$B' = \frac{B - B_{\text{equal}}}{B_{\text{monopoly}} - B_{\text{equal}}}$$

Thus, B' is 0 when all chicks receive equal amounts of provisioning, and B' is 1 when one chick monopolises all provisions from a particular parent. For each brood, we measured the B' index for each parent during each 5-day observation period in which we observed at least 10 feeding events by that parent.

We conducted all analyses using R version 2.13.1.

RESULTS

Effects of hatching order on chick survival and growth

Hatching order had a very strong influence on chick survival, with later-hatching chicks suffering greater rates of mortality (Fig. 1: Mixed-effects Cox proportional hazards regression: $Z = 5.69$, $P < 0.001$). We further investigated the timing of this hatch order effect by generating a set of Cox models with a 'change point' at different stages (Table 1). Hatch order was a strong predictor of chick survival in the first 10 days after hatching was complete (left of dashed line in Fig. 1: $Z = 6.4$, $P < 0.001$). In contrast, hatch order was not a significant predictor of survival from day 10 to the end of our censuses (right of dashed line in Fig. 1: $Z = 1.4$, $P = 0.17$). Thus, although hatch order has major effects on chick mortality, this effect is restricted to about the first 10 days after hatch completion.

The effect of hatch order on the relative body size of chicks differed before and after day 10 post-hatching. During the brood

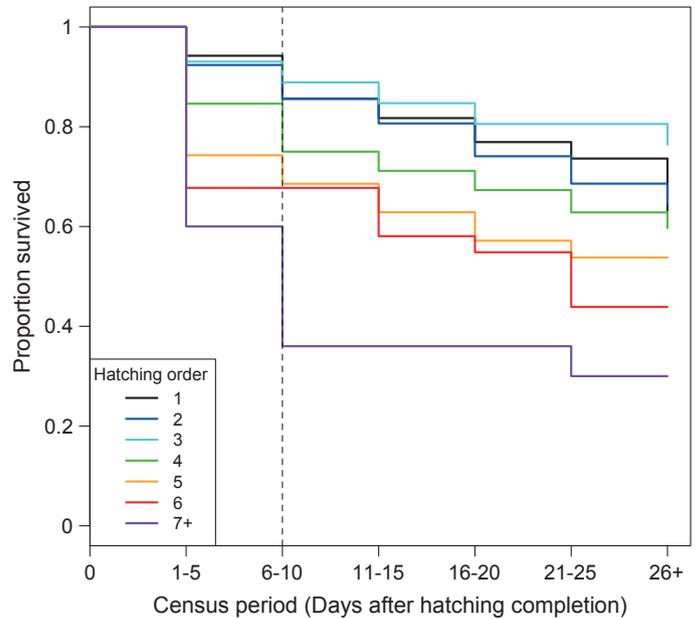


Figure 1 Hatch-order effect on offspring survival through time. Kaplan–Meier curves show that chick survival varies according to position in the hatching sequence: later-hatched chicks have lower survival. This hatch order effect is evident by the census period 6–10 days after hatching completion. However, chick mortality after Day 10 does not differ among hatch order: all chicks that survive the initial 10 day brood reduction period then have equal probability of survival through the first month, irrespective of hatch order.

Table 1 Mixed-effects Cox regression results with change points. For each model, we assess the effect of hatch order on survival before and after the change point. Day 10 is the earliest point at which we can detect a switch between hatch order-based survival to hatch order-independent survival

Change point	Before Change point		After change point	
	Z	P	Z	P
Day 5	6.2	<0.001	2.4	0.016
Day 10	6.4	<0.001	1.4	0.17
Day 15	6.4	<0.001	0.7	0.49
Day 20	6.05	<0.001	0.8	0.44

reduction period (first 10 days after last hatch), early-hatched chicks were relatively larger, regardless of the amount feedings received during this period (Fig. 2a; Mixed-effects model; effect of feedings: likelihood $Chi^2 = 0.68$, $df = 1$, $P = 0.41$; effect of hatch order: likelihood $Chi^2 = 7.18$, $df = 1$, $P = 0.007$). However, after the brood reduction period, most of the variation in size was explained by the relative amount of provisioning received, and later-hatched chicks that were still alive reached slightly larger body size than their older siblings (Fig. 2b, effect of feedings: likelihood $Chi^2 = 28.2$, $df = 1$, $P < 0.001$; effect of hatch order: likelihood $Chi^2 = 3.78$, $df = 1$, $P = 0.05$).

