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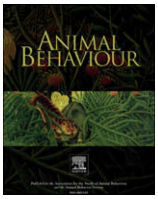

Asynchronous hatching in burying beetles: a test of the peak load reduction hypothesis

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The evolution of asynchronous hatching is a central yet controversial issue in evolutionary ecology and animal behaviour. Although asynchronous hatching has a widespread taxonomic distribution, past research has focused almost exclusively on altricial birds. We tested the peak load reduction hypothesis for the evolution of asynchronous hatching in the burying beetle *Nicrophorus vespilloides*, an insect in which parents provide their offspring with food after hatching. This hypothesis posits that caring parents benefit from asynchronous hatching because it reduces the parent's maximum workload during the peak in the offspring's demand for food. To test this hypothesis, we established three types of broods, synchronous, asynchronous and highly asynchronous, with a hatching span of 0, 24 and 48 h, respectively, and monitored effects on brood demand and female parental care. As expected, there were sharp peaks in both brood demand and female food provisioning, and the peak in brood demand decreased as a function of increasing levels of asynchronous hatching. However, in contrast to what we expected, the peak in female food provisioning was similar regardless of the level of asynchronous hatching, and offspring survival was substantially lower in highly asynchronous broods than in synchronous or asynchronous broods. We conclude that our results provide no overall support for the peak load reduction hypothesis. Further experiments are needed to establish the adaptive benefits of asynchronous hatching in this species.

Asynchronous hatching occurs when offspring from a particular reproductive event hatch or are born over several days (Stoleson & Beissinger 1995). Although asynchronous hatching has been reported in a wide range of taxa, including reptiles (While et al. 2007), amphibians (Ryan & Plague 2004), elasmobranchs (Gilmore 1993) and insects (Nalepa 1988; Smiseth et al. 2006), past research has focused almost extensively on altricial birds where parents provide their offspring with food after hatching (Lack 1947, 1954; Magrath 1990; Stoleson & Beissinger 1995; Stenning 1996). In altricial birds, asynchronous hatching is caused by the onset of incubation before the completion of the clutch, often resulting in the establishment of an age-based competitive hierarchy, within which the youngest nestling typically faces an increased risk of starvation before or after fledging (Magrath 1990; Stoleson & Beissinger 1995; Mock & Parker 1997). A major aim in avian ecology has been to understand how selection might favour asynchronous hatching despite the elevated mortality risk to the youngest nestling (Magrath 1990; Stoleson & Beissinger 1995; Stenning 1996). Despite decades of research, no consensus has been reached as to why asynchronous hatching may have evolved in altricial birds (Magrath 1990; Stoleson & Beissinger 1995; Stenning 1996).

There are currently at least 17 hypotheses for the evolution of asynchronous hatching in altricial birds (Stoleson & Beissinger 1995). One main group of hypotheses suggest that asynchronous hatching provides adaptive benefits by (1) reducing the parent's workload during the peak in the offspring's demand for food (Hussell 1972), (2) providing an effective mechanism for brood reduction when resources are limited (Lack 1947, 1954), (3) reducing the costs of sibling competition (Hahn 1981), (4) facilitating the elimination of last-laid eggs produced as insurance in case first-laid eggs fail to hatch (Stinson 1979), or (5) allowing female parents to increase the workload of their male partners (Slagsvold & Lifjeld 1989). Another main group of hypotheses explain asynchronous hatching as a by-product of selection for the early onset of incubation in order to (1) protect eggs from predation (Clark & Wilson 1981), (2) deal with limited breeding opportunities (Beissinger & Waltman 1991), (3) increase egg viability (Arnold et al. 1987), (4) increase egg protection (Beissinger et al. 1998), or (5) reduce brood parasitism (Kendra et al. 1988). It has proved difficult to distinguish between these hypotheses in altricial birds because of the close relationship between the onset of incubation and asynchronous hatching (Magrath 1990; Stoleson & Beissinger 1995).

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One way to advance our understanding of the evolution of asynchronous hatching is to extend research to nonavian species where asynchronous hatching is uncoupled from incubation of eggs. Such systems have been identified in the burying beetle *Nicrophorus vespilloides* (Smiseth et al. 2006, 2008) and White's skink, *Egernia whitii* (While et al. 2007; While & Wapstra 2008). *Nicrophorus vespilloides* provides a particularly valuable system because, as in altricial birds, parents provide their offspring with food after hatching (Eggert et al. 1998). This species breeds on carcasses of small vertebrates, which provide the sole source of food for the developing larvae (Pukowski 1933; Eggert & Müller 1997; Scott 1998). Females lay eggs in the soil near the carcass over a mean period of 27–30 h (range 8–56 h; Müller & Eggert 1990; Smiseth et al. 2006). Thus, asynchronous hatching in this species is caused by an extended period of egg laying (Smiseth et al. 2006). Upon hatching, the larvae crawl to the carcass, where they beg for predigested carrion from their parents until reaching nutritional independence at the age of 72 h (Smiseth et al. 2003). A recent study demonstrated plasticity in asynchronous hatching in relation to resource availability, suggesting that asynchronous hatching is adaptive rather than the by-product of physiological constraints on egg laying (Smiseth et al. 2008). Furthermore, asynchronous hatching has important adaptive consequences as it affects larval begging (Smiseth & Moore 2007; Smiseth et al. 2007), parental food allocation (Smiseth et al. 2007; Smiseth & Moore 2008) and larval survivorship (Smiseth et al. 2008). However, there is currently no information on the adaptive benefits of asynchronous hatching to *N. vespilloides* parents.

