



Minutes matter: brief hatching asynchrony adversely affects late-hatched hihi nestlings, but not life beyond the nest



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Size hierarchies are often seen when nestlings hatch asynchronously over a period of days. Shorter hatch periods are common across passerines, however, and while these may also give rise to asymmetries, their effects are rarely considered. Regardless of hatch period, the long-term consequences for later hatched nestlings that survive to fledge is unknown for wild birds. Here we explored the timing of hatch order in a free-living population of hihi nestlings, *Notiomystis cincta*, and followed any effects in and out of the nest. We found that while hatching time from first- to last-hatched nestlings was often less than 24 h, last-hatched individuals grew more slowly and were lighter and smaller at fledging than older siblings. Last-hatched nestlings were also less likely to fledge. These effects were greater in larger broods. Adult body size is correlated with fledging size in hihi; however, we found no evidence that hatch order affected longevity postfledging, or lifetime reproductive success. We then explored whether carotenoid availability might buffer these stressful rearing conditions (through food supplementation of parents) but found no evidence that increased access to carotenoids for mothers and/or growing nestlings influenced incubation schedules, or the effects of hatching late. Together these results suggest that while even a very short hatch period can influence adult phenotype, hatching asynchrony is not maladaptive for hihi: when last-hatched nestlings survive to fledge they can contribute as much to their mothers' fitness as first-hatched siblings.

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Sequential hatching of avian young driven by early onset of incubation (hatching asynchrony) often establishes size hierarchies within broods (Stokland & Amundsen, 1988; Wiklund, 1985). This can leave younger, smaller chicks at a disadvantage from sibling competition (Mock & Parker, 1997) if parents feed larger offspring preferentially (Rodríguez-Gironés et al., 2002), but hatching asynchrony can also be an adaptive strategy if it allows a mother to maximize the overall success of her brood (for example, through brood reduction to match unpredictable environments (Magrath, 1990; Stenning, 1996). While the effects of hatching asynchrony on life within the nest are well known, the long-term consequences of hatch order on life span or reproductive success are much less understood (Mainwaring, Blount, & Hartley, 2012), particularly for wild bird populations.

It is possible that the availability of specific nutrients may influence the potential for later hatched nestlings to catch up with

their elder siblings. Carotenoids, a class of antioxidants synthesized by plants and acquired by birds through their diet, may act as a buffer to natural stressors due to their ability to boost the immune system (Berthouly, Cassier, & Richner, 2008). In birds, carotenoids mitigate the effects of stress experimentally induced by increased sibling competition (Berthouly et al., 2008) and infestation with ectoparasites (Ewen et al., 2009). In both cases, when carotenoid concentration in eggs was increased by supplementing mothers, nestlings placed at a disadvantage from an increased brood size (Berthouly et al., 2008), or parasite infestation (Ewen et al., 2009), fared as well as nestlings from unmanipulated broods (un-supplemented nestlings fared the worst). As hatching later than siblings can increase the physiological stress levels of nestlings (de Boer, Eens, Franssen, & Müller, 2015; Costantini et al., 2006; Eraud, Trouvé, Dano, Chastel, & Faivre, 2008), carotenoids available in the nestling's diet could therefore counteract the negative effects of hatching late in a brood hierarchy.

Here we investigated whether size hierarchies observed in the hihi, *Notiomystis cincta*, are caused by sequential hatching driven by maternal incubation behaviour, and whether hatching later than siblings has long-term fitness consequences. We expected that

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early onset of incubation should result in more asynchronously hatching clutches, and that last-hatched nestlings should be smaller and grow more slowly than early hatched siblings. Body mass at fledging improves a hihi's chances of surviving its first year (Low & Pärt, 2009). Therefore, if the brood hierarchy order persists throughout the nestling period, it is likely to have long-term consequences for life span and reproductive success and not just survival to fledging, as is most commonly investigated due to the logistical challenges of tracking individuals throughout their lives.

In addition, we supplemented adult hihi with carotenoids throughout breeding (including incubation) to test whether increased availability of carotenoids to nestlings (either in eggs or also during nestling provisioning) compensates for any negative effects of late hatching. Previous research shows that carotenoids are an important dietary component for hihi nestlings, but that their effects appear to be compensatory: only when challenged by poor rearing conditions (ectoparasites) do nestlings hatched from carotenoid-rich eggs grow better (Ewen et al., 2009). This may be particularly important if brood hierarchies arise through factors other than differences in maternally driven incubation behaviour, for example, through limitation of other key egg components (Nager, Monaghan, & Houston, 2000). We therefore expected increased carotenoid availability to be most effective for nestlings in stressful conditions: those late in the hatching order.