Changes in allocation patterns through time

Parental allocation patterns to chicks of different hatch order changed across time (GLMM, hatch order \times observation period interaction: Wald $t_{606} = 3.04$; $P = 0.002$), and the timing of this shift in allocation patterns coincided with the transition from brood

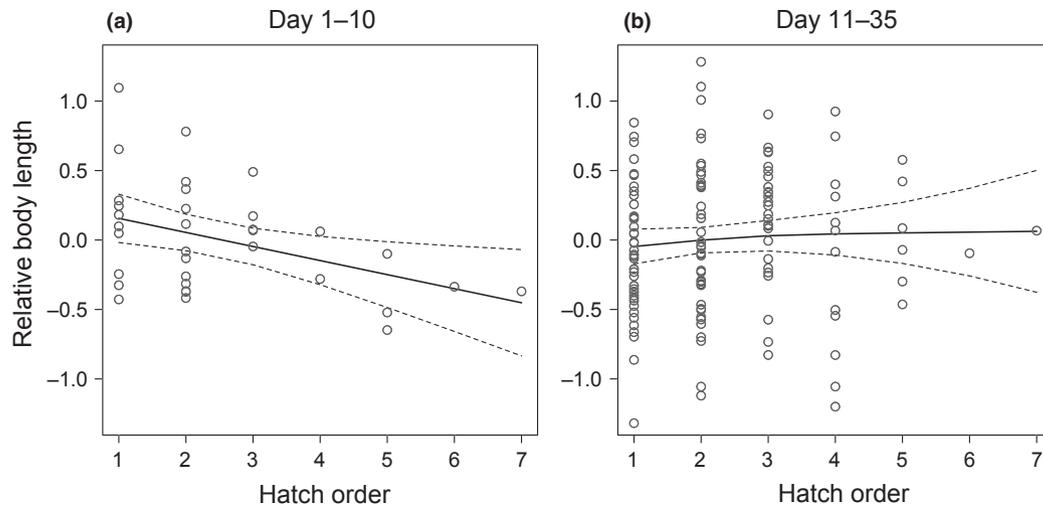


Figure 2 Changes across time in hatch order-dependent size hierarchies within broods. The plots show individual body sizes as deviance from mean offspring body size in the brood on a given day. Chicks from a given brood are photographed on the same day. Cubic spline fits with 95% confidence bands are shown, but statistical analyses incorporate nest as a random effect. (a) During the early period of brood reduction, later-hatched chicks are relatively smaller than their older siblings. (b) However, the later-hatched chicks eventually catch up to their older siblings prior to independence.

reduction to equal survival among chicks around day 10 post-hatching (Fig. 3a). Initially, the oldest chicks received the most parental provisions, as expected given the competitive advantages from their larger size. However, the youngest of the surviving brood began to receive disproportionate amounts of parental provisioning starting around day 6–10 post-hatching. This delayed parental compensation towards the youngest of the survivors explains why hatch order correlates with both chick survival (Fig. 1) and relative size (Fig. 2) during the brood reduction period, but not after.

Parental control of allocation patterns

The allocation of parental aggression towards chicks of different hatch order shifted across census periods (GLMM: hatch order \times observation period: Wald $t_{614} = 2.2$, $P = 0.03$). There were no significant differences between first-, middle- and late-hatched chicks in their tousing index during the early part of the provisioning period (Fig. 3b). However, first- and middle-hatched chicks received more tousles per interaction with parents than their later-hatched siblings after day 10 (Fig. 3b). This shift coincides with the end of the brood reduction stage (Fig. 1), and accompanies the shift in provisioning patterns (Fig. 3a).

