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Asymmetric sibling rivalry and nestling growth in red-winged blackbirds (*Agelaius phoeniceus*)

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Abstract Many birds hatch their offspring asynchronously, and the adaptive significance of this trait, if any, is controversial. David Lack suggested long ago that by facilitating brood reduction when resources are scarce, hatching asynchrony provides relief from the effects of overcrowding. Some field workers interpret this to mean that the growth and survival of survivors should rise following partial brood loss. Here we show in a 6-year study of red-winged blackbirds (*Agelaius phoeniceus*) that the presence or absence of marginal offspring in experimentally manipulated broods had virtually no effect upon the growth of core offspring, whereas alterations of the size of core brood had strong and significant effects. Nestling growth was, not surprisingly, slower in broods with partial brood loss. Intriguingly, marginal offspring showed significantly greater variation in mass. Core offspring are less sensitive to, but not exempt from, the inimical effects of resource shortfall than are marginal offspring. The phenotypic handicap appears to marginal offspring a caste of high-variance progeny whose fitness prospects rest upon levels of parental input (stochastic resources) and the size of the core brood (stochastic development).

Keywords Parental optimism · Sibling rivalry · Hatching asynchrony · Brood reduction · Blackbird

Introduction

Parent birds routinely hatch their offspring asynchronously, imposing a phenotypic handicap upon one or more of their offspring (Mock 1984; Magrath 1990; Stoleson and Beissinger 1995). Early hatched or "core" nestlings (sensu Mock and Forbes 1995) generally enjoy superior prospects for growth and survival than their later-hatched "marginal" siblings. Whether hatching asynchrony is adaptive, or simply a side consequence of other selective processes, has been hotly debated by avian ecologists (Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995; Amundsen and Slagsvold 1996; Stenning 1996). A focal point for this controversy has been David Lack's (1947) "brood reduction" hypothesis. Lack suggested that hatching asynchrony allowed parents to trim the brood efficiently during unpredictable periods of resource scarcity, while allowing them to rear additional offspring during times of plenty.

One robust prediction to emerge from the brood reduction literature is that partial brood loss should provide relief to the survivors. There is little that is controversial in this statement. But when? Some field workers assert that for brood reduction to be adaptive, the growth and survival of the remaining nestlings must rise following the death of a nestling (Stouffer and Power 1991; Hillström and Olsson 1994; Stoleson and Beissinger 1997). Or does the principle value of hatching asynchrony accrue before the onset of brood reduction by establishing the preconditions for differential resource allocation? Theory predicts that older, stronger siblings will command a disproportionate food share at the expense of their younger nestmates (Parker et al. 1989; Forbes 1993; Mock and Parker 1997). As a direct consequence, core sibs will enjoy both higher and less variable fitness prospects than marginal offspring. Within the framework of "parental optimism" (sensu Mock and Forbes 1995), parents play favourites as a hedge against ecological and developmental uncertainty. The core nestlings are the "blue chip" members of the brood, whereas the marginal nestlings are a caste of potentially expendable offspring: their fate rests upon ecological and developmental contingency, e.g. whether core offspring fail and/or prevailing resource levels (Mock and Forbes 1995; Forbes and Lamey 1996; Forbes et al. 1997; Forbes and Mock 1998, 2000).

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This logic is similar to Lack's (1947) original argument but differs in one key respect. It is not brood reduction, per se, that is adaptive, but rather differential resource allocation and the system it creates – in effect two-track offspring. To borrow an academic analogy: core offspring are effectively tenured, marginal offspring are probationary appointments that may be tenured depending upon ecological conditions. When resources are scarce, and/or all core offspring survive, marginal offspring have their appointments terminated by brood reduction.

How does this view differ from the conventional adaptive brood reduction? Under the logic of parental optimism, brood reduction is symptomatic of weakness in the family economy. Indeed, brood reduction arises as an emergent property of differential resource allocation coupled to scare resources. The death of an offspring does not, in fact, free additional resources for the remaining brood members, but simply keeps bad conditions from growing worse. Under conventional brood reduction, the death of an offspring should result in an immediate boost to the survivors (Stouffer and Power 1991; Hillström and Olsson 1994; Stoleson and Beissinger 1997) whereas under parental optimism, core offspring receive their benefit via differential resource allocation. To again use an academic analogy, the tenured offspring receive higher salaries (=growth and fitness) from the outset: the termination of marginal offspring does not result in a further increase in the salaries of core offspring. Under adaptive brood reduction, however, termination of marginal offspring would result in a salary increase for core offspring: in short, the direction of causality is reversed from the logic of parental optimism.