METHODS

Supplementation Experiment and Data Collection

We studied a breeding population of hihi, a bird endemic to New Zealand and listed by the IUCN as Vulnerable (BirdLife International, 2013), on Tiritiri Matangi Island, a 220 ha island about 25 km north of Auckland. This population is part of a conservation project, with supplementary food (sugar water) and nestboxes provided across the island. Resighting surveys were conducted each year in February (postbreeding) and in September (prebreeding) between February 2005 and February 2015, providing 21 capture occasions (for further details see Thorogood, Armstrong, Low, Brekke, & Ewen, 2013). Hihi breed between October and March, producing clutches of, on average, four eggs (this data set, 4.21 ± 0.69 eggs), which hatch into broods of, on average, three nestlings (this data set, 3.23 ± 1.05 nestlings). Previous work has shown that carotenoid supplementation does not significantly influence these parameters (Ewen, Thorogood, Karadas, & Cassey, 2008). All breeding attempts were closely monitored so the parentage of all offspring that reach fledging age (30 days, blood-sampled at 21 days) could be determined via genotyping and assignment using Colony 2.0 software (Brekke, Ewen, Clucas, & Santure, 2015).

Our data were collected during the 2004–2005 and 2005–2006 breeding seasons (hereafter Seasons 1 and 2) as part of carotenoid supplementation experiments designed to investigate effects on maternal egg investment (Ewen, Surai, et al., 2006), parental provisioning of nestlings (Ewen et al., 2008) and effects of ectoparasites on nestling health (Ewen et al., 2009). Our supplementation regime differed between years, with females in 'Season 1' receiving supplementation from nest building to offspring fledging, whereas in 'Season 2', supplementation was stopped after completion of egg laying (Table 1). This allowed us to test any effect of carotenoid supplementation at different times during development. Breeding pairs were allocated to treatment or control groups once they settled on a nest site. Control pairs were provided with a supplementary food source (sugar water), while treatment pairs were provided with sugar water supplemented with carotenoids (lutein and zeaxanthin) at a concentration of 100 µg/ml (Ewen et al., 2008),

in both cases within 10 m of the nestbox. Hihi defend food resources in their territories, and food was provided ad libitum, so feeders were rarely used by either conspecifics or other nectarivorous species, nor did use of feeders differ between treatment groups (Ewen et al., 2008). Furthermore, supplementation of female hihi with carotenoids during laying has been shown to positively influence yolk carotenoid concentration (Ewen, Thorogood, Karadas, Pappas, & Surai, 2006), and supplementation of parents during nestling rearing increases circulating plasma carotenoid levels of both nestlings and parents (Thorogood et al., 2008; Thorogood, Ewen, & Kilner, 2011).

Hihi females lay one egg per day, and incubate for 14 days after clutch completion, but whether they begin incubation during laying (and therefore, whether they may adaptively adjust hatching synchrony) is unknown. Incubation behaviour was recorded in Season 2 using temperature loggers (Thermochron iButtons DS1921G, Maxim), which were inserted into the nest cup and secured around nest material either the day before or the day the first egg was laid. A second logger was attached inside the nestbox (20 cm from the nest cup) to record ambient temperature. Both loggers recorded temperature (°C) in 2 min intervals for up to 7 days. We counted the onset of incubation from the first night when the nest cup, but not box, temperature rose above 25 °C for more than 1 h (Cooper & Mills, 2005; Wang & Beissinger, 2009). This is 'physiological zero temperature', when embryonic growth begins (Wilson, 1990). Our measurement therefore recorded incubation effort in nights until clutch completion.

After 13 days of incubation (day final egg laid = day 1) nests were monitored to determine hatching order of each egg. Nests were visited in the late afternoon (after 1600 hours) on day 13, and then at no more than 2 h intervals from dawn until dusk on day 14. If any eggs remained intact by dusk on day 15 we checked only once more on day 16 before removing eggs for other analyses (Season 1, $N = 39$; Season 2, $N = 78$; Thorogood & Ewen, 2006): a small proportion of each clutch often fails to hatch due to unviability (Brekke, Bennett, Wang, Pettorelli, & Ewen, 2010; Thorogood & Ewen, 2006). From these checks the time between hatching events was recorded accurate to within 120 min.

Once nestlings hatched (day 0) they were marked on the tarsus using a permanent nontoxic marker pen. This identifier was refreshed every 2 days until nestlings were 21 days old, when birds were given numbered metal rings and plastic colour ring combinations as part of standard management practice to enable identification. Nestlings were weighed and the length of their tarsi measured (with Vernier callipers) throughout the nestling period (Table 1). Measurements were taken every 3 days until day 24, after which measurements ceased to avoid causing the premature fledging of offspring. Tarsus length does not change after 21 days so measurements at day 24 indicate adult tarsus length (Low, 2006).

For our analyses of the effects of hatch order (and mitigating effects of carotenoids), we restricted our data set to first clutches ($N = 82$ clutches); hihi sometimes produce second clutches in a season, but these often fail completely (Thorogood et al., 2011). We further restricted our data set to clutches that hatched at least two nestlings as by definition, broods of one cannot hatch asynchronously. Of these clutches, full data on mass and size were available for 167 nestlings from 64 nests, and full data on growth rate were available for 96 nestlings from 38 nests. Reported brood sizes represent brood size at hatching.

Statistical Analyses

Onset of incubation and hatching spread

To investigate whether hatching asynchrony is influenced by females' incubation behaviour, and to rule out the possibility that

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