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## Olfactory imprinting as a mechanism for nest odour recognition in zebra finches

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Olfactory communication is widespread across the animal kingdom but until recently was believed to be unimportant in songbirds. However, recent studies of zebra finches, *Taeniopygia guttata*, have found that fledglings are capable of recognizing their own nest based on olfactory cues alone. This raises the important question of whether this knowledge is learned or innate. To discriminate between these two hypotheses, we experimentally fostered single eggs into foreign, unrelated broods, and subsequently tested the odour preferences of the respective fledglings. In contrast to a previous study in which individuals were fostered as chicks, we found a strong preference for the host nest odour. This suggests that olfactory imprinting occurs and is based on a familial template learnt within a narrow time window around hatching.

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Despite the fact that birds in general and passerines in particular have, for many years, been thought to be anosmic, evidence is now mounting that many avian species are able to perceive olfactory cues (Roper 1999; Hagelin & Jones 2007; Caro & Balthazart 2010; Campagna et al. 2012). Birds use these cues in a variety of different circumstances, such as foraging (Nevitt et al. 1995), homing and orientation (Papi et al. 1974; Holland et al. 2009), predator avoidance (Amo et al. 2008, 2011) and nest construction (Gwinner & Berger 2008). In addition, recent studies have also shown that birds of certain species have individually distinctive body odours (Campagna et al. 2012) that may play a crucial role in social communication (Hagelin 2007; Whittaker et al. 2010; Coffin et al. 2011; Amo et al. 2012a, b; Bonadonna & Sanz-Aguilar 2012; Krause et al. 2012). For example, olfactory cues may be important for nest recognition (Minguez 1997; Bonadonna & Bretagnolle 2002; Bonadonna et al. 2003; Cunningham & Nevitt 2011; Caspers & Krause 2011; Krause & Caspers 2012).

Nest recognition could be important for fledglings of some altricial bird species because, although they spend increasing amounts of time away from their home nest, they still need to be able to return faithfully in order to obtain parental care and shelter. The ability to recognize the home nest, based on olfactory cues, has

been experimentally demonstrated in two altricial bird species (Caspers & Krause 2011; Cunningham & Nevitt 2011). However, the mechanism by which this is achieved remains unclear. The aim of this study was to distinguish whether knowledge of the home nest odour is learnt or innate, using an egg-fostering experiment in zebra finches, *Taeniopygia guttata*, since this approach allows the separation of prenatal from postnatal influences.

The zebra finch is a colonially breeding, altricial songbird with biparental care (Zann 1996). Chicks fledge at around 19 days of age and then return regularly to the home nest for parental care, until they become fully independent around 2 weeks later (Zann 1996; Rehling et al. 2012). Odour appears to play an important role in nest recognition, since fledglings have been experimentally shown to recognize, and prefer, the odour of their own nest over that of a foreign nest (Caspers & Krause 2011). Surprisingly, fledglings that were fostered into foreign nests shortly after hatching did not show a preference for the nest they were raised in, but instead preferred the odour of their familial nest (Krause et al. 2012). This suggests that information about the familial nest is either innate or acquired early in life. To distinguish between these two possibilities, we experimentally fostered single eggs several days prior to hatching into unrelated clutches of the same developmental stage and tested the fledglings' odour preferences. If odour recognition is based on innate cues such as recognition alleles, foster fledglings should prefer their genetic nest odour over the foster nest odour. In contrast, if chicks learn the nest odour early in life, we predicted that foster fledglings would show a clear preference for the host nest odour.

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## METHODS

*Breeding and Egg Fostering*

Experiments were conducted from August 2011 to June 2012, in the Department of Animal Behaviour at Bielefeld University. We used zebra finches belonging to our domesticated laboratory stock (referred to as 'Bielefeld' in Forstmeier et al. 2007b). Randomly selected pairs of zebra finches were allowed to breed in two-compartment breeding cages (Fig. 1a) with attached wooden nestboxes (15 × 15 × 15 cm) on a 14:10 h dark:light cycle. The temperature during the experiments was kept stable in the range 24.5–25.5 °C. The birds received water and standard seed food ad libitum plus additional egg food and germinated seeds three times per week. Coconut fibres were provided as nest material. The birds used in this study were all from the same laboratory stock and were subject to identical conditions during breeding as those used in an earlier study (Krause et al. 2012), but were different individuals and were not closely related to each other. We checked nestboxes daily to count eggs and/or chicks. Eggs of each clutch were given distinctive markings using a nontoxic pen. All birds, eggs and nestboxes were handled using new nitrile gloves to avoid olfactory contamination. When the eggs of a donor clutch were readily incubated by the parents and the embryo appeared to be developing normally as indicated by a change in egg coloration (about 5–7 days before hatching), a single egg was randomly selected and transferred from a donor nest to a host nest containing a clutch at a similar developmental stage. Egg fostering was unidirectional, with no eggs being transferred back into the donor nest, to avoid contaminating it with odour. Each breeding pair was used at most once as an egg donor and once as an egg host. On the day the first chick hatched in the host nest, the parent birds and the entire nestbox with the remaining eggs and chicks were transferred to

three-compartment cages (Fig. 1b). Here, the nestbox was placed centrally and food and water were symmetrically placed in both sides of the cage (Caspers & Krause 2011; Krause & Caspers 2012).

