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Monogamy on the fast track

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Social monogamy has evolved multiple times and is particularly common in birds. It is not well understood why some of these species are continuously and permanently paired while others occasionally ‘divorce’ (switch partners). Although several hypotheses have been considered, experimental tests are uncommon. Estrildid finches are thought to be permanently paired because being short-lived opportunistic breeders, they cannot afford the time to form a new pair relationship. Here it is shown through a controlled experimental manipulation that zebra finches (*Taeniopygia guttata*) allowed to remain with their partners to breed again are faster to initiate a clutch (by approx. 3 days) than birds separated from their mates that have to re-pair, supporting the hypothesis that continuous pairing speeds up initiation of reproduction, a benefit of long-term monogamy in a small, short-lived, gregarious species.

Keywords: monogamy; mating systems; opportunistic breeder; zebra finch; clutch initiation

1. INTRODUCTION

Social monogamy, the mating system in which males and females pair exclusively for at least one breeding episode, has evolved multiple times. It is most prevalent in birds; more than 90% are socially monogamous (Lack 1968). Some progress has been made in understanding social monogamy by viewing ‘divorce’ (change of partner) as a fitness-increasing strategy, the outcome of a decision based on the costs and benefits of switching to a better quality partner (Trivers 1972; Black 1996; Dhondt 2002; Dubois & Cézilly 2002).

However, not all socially monogamous species divorce; pair relationships terminated only by the partner’s death are also common, as is continuous pairing even when not breeding (Mock & Fujioka 1990; Black 1996). Such birds presumably face high costs and/or insufficient benefits of divorce, and remaining with the partner improves reproduction compared with mate switching. This hypothesis has seldom been tested experimentally, however, to rule out greater age or experience (confounded with pair continuity) as the cause of the improvement (Fowler 1995; Black 1996). Furthermore, both observational and mate removal studies have tended to focus on long-lived birds with slow reproduction, and species

with pair defence of a foraging territory (Fowler 1995; Dhondt 2002). How well these results apply to other birds is unclear.

Estrildid finches form behaviourally conspicuous pairs (Goodwin 1982). In the best-studied species, the zebra finch, divorce has never been observed in wild populations (Zann 1994). Zebra finches are gregarious and breed colonially. They are relatively short lived, able to breed opportunistically in response to unpredictable rainfall and are continuously paired even when not actively breeding (Zann 1994, 1996; Perfeto *et al.* 2007). Offspring can breed at a remarkably early age (60 days). Intraspecific nest parasitism and extra-pair fertilizations occur, the latter infrequently (Birkhead *et al.* 1990). The prevailing hypothesis for the permanence of the pairs is the need to be ready to produce a clutch rapidly without having to spend time forming a pair relationship (Rowley 1983; Zann 1996). Like birds with ‘fast-track’ reproductive life histories, zebra finches and other short-lived birds might be especially vulnerable to temporal costs of mate switching.

This hypothesis has not been tested experimentally. Zebra finches form pairs quickly (Silcox & Evans 1982; Oliva-Purdy & Harding 1997). Gonads are partially activated when not breeding (Sossinka 1980; Perfeto *et al.* 2007). Therefore, it cannot be assumed without evidence that changing partners would introduce a biologically significant delay. Any delay caused by pairing time that does occur should be detectable even in a captive colony.

We tested this fast-track hypothesis by allowing birds to pair and breed, then assigning them to two groups that differed only in whether birds could continue with their partner to produce a clutch again. If the hypothesis is correct, continuing pairs should initiate a clutch sooner and improve more in speed of clutch initiation when breeding again.

2. MATERIAL AND METHODS

Male and female subjects were produced in separate aviary colonies at Cornell University, removed from their natal aviaries when 45–50 days old, and placed in single-sex aviaries until entering phase 1 at 90–120 days. The diet throughout was mixed seed plus supplements of eggs and carrots. All procedures were approved by the university’s IACUC.

To begin phase 1, six males and six females were placed in each of three aviaries (1.8 × 1.8 × 1 m) containing nest boxes and nest material located in three rooms. Birds were observed daily for 5 days to determine pair formation based on (i) allopreening, (ii) clumping and (iii) being in a nest box together. On the fifth day, pairs were transferred to individual pair cages (61 × 36 × 41 cm) containing a nest box and nest material located in the same rooms as the aviaries. The separate cages ensured the identity of the females producing the eggs. Nests were then checked daily. After 84 days, allowing the pairs to gain breeding experience together, the nest box, material and offspring were removed. The pairs remained in their cages for two additional weeks, unable to nest, so that all were in a similar state to begin phase 2. Only pairs that produced chicks went on to phase 2 to eliminate those whose pair relationship did not continue after removal from the aviary.