Here we present the results of a 6-year study of the growth performance of core and marginal red-winged blackbirds (*Agelaius phoeniceus*) in relation to experimental alterations of brood size. We show that: (1) the phenotypic handicap of hatching asynchrony creates an effective buffer – albeit incomplete – for core offspring that protects them, but not marginal offspring, from the inimical effects of resource shortfall, and (2) brood reduction arises as an emergent property of scarce resources and differential resource allocation.

Methods

We studied red-winged blackbirds nesting in wetlands near Winnipeg, Manitoba, from 1993 to 1998. Nests were followed from the time of discovery, usually during nest-building, until the eldest nestlings reached 10 days of age, just prior to fledging. At this point, marginal nestlings hatching 2 days after core nestlings were 8 days of age. Each nest was censused daily; eggs and nestlings were marked for individual identification. Broods where one or more nestlings died before reaching 8 days of age were considered to have undergone partial brood loss; broods where all nestlings disappeared simultaneously, usually due to predation, were excluded from this sample. Nestlings were weighed between 0600 and 1500 hours CST to the nearest 0.1 g with portable electronic balances; Pesola spring balances, accurate to 0.5 g, were used as back-ups. Nestlings were handled lightly before weighing to induce them to release fecal sacs.

The mean clutch size between 1993 and 1998 ranged from 3.72 to 4.11 $\bar{x}$=3.92 eggs/clutch per year, SE=0.05, *n*=7 years, 749 clutches). The modal clutch size was four (65.8% of 553 clutches, range 2–6), and the first two laid eggs almost always hatched (~99% of all four-egg clutches) on the same day, and thus were designated "core" eggs; the last-laid egg in clutches of four or more almost always hatched 1 or more days later, and was designated as a marginal egg. In experimentally manipulated clutches, third-laid eggs were assigned as core or marginal based upon when the nestling hatched in the foster nest, ensuring in the manipulations that an incubated egg was not transferred into a nest where incubation had not commenced.

Most broods hatched asynchronously in our population. For 210 broods where four eggs hatched, 8.1% hatched synchronously (over 0 days), 41.9% hatched over 1 day, 43.3% hatched over 2 days, and 6.7% hatched over 3 or more days. The average brood size at hatching ranged from 3.46 to 3.71 nestlings; ($\bar{x}$=3.57 nestlings/brood per year, SE=0.41, *n*=7 years, 462 broods). Substantial partial brood loss occurred in the population, as the number of 8-day-old nestlings/brood (an approximate index of fledging success) ranged from 2.50 to 3.06 nestlings; ($\bar{x}$=2.77 nestlings/brood per year, SE=0.08, *n*=7 years, 367 broods).

Nestling red-winged blackbirds compete non-aggressively for food items that are delivered primarily by the parent female; in our population, males contributed occasionally to the feeding of older broods. Nestlings fledge when 10–12 days of age, and are sexually dimorphic with males substantially larger than females.

Experimental design

We experimentally enlarged or reduced the core or marginal brood by transferring eggs across clutches, usually within a day of laying. In a small number of cases, broods were enlarged or reduced by moving a chick on the day of hatching. By moving eggs, our intent was to maximize the effect of the manipulation on nestling growth.

