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Incubation behaviour and hatching synchrony differ in wild and captive populations of the zebra finch

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Hatching asynchrony is widespread in birds laying clutches containing multiple eggs, yet is seemingly paradoxical as the age and size hierarchies result in asymmetric sibling competition and low survival prospects for late-hatched nestlings. We examined the causes of variation in hatching asynchrony between broods of zebra finch, *Taeniopygia guttata*, in three environments: domesticated, captive wild and wild free-living. We found that broods of both domesticated and wild birds taken into captivity hatched more asynchronously than wild free-living broods. This was directly attributable to both male and female parents of domesticated and captive wild broods initiating incubation as soon as the first egg was laid as opposed to when the clutch was virtually complete in wild free-living broods. Wild free-living birds that were transferred to captive environments immediately switched to the incubation onset behaviour seen in domesticated birds, thereby demonstrating a previously unsuspected level of intraspecific plasticity in incubation behaviour. This finding suggests that something about the captive environment is driving the early onset of incubation and contributing to an elevated level of hatching asynchrony in captive birds. Across all populations and environments males contributed almost equally to incubation, and the onset of incubation by males was highly coordinated with that of their partner.

Hatching asynchrony, whereby offspring from the same reproductive event are either born or hatch over an extended period of time, is taxonomically widespread, yet is seemingly an evolutionary paradox as it appears to result in the increased mortality of younger siblings (Magrath 1990; Stoleson & Beissinger 1995; While et al. 2007; Smiseth & Morgan 2009). Within avian broods, hatching asynchrony creates structured family units consisting of both early and late-hatched nestlings (Mock & Forbes 1995). It has been argued that early hatched nestlings represent the minimum number of nestlings that the parents are capable of rearing and exhibit little variation in survival and growth rates, while late-hatched nestlings are much more likely to be adversely affected by poor conditions during development and typically exhibit lower survival and growth rates within asynchronously hatched broods (Magrath 1990; Stoleson & Beissinger 1995). Furthermore, parents and offspring can facilitate the outcome of hatching asynchrony through parental provisioning rules and sibling competition, respectively (Royle et al. 2002).

The causes and consequences of hatching asynchrony within avian broods have been extensively studied and debated. Variation in hatching asynchrony between individuals within species is thought either to have evolved as a consequence of food availability or selection on faster reproductive cycles or to be a maladaptive consequence of selection for some other trait (Lack 1947; Clark & Wilson 1981; Magrath 1990; Stoleson & Beissinger 1995). There is a substantial amount of variation in hatching asynchrony between individuals within species (Wang & Beissinger 2009; Nord & Nilsson 2012). For example, both blue tit, *Cyanistes caeruleus*, and tree swallow, *Tachycineta bicolor*, broods hatch out over periods of 0–2 days (Nilsson & Svensson 1993; Ardia et al. 2006). The timing of the initiation of incubation is widely invoked as being the primary determinant of hatching asynchrony as, while unattended eggs are too cold to develop, the heat transferred to eggs from the brood patch of an incubating parent causes eggs to start developing (Magrath 1990; Stoleson & Beissinger 1995; Stenning 1996). The onset of incubation is influenced by a variety of factors, including maternal age, experience and body condition (Bortolotti & Wiebe 1993; Soler et al. 2001; Hanssen et al. 2002; Badyaev et al. 2003; Ardia et al. 2006; Ardia & Clotfelter 2007; Kim et al. 2010), social influences including the risk of intraspecific brood parasitism and mate attractiveness (Beissinger et al. 1998; Soler et al. 2001) and environmental factors such as ambient temperatures, precipitation, predation risk and food availability (Perrins 1991; Nilsson 1993; Wiebe & Bortolotti 1994; Ghalambora & Martin 2002; Eikenaar et al. 2003; Wang & Beissinger 2009; Arnold 2011). Another possible, but previously unexplored, determinant of intraspecific

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variation in incubation behaviour is the domestication process, because this has the capacity to change both the environment and, through artificial selection, the genes underlying incubation behaviour or broodiness.

Zebra finches, *Taeniopygia guttata*, are a good model species for examining maternal effects, hatching patterns and parental care because they tolerate a relatively high level of observational and experimental work under laboratory conditions (Griffith & Buchanan 2010a, b). As a result of this amenability, research into the effect of hatching asynchrony and other parental effects on offspring fitness has focused disproportionately on the domesticated zebra finch, a well-used laboratory system (Griffith & Buchanan 2010a, b). Indeed, many empirical studies on domesticated zebra finches report strong effects of a range of parental effects, including hatching order and patterns, on various components of offspring growth and development (e.g. Skagen 1988; Kilner 1998; Gil et al. 1999; Royle et al. 2003; Gorman & Nager 2004; Rutkowska & Cichoń 2005; Blount et al. 2006; Gilby et al. 2011a; Mainwaring et al. 2011, 2012). Previous studies have shown that domesticated zebra finch broods hatch out over periods of up to 4 days, which creates size hierarchies that are maintained until the prefledging period (Mainwaring et al. 2010), and affect sibling competition and access to resources (Gilby et al. 2012). These differences may have occurred as a result of domestication, through two potential processes. First, aviculturists might have effected a genetic change in female behaviour by selecting for 'broody' females that exhibit early or continual nest attentiveness, with the consequence that, because zebra finches lay one egg per day, domesticated females are likely to begin incubating their eggs as soon as the first egg is laid. Alternatively, some aspect of the captive environment itself might stimulate early onset of incubation, and the observed difference in hatching asynchrony might be a phenotypically plastic response that is not the result of genetic change in domesticated birds.