To begin phase 2, pairs were categorized for the purposes of group assignment based on the number of days to initiate a clutch in phase 1 after transfer to pair cages (fast = 7 or less; medium = 8–14; slow = more than 14). Pairs within each category were assigned to two groups, Same Partner and Different Partner, such that twice as many were assigned to Different Partner but otherwise assignment was random. (Different Partner was designed to be larger in case any of those birds failed to re-pair.) Birds were then moved to two aviaries in different rooms such that (i) Same Partner birds were moved to the same aviary as their phase 1 partners, (ii) Different Partner birds were moved to a different aviary and room

from their phase 1 partners, (iii) each aviary contained birds from both the groups, an equal number of each sex and the same density and (iv) all birds were moved to a different room and aviary than they had been in for phase 1. Thus, both the groups experienced any effects of being moved to a different room and into an aviary with unfamiliar unpaired individuals. Once located in their new aviaries, the same procedures as in phase 1 occurred: 5 days for pair formation by Different Partner birds (and confirmation of continuity of Same Partner pairs); transfer of pairs to individual pair cages; and monitoring nests daily. A few eggs were laid in the aviaries; these were not transferred to the pair cages because they will not be incubated.

The entire experiment was then repeated twice with new birds, but with 16 instead of 12 birds to begin the third iteration. Thus, a total of 60 males and 60 females entered phase 1. Of these, 21 of each sex failed to pair within 5 days in phase 1, five pairs failed to reproduce in phase 1, one Different Partner bird of each sex failed to pair within 5 days in phase 2 and one pair was eliminated due to illness, leaving 20 pairs in Different Partner and 12 in Same Partner.

Latencies to produce the first egg were log transformed prior to the analysis with a two-way ANOVA (group \times phase) with repeated measures on the phase factor, using females (the egg producers) as the within-subjects for Different Partner pairs. The prediction of a group difference in phase 2 was then tested with an unequal variance *t*-test.

3. RESULTS

In phase 2, five Same Partner pairs and one Different Partner pair had already produced one or more eggs in the aviary (assigned a latency of 0). Both groups were much faster to initiate clutches in phase 2 than phase 1, as might be expected now that they were older and more experienced ($F=75.4$, d.f. = 1,30, $p<0.0001$). Also as expected, the main effect of group was not significant ($F=2.5$, d.f. = 1,30, $p=0.1262$). More importantly, the predicted interaction between group and phase was significant, with Same Partner pairs improving more in speed of clutch initiation ($F=6.3$, d.f. = 1,30, $p=0.018$; figure 1).

Same Partner pairs began their phase 2 clutches approximately 3 days sooner on average than Different Partner pairs (means \pm s.e.m. 4.2 ± 0.8 and 1.3 ± 0.5 days, respectively; $t=3.4$, d.f. = 25, $p=0.0025$; figure 2). The difference remained significant if the extreme outlier (latency 16 days) in the Different Partner group was excluded ($p=0.0045$). The group difference in latency was also still significant if pairs laying eggs in the aviary were excluded ($t=2.5$, d.f. = 17, $p=0.0256$). There was no difference in phase 2 clutch size (mean egg numbers were 4.7 for both groups; $p=0.96$).

4. DISCUSSION

Latencies to the first egg supported the fast-track hypothesis proposed by Zann for this short-lived species capable of breeding opportunistically (Zann 1994; Perfito *et al.* 2007). Birds continuing with their previous partner initiated a clutch faster than birds that had to re-pair, even though the latter re-paired quickly. Continuing pairs realized greater improvement in speed of clutch initiation from the first to second breeding phases. Given the importance of rapid reproduction in the life history of this species, faster clutch initiation is likely to be a biologically significant benefit of pair continuity selecting against divorce in this and other opportunistically breeding estrildid finches. Delesalle (1986), using a similar design but with a fewer pairs and several important procedural differences, found