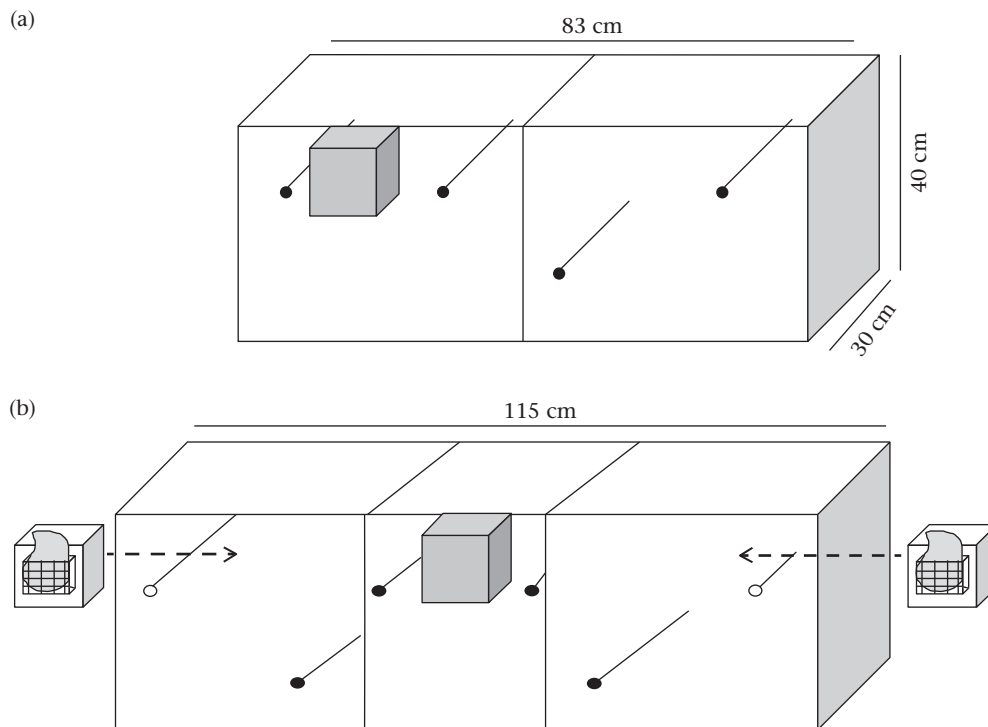
Chicks were not marked after hatching to minimize any potential experimental bias with respect to genetic origin (foster or nonfostered chick). Moreover, sometimes more than one chick hatched between sightings, meaning that it was also not always possible to determine the status of chicks without genetic analysis. Similarly, hatching order of the chicks could not be reconstructed for the majority of nests, meaning that the foster chick could be the first, middle or last hatching chick within the host nest.

All successfully fledged birds were tested in the olfactory preference tests. Experimental tests were conducted 'blind' with respect to the origin of the chicks, which were subsequently assigned to either fostered ( $N = 16$ ) or nonfostered ( $N = 43$ ) treatments using genetic parentage analysis. The average number of unrelated host chicks accompanying the foster chick in the brood  $\pm$  SD was  $2.7 \pm 1.7$  chicks.

*Olfactory Preference Tests*

As fledging occurs at around 19 days of age (see Introduction), to ensure that all of the experimental chicks had fledged we conducted olfactory preference tests on day 23 as detailed by Caspers & Krause (2011). Tests were conducted in the home cages after temporarily removing all but the focal individual. We used nest material that was partially soiled with faeces (approximately 2.5 g) from the host and genetic nests as odour stimuli, which were transferred into synthetic gauze bags.

Following Krause et al. (2012), samples of the familiar nest odour from the host nest were designated as the 'host nest odour' (HNO), whereas those of the unfamiliar odour (i.e. from the foster chick's genetic nest) were designated as the 'nonhost nest odour'



**Figure 1.** (a) A two-compartment breeding cage in which the experimental clutches were incubated until hatching. The natal nestbox containing the chicks together with the parents was then transferred to (b) a three-compartment cage, which was subsequently used to rear the brood and for odour preference testing. During an odour preference test, the natal nestbox was removed and two artificial test nestboxes with the odour stimuli were attached (indicated by dashed arrows). Preference zones in the odour preference tests were defined as the artificial test nestboxes plus the perches in front of them (indicated by open circles).

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