Parental aggression had an effect on the amount of food that early-hatched chicks receive in the *subsequent* observation period, but not the late-hatched chicks (GLMM: hatch order \times tousle index: $t_{138} = 2.3$, $P = 0.02$). Thus, parents use parental aggression as a way to modulate the amount of feedings that are allocated to older vs. younger offspring.

Both the male and female increasingly skewed their allocation of food within the brood over the course of the parental care period. The skew index (B) reaches an asymptote around day 11–15 post-hatching (Figs 3a and 4a: mean skew for Days 11–15, female: 0.67 ± 0.03 ; male: 0.68 ± 0.03). During this period of maximal skew, each parent typically allocated the vast majority of their feedings to a single chick, hereafter the ‘favourite’ chick (Fig. 4b, c; proportion of total uniparental feeds received by favourite chick = 0.80 ± 0.03 for female feeds; 0.82 ± 0.03 for male feeds).

Moreover, each parent chooses a different ‘favourite’ chick. During the interval day 11–25, each parent rarely ever fed the chick that the other parent favoured (proportion of male feeds received by female favourite: 0.024 ± 0.012 ; proportion of female feeds received by male favourite: 0.006 ± 0.003). Finally, each parent favours a chick that is among the youngest of the survivors (Table 2: Fisher tests for bias in hatch order: female favourite vs. not favoured, $P = 0.002$; male favourite vs. not favoured, $P = 0.012$). There was no difference between the sexes in their tendency to favour a later-hatched chick (female favourite vs. male favourite, $P = 1.0$). The lone case in which both parents favoured the same chick (Table 2) occurred in a brood of two chicks, and both chicks received provisions from both parents. Therefore, coots show an extreme form of brood division whereby each parent favours a different single chick, and the favourites are among the youngest of the brood to survive past brood reduction.

DISCUSSION

Our results show striking congruence in the timing between the end of brood reduction (Fig. 1) and a dramatic shift in parental allocation patterns (Fig. 3a). Initially, early-hatched chicks receive more food than their later-hatched siblings, presumably because they are at a competitive advantage and because parents do not exert control. Although the exact timing may differ across broods, coot parents begin to favour the youngest chicks of their brood around 6–10 days after hatching is complete (Fig. 3a). The shift in allocation pattern is accompanied by increased parental aggression towards senior chicks (Fig. 3b) and extreme favouritism: each parent favours a single chick, and these chicks tend to be among the youngest of the brood to survive (Fig. 4, Table 2). This strategy results in equal-sized chicks prior to independence (Fig. 2), evidence that adjustment of brood size can be coupled with flexible parental allocation rules that mitigate the effects of competitive asymmetries among offspring.

Life histories of asynchronously hatching birds have classically been categorised into two distinct strategies: ‘brood reducing’ and