In this study, for the first time, we formally characterized and investigated differences in incubation patterns and hatching asynchrony in the zebra finch, and attempted to distinguish between the two potential processes given above, by studying zebra finches breeding in the wild, wild zebra finches breeding in captivity and domesticated birds originating from aviculturists. If incubation patterns and hatching asynchrony are determined as a result of genetic selection by aviculturists, then we would expect captive wild birds to behave like wild birds and if they are determined by some aspect of the captive environment, then we expect captive wild birds to behave like captive birds.

METHODS

Field Sites and General Methods

Wild free-living zebra finches were studied from September to December 2008 at Fowlers Gap Arid Zone Research Station, New South Wales, Australia. We studied wild nestbox-breeding birds at Saloon tank (31°03′90″S, 141°50′60″E) and West Mandelman (31°01′S, 141°50′E); further details regarding the study site are provided elsewhere (Griffith et al. 2008). The captive wild birds were either adult zebra finches taken from the wild in Sturt National Park, New South Wales, Australia (29°05′37″S, 141°30′31″E) in September 2007, or their mature (F1) offspring (that had been bred in our facility in Sydney). The captive wild birds were originally caught with mist nets near a water hole and transported to Sydney by road in carrying boxes in an air-conditioned vehicle (and were taken and held under a scientific licence from the New South Wales National Parks and Wildlife Service, Licence No. S11374). The captive wild birds had been held in Sydney for at least 12 months prior to this work being conducted. Meanwhile, the domesticated birds were the descendants of zebra finches originally obtained from aviculturists in the Sydney region in 2005 and which had been domesticated by Australian aviculturists over the past century (Tschirren et al. 2009). All captive birds used in this study (domesticated or captive wild) were maintained in captivity after this work for the remainder of their natural lives.

The incubation behaviour of parents from domesticated and captive wild zebra finches was studied between January and April 2009, and data on natural (unmanipulated) hatching patterns in captive birds were collected from January to March 2010. The same population of birds was used across years but the pairing of the birds differed. In the 2 months prior to data collection, the domesticated and captive wild birds were housed in four large outdoor flight aviaries (10 × 8 m and 2.5 m high), separated by both origin and sex. Aviaries were provided with ad libitum commercial finch seed, sprouted seed, water, cuttlefish bone, grit and two heat lamps. In the first week of January (of each of the 2 years of experimental set-up), males and females were placed in the four aviaries each containing 25 nestboxes (40 birds were in each aviary, 20 males and 20 females of the same origin). Breeding pairs of captive wild and domesticated birds were kept in separate aviaries to prevent birds from different origins pairing up and breeding together. The four aviaries were in a line with domesticated birds in aviaries 1 and 3 and captive wild birds in aviaries 2 and 4.

Quantifying Incubation Behaviours and Hatching Patterns

Once parents initiated nest building, nestboxes were checked daily in all three environments. Natural hatching patterns were closely monitored for 33 domesticated, 31 captive wild and 11 wild free-living broods; except for the hatch checks, no other work was conducted on these birds to avoid disturbance of natural patterns of behaviour. To obtain the time difference between the time at which the first and last nestling hatched, nestboxes were checked twice daily from 13 days after the first egg in the clutch was laid (Zann & Rossetto 1991).

For a different set of nests, parental incubation behaviours were filmed from the morning the first egg was laid using an infrared camera (colour CCD camera HK-C3, Handykam, U.K.), which was attached on the inside of the nestbox lid pointing down into the nest cup. Videos were recorded onto an external hard drive (Archos 605, 160 GB memory), which allowed continuous filming for long periods (Gilby et al. 2011a, b). Nests of domesticated and captive wild parents were filmed from sunrise to sunset on each day a new egg was laid (i.e. across at least 5 days). Although we also attempted to film wild nests for the full day when an egg was laid, the filming of parental incubation by wild free-living birds lasted 5–9 h with a mean ± SD of 7.26 ± 1.89 h of filming time on each day, because the batteries and hard drives were sometimes unstable in the harsh field conditions and intermittently stopped recording. A total of 55 nests were filmed across their entire egg-laying period: 25 domesticated, 15 captive wild and 15 wild free-living. All wild free-living nests that were filmed for parental incubation behaviour had clutches of five eggs, whereas captive nests had clutches of five or six eggs (domesticated: five eggs, $N = 12$, six eggs, $N = 13$; captive wild: five eggs, $N = 9$, six eggs, $N = 6$), matching the mean clutch size normally found across both environments: wild free-living, mean clutch size ± SD = 4.87 ± 1.05 (Griffith et al. 2008); captive domesticated Australian population, mean clutch size ± SD = 5.08 ± 1.2 (Tschirren et al. 2009). Parental incubation behaviours were measured as beginning when a parent was observed to enter the nestbox and sit directly on the egg/s, and end when they moved away from the egg/s. If the parent entered the nest and carried out a task that did not involve sitting on the eggs