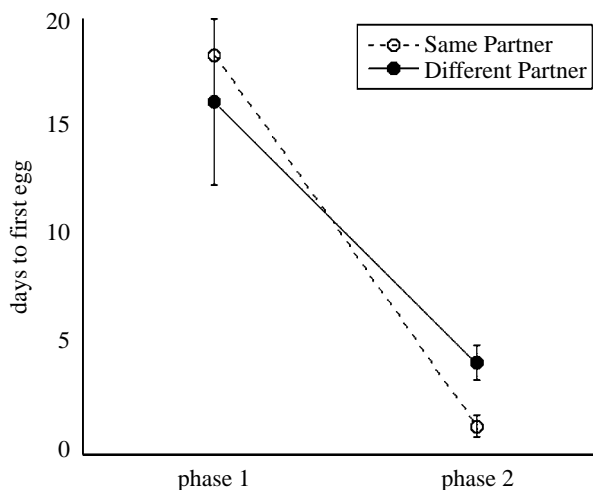


Figure 1. Clutch initiation latencies (untransformed, means \pm s.e.m.) before (phase 1) and after (phase 2) assignment to groups. Day 0 was the day the pairs were moved to pair cages for daily nest checks (latencies from the beginning of the aviary period would be 5 days longer). The group \times phase interaction was significant (means \pm s.e.m.; $p=0.018$).

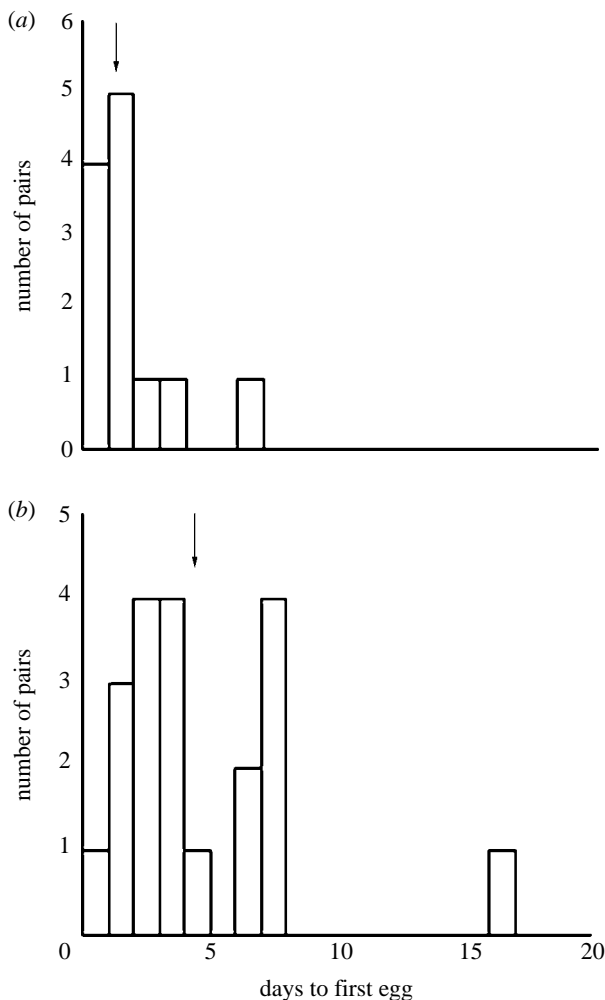


Figure 2. Distributions of phase 2 clutch initiation latencies (untransformed) for (a) Same Partner and (b) Different Partner pairs. Arrows indicate means. Latencies in (a) were significantly shorter ($p=0.0025$).

that continuing pairs fledged more young over a 126-day period. It was not reported whether those pairs initiated a clutch sooner, a key prediction of the fast-track hypothesis. Continuing pairs of some seasonally

breeding, long-lived, slowly reproducing species also lay earlier than newly formed pairs, but in these observational studies the causal link between pair continuity and clutch timing is unclear (Fowler 1995). A mate removal experiment with oystercatchers (*Haematopus ostralegus*), which are longer lived seasonally breeding birds, suggested an earlier laying date benefit of pair continuity. The mediator of the benefit was probably not pair formation time saved, however, because mates were removed during incubation and re-pairing occurred long before the next year's breeding began (van de Pol *et al.* 2006).

Separation of paired zebra finches elevates circulating corticosterone, a hormone that increases in response to stress or energetic challenges (Remage-Healey *et al.* 2003). Corticosterone delays or inhibits egg laying in this species (Salvante & Williams 2003). Increased corticosterone may be a mechanism producing the delay in beginning the clutch in Different Partner pairs. Although wild zebra finches do not divorce, partner mortality does occur (Zann 1996), which should produce a similar delay if it occurs at the onset of breeding.

These results with zebra finches indicate a benefit of continuous pairing relevant to small, rapidly reproducing, short-lived species to add to those applicable to larger, slowly reproducing animals. This benefit is large enough to be detectable even in a captive colony with minimal foraging demands.

All procedures were approved by the university's IACUC.

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