To avoid pseudoreplication (Hurlbert 1984), we assessed growth performance based upon brood means for 5-day-old core or marginal nestlings whenever there was more than one nestling in either category. Masses were standardized to mass at 1200 hours to correct for time-of-day differences. We used day 5 mass as the performance measure for five reasons. First, it represents the end of the ectothermic phase of the nestling period (Olson 1992), an obvious developmental landmark. Second, it represents the onset of sexually dimorphic growth (Holcomb and Twiest 1970), where growth performance is complicated by the diverging trajectories of male and female nestlings. Third, mass at day 5 is highly correlated with the mass of older nestlings (see below). Fourth, it represents a simple, interim point estimate of growth performance that is easier to interpret than growth curves, which are non-linear and in our population did not reach an asymptote while we could collect still growth measurements (nestlings 8–10 days of age). And fifth, whole-brood loss due to predation was relatively common in this population; thus, using day 5 masses allows for larger sample sizes than growth measured closer to fledging age.

We used nestling mass as a proxy for fitness in our study, which we believe a reasonable assumption. Earlier experimental work on red-winged blackbirds has established a positive relationship between fledging mass and subsequent survival (Hengeveld 1989; see Magrath 1991 for a general review of the relationship between nestling mass and survival).

Results

We computed the correlations between the mass of nestlings at day 5 and at day 8. The data were subdivided into males and females, and core and marginal nestlings, and to avoid the potential for pseudoreplication, brood

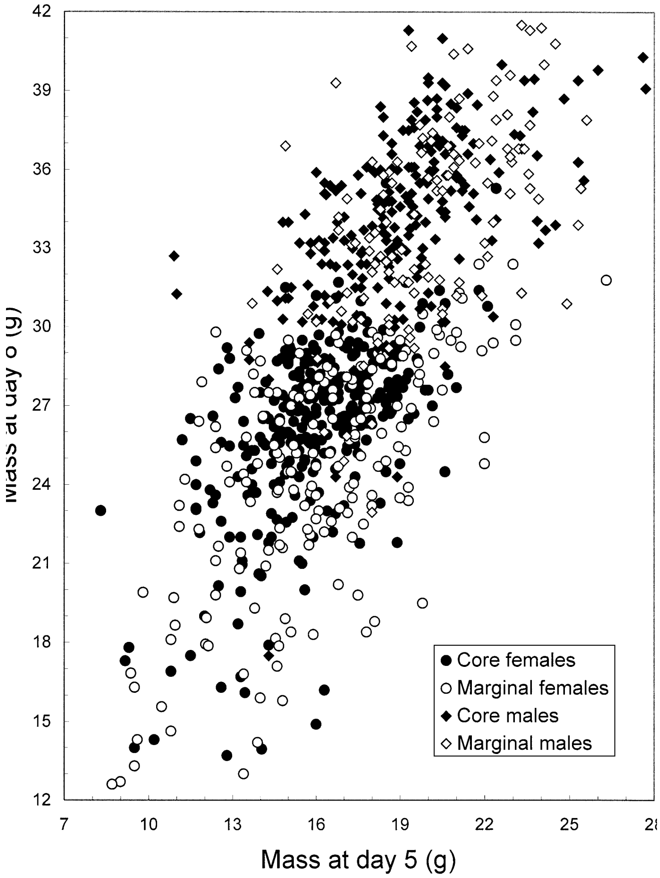

Fig. 1 Relationship between the mass (g) of a nestling red-winged blackbird (*Agelaius phoeniceus*) at 5 days of age, and its subsequent mass at 8 days of age. The data for core males (n=236), core females (n=325), marginal males (n=118), and marginal females (n=178) are shown

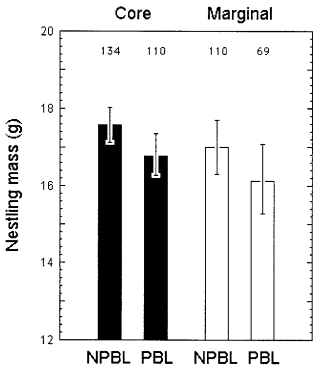

Fig. 2 Average mass of 5-day-old core (*black bars*) and marginal (*open bars*) nestling red-winged blackbirds in unmanipulated broods with partial brood loss (*PBL*) and no partial brood loss (*NPBL*). *Vertical lines* show 95% confidence intervals. Sample sizes are shown above bars