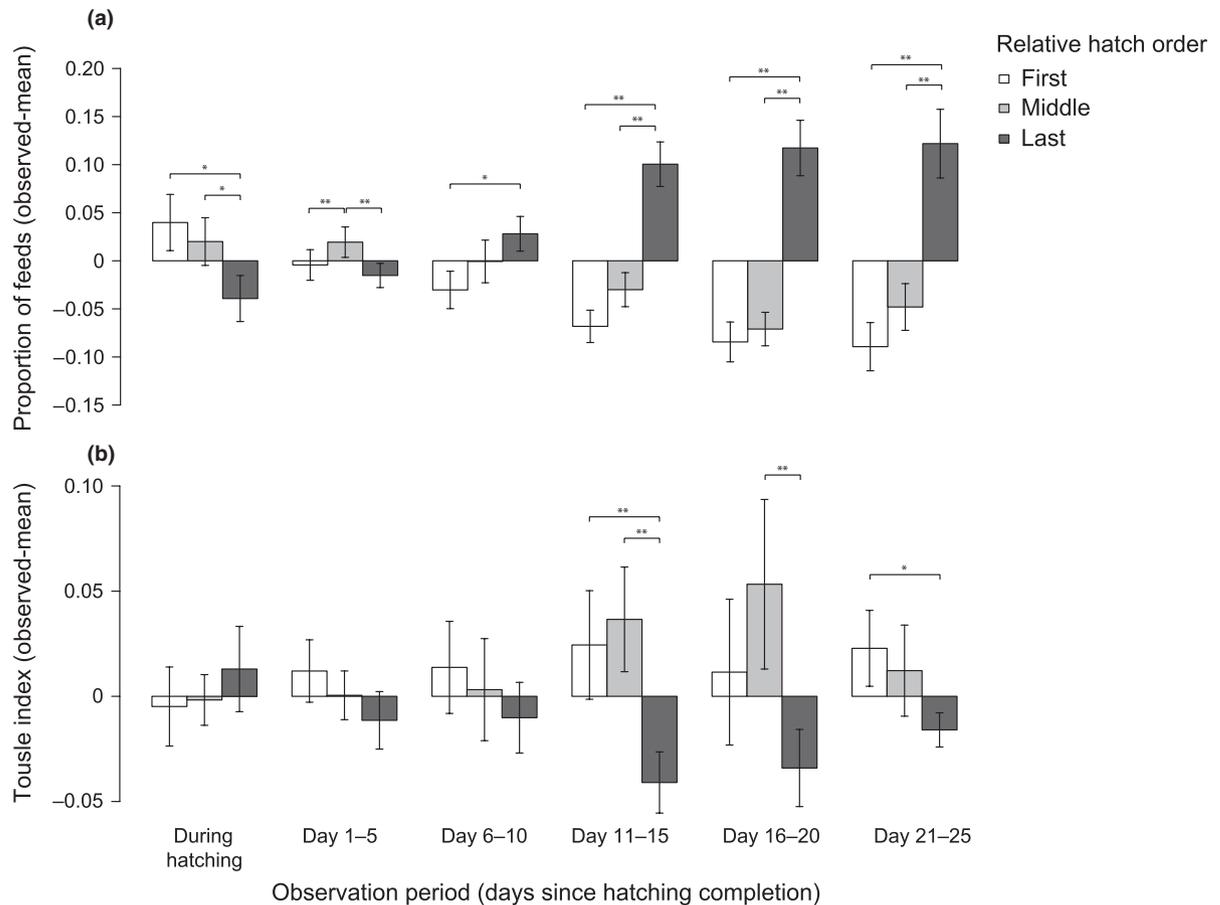


Figure 3 Changes across time in parental allocation of food and aggression with respect to hatching order. (a) The proportion of feeds received by chicks in each hatch order class, relative to the mean proportion received by each chick in the brood. (b) The touse index (see Methods) relative to the mean touse index of the brood during each observation period. Parents initially feed relatively early-hatched chicks more than the late-hatched chicks and do not differentially touse chicks by age. Later (particularly after day 10), parents allocate more food towards the last-hatched of the surviving chicks and increase tousing towards early-hatched chicks. Error bars represent \pm SE. ** $P < 0.01$, * $P < 0.05$ based on Tukey multiple comparisons of mixed-effects models.