The peak load reduction hypothesis is relevant for species with sharp peaks in the offspring's demand for food (Hussell 1972; Mock & Schwagmeyer 1990), such as *N. vespilloides*, in which larval begging and parental food provisioning peak sharply about 24 h after hatching (Smiseth et al. 2003, 2007). The peak load reduction hypothesis suggests that asynchronous hatching provides the parents with a means of saving energy by spreading out and thus reducing the peaks in the offspring's demands and the parents' workload (Hussell 1972; Mock & Schwagmeyer 1990; Wiebe & Bortolotti 1994). Theoretical considerations suggest that the energy savings to caring parents from asynchronous hatching are greatest in species with large broods and large hatching intervals (Mock & Schwagmeyer 1990). *Nicrophorus vespilloides* has an average brood size of 21 larvae (Smiseth & Moore 2002), and an average hatching span of 27–30 h (Müller & Eggert 1990; Smiseth et al. 2006), which is considerable given that the larvae have reached nutritional independence by the age of 72 h (Smiseth et al. 2003). Thus, the peak load reduction hypothesis provides a plausible adaptive explanation for the evolution of asynchronous hatching in *N. vespilloides*.

To test the peak load reduction hypothesis, we generated experimental broods with the same number of larvae but with three levels of asynchronous hatching: synchronous, asynchronous and highly asynchronous broods with a hatching span of 0, 24 and 48 h, respectively. We then monitored effects on brood demand and female parental care at 24 h intervals throughout the period when the larvae depend on their parents for food. We first verified the presence of sharp peaks in brood demand and female parental care by testing whether and how these behaviours changed over time. We next tested whether the changes in brood demand and parental care over time depended on the level of asynchronous hatching, and whether the peaks in brood demand and parental care decreased as a function of increasing levels of asynchronous hatching. Finally, we tested for adaptive consequences of the level of asynchronous hatching to the parents. Although *N. vespilloides* will breed repeatedly when given access to additional resources, suitable resources are extremely limited in the wild (Scott 1998). Thus, adaptive benefits derived from the current reproductive event may be more important to the parents than benefits derived from future reproductive events. Consequently, we tested for effects of asynchronous hatching on the survival and growth of larvae from the current reproductive event.

METHODS

Origins and Husbandry of Beetles

The adult beetles used in the experiments were from an outbred laboratory population derived from over 100 wild-caught females trapped in deciduous woodland at Sunbank Wood, Manchester, U.K. Laboratory-bred beetles were kept individually in transparent plastic containers (17 × 12 cm in area and 6 cm high) under a 16:8 h light:dark cycle at 20 ± 1 °C. The beetles were fed scraps of meat twice a week.

Experimental Procedures

We randomly selected pairs of nonsibling virgin male and female beetles for use in the experiment. Once pairs had been selected, they were moved to a new container filled with 2 cm of moist soil. We provided each pair with a previously frozen mouse carcass (range 20–25 g) supplied from Livefoods Direct Ltd, Sheffield, U.K.

Approximately 60 h after a pair had been set up for breeding, the female was transferred to a new container along with the carcass. The male was removed at this stage because male care has no effect on larval growth or survival under laboratory conditions (Smiseth et al. 2005). The eggs were left to hatch in the old container, which was searched for newly hatched larvae four times each day. Although these larvae would have hatched over a period of about 4 h, they gained access to food and started growing at the same time (i.e. when placed on a carcass). We used the newly hatched larvae to generate synchronous, asynchronous and highly asynchronous broods with a hatching span of 0, 24 and 48 h, respectively. We generated synchronous broods by placing 20 larvae simultaneously with a female, asynchronous broods by providing a female with 10 larvae followed by another 10 larvae 24 h later, and highly asynchronous broods by providing a female with 10 larvae followed by another 10 larvae 48 h later. Thus, we set up the asynchronous and highly asynchronous broods such that they comprised two separate age classes with an equal number of larvae. This design is similar to previous designs used to study the effects of asynchronous hatching on larval begging (Smiseth & Moore 2007, Smiseth et al. 2007) and parental food allocation (Smiseth et al. 2007; Smiseth & Moore 2008). However, hatching in natural broods occurs continuously and is highly biased towards the early part of the hatching period (Smiseth et al. 2006). In other respects, the treatments were well within the natural variation for asynchronous hatching (mean 30; range 8–56 h; Müller & Eggert 1990; Smiseth et al. 2006) and brood size (mean 21 larvae; range 2–47 larvae; Smiseth & Moore 2002) in this species. Because broods hatch asynchronously, we could generate our experimental broods only by mixing larvae of different females. We therefore always generated broods of mixed maternity by picking larvae at random from the pool of all available newly hatched larvae. Müller & Eggert (1990) found that parents do not distinguish between their own and foreign larvae when these appear on the carcass at the same time, but that parents kill larvae arriving before their own brood hatch. We therefore provided females with an experimental brood only after their own eggs had started hatching.

Behavioural Observations

We conducted observations at 24 h (±15 min) intervals, starting 1 h after the larvae were placed on the carcass (to avoid