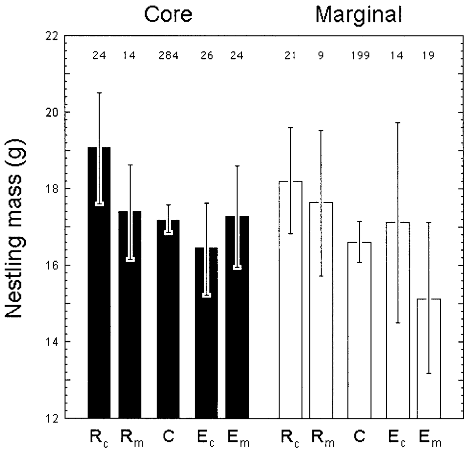

Fig. 3 Average mass of 5-day-old core (*black bars*) and marginal (*open bars*) nestling red-winged blackbirds in relation to experimental treatment. R_c and R_m indicate reductions of core and marginal brood, respectively; E_c and E_m indicate enlargement of the core and marginal brood, respectively; *C* indicates unmanipulated control broods. *Vertical lines* indicate 95% confidence limits. Sample sizes are shown above bars

means were taken when more than one nestling of one type was found in a brood (e.g. core males). The data are presented in Fig. 1 and all correlations were significant (P<0.01): core males: r=0.590, marginal males: r=0.536, core females: r=0.603, marginal females: r=0.670)

We compared the average mass of core and marginal nestlings in unmanipulated broods with and without partial brood loss on or before marginal nestlings reached 8 days of age (Fig. 2). Core nestlings in broods without partial brood loss were heavier than those in broods experiencing partial brood loss (F=4.795, df=1, 242, P=0.029); a similar but statistically weaker trend was observed for marginal nestlings (F=2.267, df=1, 177, P=0.134; $1-\beta=0.322$) where we note that the power of the test was low even though the sample size was very large. Part of the reason for the lack of a significant effect here likely stems from the fact that marginal offspring showed greater variability in mass. This also reveals a biologically interesting point. Bartlett's test (Walpole 1968) revealed that there was significant heterogeneity in the variances of the four samples in Fig. 2 (core nestlings – no partial brood loss: S^2=6.636, n=134; partial brood loss: S^2=8.214, n=110; marginal nestlings – no partial brood loss: S^2=13.687, n=109; partial brood loss: S^2=14.430, n=68; Bartlett's b-statistic=22.79, df=3, P<0.001). From inspection of the data, the primary difference clearly exists between core and marginal offspring. Marginal offspring were, evidently, substantially more variable in mass than core nestlings in both manipulated and unmanipulated broods.

One-way analysis of variance indicated that the mass of 5-day-old core nestlings varied significantly across experimental groups (F=2.912, df=4,360, P=0.022; Fig. 2). Pairwise post hoc comparisions, using a Bonferroni adjustment for multiple comparisons, revealed that only manipulations involving the core brood (enlargement and reduction) had any effect on the average mass of core nestlings: the control group differered only from core reductions (P=0.018); the core addition group differed only from the core reduction group (P=0.027), and the core reduction group differed only from the control and core addition groups. Manipulating the marginal brood had virtually no effect on nestling mass (Fig. 3).

One-way analysis of variance indicated a weaker, non-significant effect of experimental manipulation on the mass of 5-day-old marginal nestlings, (F=1.823, df=4,257, P=0.125; Fig. 3), which is perhaps attributable to smaller sample sizes and greater variance for marginal nestlings resulting in a low-power test ($1–\beta$=0.55). Post hoc pairwise comparisons (Bonferonni corrected) revealed no significant differences.

Discussion

Is brood reduction adaptive? Some have suggested that it is not, based on the inferior growth performance of broods experiencing partial brood loss relative to broods where all nestlings survive (Stouffer and Power 1991; Hillström and Olsson 1994; Stoleson and Beissinger 1997), as was the case here. But this simple comparison of growth is potentially confounded by differences in provisioning rates across broods, e.g. due to differences in territory or parental quality, random effects, and/or short-term differences in resource availability (see Amundsen and Slagsvold 1996 for a cogent discussion). And from a mechanistic point of view, we expect more frequent brood reduction when provisioning is deficient.