Table 2 Females and males both favour later-hatching survivors. Favouritism is determined from observations from Day 11 to the end of the observation period, and relative hatch order is based on surviving offspring at end of observation for each brood ($n = 24$ broods). Last-hatched chicks include the last two hatched because there are two parents, each of which favours a single chick. By definition, each parent has one 'favourite' chick, and all other surviving chicks are classified as 'not favoured'. Two chicks that lost their nape tags are classified as unknown hatch order

Relative hatch order	Female favourite	Male favourite	Not favoured	Favoured by both
First	4	5	32	1
Middle	3	4	25	0
Last 2	16	15	22	0
Unknown	1	0	1	0

'brood survival' strategies (Slagsvold *et al.* 1984). Brood reducers are thought to skew investment towards earlier hatching chicks and promote the death of late-hatching chicks (e.g. Drummond *et al.* 1986; Ploger & Mock 1986; Schwabl *et al.* 1997), whereas the brood survival strategy entails compensating for hatching asynchrony by increasing allocation towards later-hatching chicks (e.g. Stamps *et al.* 1985; Krebs *et al.* 1999; Budden & Beissinger 2009). In some cases,

the optimal parental strategy may be to utilise both strategies at different times in the same reproductive bout, but such flexibility has rarely been shown empirically or considered in theoretical models. We show that American coots exhibit the attributes of both a 'brood reducing' and 'brood survival' strategy, and they employ these allocation patterns at different stages of the nesting cycle. This particular mix of parental strategies may be advantageous because it simultaneously allows for adjustment of offspring number through brood reduction and adjustment of offspring size through parental compensation.

Previous studies of coots showed that maternal investment in eggs favours the early-hatching coot eggs, potentially exacerbating the competitive asymmetry among offspring (Reed & Vleck 2001; Reed *et al.* 2009). Therefore, early-hatching chicks can initially out-compete their later-hatching siblings for more provisions early on in the parental care period (Fig. 3a). Later, parental aggression appears to cause early-hatched chicks to begin feeding independently – they do not suffer increased mortality despite receiving less food from the parents – and this frees up parents to shift resources towards the later-hatching chicks. Such parental control behaviours have been reported for other subprecocial water birds such as European coots (Horsfall 1984), moorhens (Leonard *et al.* 1988) and red-necked grebes (*Podiceps grisegena*) (Kloskowski 2001). Moreover,

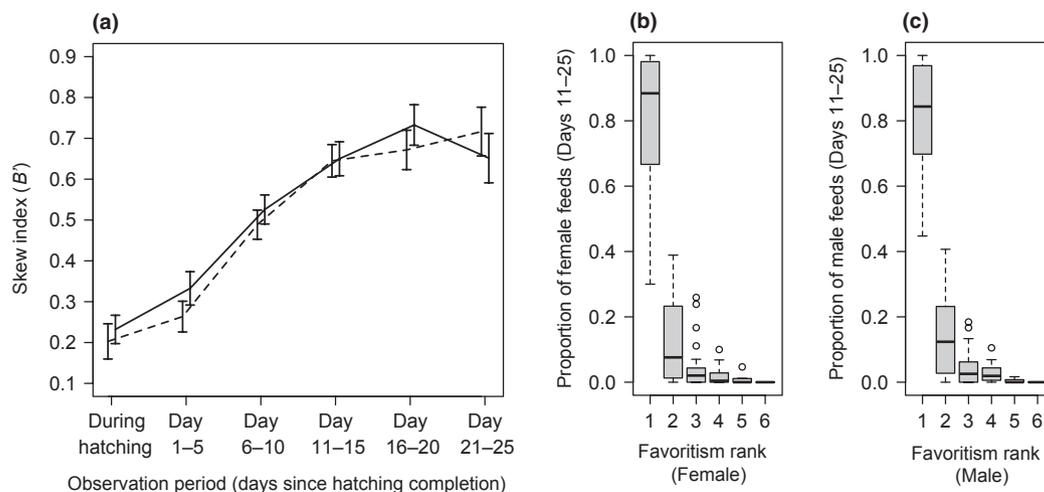


Figure 4 Skewed allocation of resources by females and males. (a) The skew in the distribution of food among offspring by males (solid line) and females (dashed lines). Error bars represent mean \pm SE of the scaled binomial skew index, B' (see Methods). The skew index ranges from 0 (all chicks fed equally) to 1 (a single chick monopolises food). Parental provisioning becomes skewed towards a small subset of chicks as the brood becomes older. (b, c) Box plots showing the proportion of feeds received from the female (b) or male (c) parent by each chick during days 11–25, assorted by rank order from most-fed to least-fed ('favouritism rank'). Single 'favourite' chicks monopolise most of the parental feedings during this period.

parental aggression has been observed in fledgling stages of altricial birds (Leonard *et al.* 1991; Raihani & Ridley 2008), suggesting that some of these parental control dynamics may be widespread in birds. The general pattern here appears to be that the timing of the onset of parental aggression is associated with chick mobility and transition to independence. Further work, particularly with altricial species after fledging, is needed to test this hypothesis and confirm the generality of the shifting priorities in distribution of resources we have documented here.

Parental favouritism towards later-hatched chicks after brood reduction is associated with a combination of brood division (each parent feeds different set of chicks) and single-chick favouritism (each parent favours one particular chick). These two patterns need not occur together, but both forms of skewed allocation have interesting implications for parent–offspring dynamics. In altricial birds, brood division is rare in the nestling stage, but is apparently common in the fledgling stage (Slagsvold 1997; Lessells 2002). The selective advantages of brood division are not well understood, but some hypotheses suggest a role of conflict, either between parents and offspring or between parents (Lessells 2002). Parents may also benefit from the informational advantage of exclusively feeding a different 'favourite' chick – each parent will have exact information on how much provisioning its favoured chick has received. Theory is now needed to determine if brood division and single-chick favouritism make sense in terms of 'information warfare' between parents and offspring (Kilner & Hinde 2008).

Parental allocation strategies are shaped by the fitness effects of both offspring size and number (Smith & Fretwell 1974; Lloyd 1987). Our results indicate that flexibility in allocation patterns can play an important role in balancing this life history trade-off. However, questions remain over which fitness benefit drives the evolution of parental compensation: equalising offspring size, increasing offspring number by stemming excess brood reduction or both. That is, do parents begin to favour late-hatching chicks after brood reduction via sibling competition has run its course, or does favouritism directly stop the process of brood reduction? This distinction is of

particular interest given the suggestion that hatching asynchrony will always have costs in terms of lower offspring numbers when conditions are good because the hatching pattern alone determines chick survival (Forbes 1994; Amundsen & Slagsvold 1996). Our results clearly demonstrate that parental allocation patterns reduce variance in offspring size (Fig. 2), but we do not yet know what role parental compensation has on controlling brood size. Determining this role will be difficult because it would require that one experimentally suppresses parental aggression to examine provisioning and chick survival patterns in the absence of parental control mechanisms.

Current models of optimal parental allocation do not account for changes that occur across the period of parental care, such as changes in brood size, parental condition or offspring age and condition, and there is a need for more dynamic models (Johnstone 1996; Godfray & Johnstone 2000; Mock *et al.* 2011). Our analysis demonstrates one way in which parental investment can shift across time. As some offspring die and others reach the critical size for independence, the optimal patterns of resource allocation may shift such that exclusively feeding the smallest chicks becomes favourable. Theoretical models that allow for such flexibility in allocation patterns may resolve some of the current debates surrounding the parent–offspring conflict, communication and parental investment (Mock *et al.* 2011). Detecting similar patterns of shifting parental allocation strategies in other systems would require detailed data on provisioning to individual offspring across the entire parental care period, including parental care outside the nest. Such data will be labour intensive to collect, but will help yield a more complete picture of parental strategies underlying life histories in birds.