But if by adaptive we mean that the surviving offspring in broods experiencing brood reduction are better off than they would have been had it not occurred, then this question cannot be usefully addressed from non-experimental data. The appropriate protocol is to experimentally replace victims of brood reduction within the brood, as Husby (1986) and Hengeveld (1989) have done. Their results were clear-cut: replacement resulted in reduced growth and elevated mortality of nestlings and/or fledglings, i.e. brood reduction kept a bad situation from getting worse.

But here we argue that the phenotypic handicap – hatching asynchrony – is not designed to facilitate brood reduction per se, but rather to keep the costs of rearing marginal offspring low. According to resource allocation theory (Parker et al. 1989; Forbes 1993; Mock and Parker 1997), a brood hierarchy ensures that marginal offspring will only be reared after the needs of senior sibs have been satisfied. Brood reduction simply arises as a side consequence of differential resource allocation and deficient levels of provisioning. Our results support this view strongly. The presence or absence of marginal offspring had virtually no effect on the growth of core nestlings in red-winged blackbirds. Earlier work in the same system (Forbes et al. 1997) revealed a parallel pattern for nestling mortality. The presence or absence of core nestlings, however, did have strong effects on the growth of core nestlings (Fig. 3), and modest effects on survival (Forbes et al. 1997). Not surprisingly, brood reduction was more frequent in broods with lower growth (Fig. 3).

Thus our results are consistent with “cascade” models of within-brood resource allocation (the hierarchy model of Parker et al. 1989; see also Mock and Parker 1997; the despotic allocation model of Forbes 1993). Parental resources are channeled into the brood hierarchy – established here by hatching asynchrony – allowing the dominant, senior sibs (the core brood) first access; the marginal offspring then receive the residual food share. This provides a tidy explanation for why the addition of core, but not marginal offspring influenced the growth of core nestlings. Marginal nestlings only received resources when the needs of core sibs were, evidently, satisfied. Thus hatching asynchrony “assures the quality” of at least a portion of the brood as Slagsvold (1986) originally suggested (see also Amundsen and Slagsvold 1996).

But does the phenotypic handicap of hatching asynchrony exempt core offspring from the inimical effects of food shortfall? The average mass of core nestlings in broods with partial brood loss fell below those in broods without loss (Fig. 2), a result consistent with earlier studies (Stouffer and Power 1991; Hillström and Olsson 1994; Stoleson and Beissinger 1997). Does this result conflict with theory? Both game-theoretical models of hierarchical resource allocation among siblings predict this effect (Parker et al. 1989; Forbes 1993). Both are based upon permutations of Hamilton’s rule. When food supplies decline, the fitness of the senior members of the hierarchy falls – in this case the core siblings. The key prediction is that the fitness of marginal siblings falls faster; food shortfalls impact them disproportionately. Partial brood loss arises as an emergent property of food shortfall and hierarchical resource allocation, and under hierarchical food allocation, core offspring are less sensitive to the effects of food shortfall, as can be seen from their higher growth rates (this study) and lower mortality (Forbes et al. 1997), than marginal offspring.

Overall, our results provide further empirical support for what we call the principle of asymmetric sibling rivalry. Within-brood phenotypic handicaps cosset a portion of the brood from developmental uncertainty (Mock and Forbes 1995). As a consequence, parents are left with a caste of “low-variance” progeny – the core brood – whose prospects for growth and survival are *relatively* secure, and a caste of “high-variance” progeny – the marginal offspring – whose fitness prospects rest upon ecological and developmental contingency (Mock and Forbes 1995; Forbes et al. 1997).

To return to the academic analogy developed at the outset, core offspring receive their benefit – effective “tenure” within the brood and all of the benefits associated with that status (superior prospects for growth and fitness) – simply by hatching first. The probationary marginal offspring, however, face a greater and somewhat arbitrary challenge: their future depends upon the current family economy, which in turn is influenced both by intrinsic (the number of core offspring), and extrinsic (levels of parental input) conditions. Brood reduction does not function to increase the growth and fitness (=salaries) of core offspring, but rather prevents future decreases. Under this view, brood reduction is not functional at all, but arises simply as an epiphenomenon of a system of differential resource allocation. Unaffordable marginal offspring become expendable and have their "appointments" terminated by brood reduction.

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