ACKNOWLEDGEMENTS

We thank J. Herrick and W. Messner for access to their property. We thank B. Bair, L. Cargill, E. Clancey, J. Clark, J. Click, R. Drobek, S. Everding, K. Funk, J. Garcia, L. Hamilton, D. Hansen, E. Hooshair, M. Magrath, J. Mehlhaff, C. Morill, C. Nelson, A. O'Brien, E. Orr, G. Peters, G. Taylor, K. Tjernell, J. Sapp and

W. Wong for assistance in the field. We thank G. Nuechterlein for sharing his floating blind design. J. Eadie and B. Sinervo commented on early drafts of this manuscript. Field work was conducted under permits from the Canadian Wildlife Service and the UCSC Institutional Animal Care and Use Committee. This work was supported by the National Science Foundation (DDIG IOS-0808579 to D.S. and IOS 0443807 to B.E.L.), the National Geographic Society, the Chapman Fund, and the Sigma Xi Society. DS was supported by the Chicago Fellows postdoctoral fellowship during the preparation of this manuscript.

AUTHORSHIP

Both authors conducted research and wrote the manuscript, and DS conducted all analyses.

REFERENCES

- Amundsen, T. & Slagsvold, T. (1996). Lack's brood reduction hypothesis and avian hatching asynchrony: what's next? *Oikos*, 76, 613–620.
- Arnold, T.W. (2011). Onset of incubation and patterns of hatching in the American coot. *Condor*, 113, 107–118.
- Arnold, T.W., Shizuka, D., Lyon, B.E., Pelayo, J.T., Mehl, K.R., Traylor, J.J. *et al.* (2011). Use of nape tags for marking offspring of precocial waterbirds. *Waterbirds*, 34, 312–318.
- Budden, A.E. & Beissinger, S.R. (2009). Resource allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet (*Forpus passerinus*). *Behav. Ecol. Sociobiol.*, 63, 637–647.
- Clark, A.B. & Wilson, D.S. (1981). Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.*, 56, 253–277.
- Cotton, P.A., Wright, J. & Kacelnik, A. (1999). Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am. Nat.*, 153, 412–420.
- Drummond, H., González, E. & Osorno, J.L. (1986). Parent-offspring cooperation in the blue-footed booby (*Sula nebouxi*): social roles in infanticidal brood reduction. *Behav. Ecol. Sociobiol.*, 19, 365–372.
- Forbes, L.S. (1994). The good, the bad and the ugly: Lack's brood reduction hypothesis and experimental design. *J. Avian Biol.*, 25, 338–343.
- Godfray, H. (1991). Signalling of need by offspring to their parents. *Nature*, 352, 328–330.
- Godfray, H.C.J. & Johnstone, R.A. (2000). Begging and bleating: the evolution of parent-offspring signalling. *Philos. T. Roy. Soc. B.*, 355, 1581–1591.
- Guillon, G.W. (1950). Voice differences between sexes in the American Coot. *The Condor*, 52, 272–273.
- Horsfall, J.A. (1984). Brood reduction and brood division in coots. *Anim. Behav.*, 32, 216–225.
- Johnstone, R.A. (1996). Begging signals and parent-offspring conflict: do parents always win? *Proc. Roy. Soc. B.*, 263, 1677–1681.
- Kilner, R.M. & Hinde, C.A. (2008). Information warfare and parent-offspring conflict. *Adv. Stud. Behav.*, 38, 283–336.
- Kloskowski, J. (2001). Temporal patterns of parental resource distribution in the red-necked grebe: equalizing the share of the survivors. *Behaviour*, 138, 1355–1370.
- Krebs, E.A., Cunningham, R.B. & Donnelly, C.F. (1999). Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. *Anim. Behav.*, 57, 753–763.
- Lack, D. (1947). The significance of clutch-size. *Ibis*, 89, 302–352.
- Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Leonard, M., Horn, A. & Eden, S. (1988). Parent-offspring aggression in moorhens. *Behav. Ecol. Sociobiol.*, 23, 265–270.
- Leonard, M., Horn, A. & Ratcliffe, L. (1991). Parental aggression in black-capped chickadees. *Behav. Ecol.*, 2, 228–233.
- Lessells, C.M. (2002). Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philos. T. Roy. Soc. B.*, 357, 381–403.
- Liang, K.Y., Self, S.G. & Liu, X.H. (1990). The Cox proportional hazards model with change point: an epidemiologic application. *Biometrics*, 46, 783–793.
- Lloyd, D.G. (1987). Selection of offspring size at independence and other size-versus-number strategies. *Am. Nat.*, 129, 800–817.
- Lyon, B.E. (1993). Conspecific brood parasitism as a flexible female reproductive tactic in American coots. *Anim. Behav.*, 46, 911–928.
- Lyon, B.E. (1994). A technique for measuring precocial chicks from photographs. *Condor*, 96, 805–809.
- Magrath, R.D. (1990). Hatching asynchrony in altricial birds. *Biol. Rev.*, 65, 587–622.
- Mock, D.W. (1984). Siblicidal aggression and resource monopolization in birds. *Science*, 225, 731–733.
- Mock, D.W. (1994). Brood reduction: narrow sense, broad sense. *J. Avian Biol.*, 25, 3–7.
- Mock, D.W. & Parker, G.A. (1986). Advantages and disadvantages of egret and heron brood reduction. *Evolution*, 40, 459–470.
- Mock, D.W. & Parker, G.A. (1997). *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.
- Mock, D.W., Dugas, M.B. & Strickler, S.A. (2011). Honest begging: expanding from signal of need. *Behav. Ecol.*, 22, 909–917.
- Nonacs, P. (2000). Measuring and using skew in the study of social behavior and evolution. *Am. Nat.*, 156, 577–589.
- Parker, G.A., Royle, N.J. & Hartley, I.R. (2002). Intrafamilial conflict and parental investment: a synthesis. *Philos. T. Roy. Soc. B.*, 357, 295–307.
- Ploger, B.J. & Mock, D.W. (1986). Role of sibling aggression in food distribution to nestling cattle egrets (*Bubulcus ibis*). *Auk*, 103, 768–776.
- Pons, O. (2003). Estimation in a Cox regression model with a change-point according to a threshold in a covariate. *Ann. Stat.*, 31, 442–463.
- Price, K., Harvey, H. & Ydenberg, R. (1996). Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim. Behav.*, 51, 421–435.
- Raihani, N.J. & Ridley, A.R. (2008). Parental aggression against dependent young results in task partitioning in a cooperatively breeding bird. *Biol. Lett.*, 4, 23–26.
- Reed, W. & Vleck, C. (2001). Functional significance of variation in egg-yolk androgens in the American coot. *Oecologia*, 128, 164–171.
- Reed, W.L., Clark, M.E. & Vleck, C.M. (2009). Maternal effects increase within-family variation in offspring survival. *Am. Nat.*, 174, 685–695.
- Ryan, M.R. & Dinsmore, J.J. (1979). A quantitative study of the behavior of breeding American coots. *Auk*, 96, 704–713.
- Schwabl, H., Mock, D.W. & Gieg, J.A. (1997). A hormonal mechanism for parental favouritism. *Nature*, 386, 231–231.
- Shizuka, D. & Lyon, B.E. (2010). Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature*, 463, 223–226.
- Slagsvold, T. (1997). Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Anim. Behav.*, 54, 1357–1368.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, O. & Husby, M. (1984). On the adaptive value of intraclutch egg-size variation in birds. *Auk*, 101, 685–697.
- Smith, C.C. & Fretwell, S.D. (1974). The optimal balance between size and number of offspring. *Am. Nat.*, 108, 499–506.
- Stamps, J., Clark, A., Arrowood, P. & Kus, B. (1985). Parent-offspring conflict in budgerigars. *Behaviour*, 94, 1–40.
- Stenning, M.J. (1996). Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trend. Ecol. Evol.*, 11, 243–246.
- Stoleson, S.H. & Beissinger, S.R. (1997). Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecol. Monogr.*, 67, 131–154.
- Trivers, R.L. (1974). Parent-offspring conflict. *Am. Zool.*, 14, 249–264.

Editor, John Fryxell

Manuscript received 23 October 2012

Manuscript accepted 30 October 2012