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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.

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 ($15 \times 15 \times 15$ 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 ± SD was 2.7 ± 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'

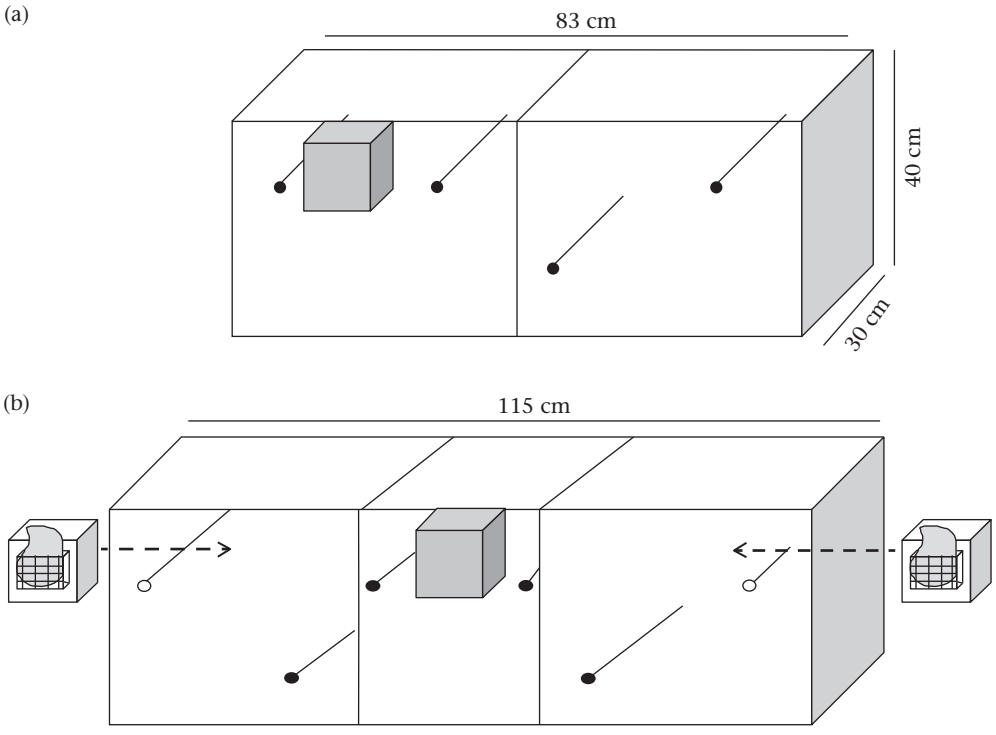

Figure 1. (a) A two-compartment breeding cage in which the experimental clutches were incubated until hatching. The natal nestbox containing the chicks together with the parents was then transferred to (b) a three-compartment cage, which was subsequently used to rear the brood and for odour preference 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).

(nHNO). Chicks were tested for their odour preference in a randomized order. We conducted the experiment blind with respect to the identity of the chick (i.e. foster chick or host chick). The foster chicks were allowed to choose between the odour of a nest used by familiar but unrelated conspecifics (HNO) and the odour of a nest used by unfamiliar but closely related conspecifics (full sibs and parents; nHNO).

During the olfactory preference tests, the nestbox from the central compartment of the three-compartment cage was removed and two new artificial nestboxes filled with fresh unused coconut fibres imitating the shape of a nest were added, one to each side of the cage (Fig. 1b). The odour samples in synthetic gauze were placed in wire baskets attached behind each of the artificial nestboxes. These were of identical appearance and were not visible to the fledgling. A 7.5 cm hole in the rear wall of each of the nestboxes allowed a fan, installed behind the wire basket, to pass air through the sample into the nestbox and the preference zone beyond. The preference zone was defined as the respective nestbox and the perch in front of it, whereas all other locations in the three-compartment cage were regarded as neutral nonchoice areas. We ran the fans for 20 min prior to each experiment as well as during the preference tests, allowing the odours to permeate the preference zones. During this period, the test bird was kept in the central compartment which was separated by plastic dividers from the two side compartments. When the test was started, the dividers were removed and the location of the test individual was recorded in 3 s intervals over a 5 min period. Thereafter, odour samples were switched between the two sides and the same procedure was repeated, such that each olfactory preference test lasted a total of 10 min. All experiments were recorded by a video camera and the total amount of time spent at the HNO and the nHNO was recorded for each individual. Data were partitioned into 3 s intervals. If the focal animal remained stationary for the full 3 s, it was scored as '3', whereas if it changed its position, it was scored as '1.5' following Witte & Caspers (2006). Finally, we classified each individual as preferring the HNO if choice for the HNO was >50%, or preferring the nHNO if choice for the HNO was <50%. In cases where exactly the same amount of time was spent in both choice areas, the fledglings were defined as having no preference.

Blood Sampling, DNA Extraction and Microsatellite Genotyping

A small blood sample (5–10 μl) was taken from each adult and fledgling by brachial venipuncture using a 26-gauge needle and the blood was stored in 70% ethanol. Total genomic DNA was extracted using an adapted phenol–chloroform protocol. Each sample was then genotyped at eight polymorphic microsatellite loci: Indigo41 (d), Tgu01, Tgu03, Tgu04, Tgu05, Tgu08, Tgu09 and Tgu12 (Forstmeier et al. 2007a) using a Qiagen Type-it Mastermix kit. The following PCR profile was used: 95 °C for 5 min, eight cycles of 95 °C for 30 s, 60 °C for 90 s (minus 1 °C per cycle) and 72 °C for 60 s, followed by 30 cycles of 95 °C for 30 s, 56 °C for 90 s and 72 °C for 60 s. Final extension was performed at 70 °C for 15 min. Fragment sizes were scored using the automated software Genemarker v1.7 (Softgenetics, State College, PA, U.S.A.). All of the scores were checked manually and adjusted wherever the genotype call was deemed to be in error.

Parentage Analysis

Molecular parentage analysis was used to determine which of the chicks were fostered and which were host chicks. The program Genepop (http://genepop.curtin.edu.au) was used to quantify the number of alleles, observed and expected heterozygosity and to test each locus for conformity to Hardy–Weinberg equilibrium (HWE). For each test, the dememorization number was set to 10 000, the number of batches to 1000 and the number of iterations per batch to 10 000. Multilocus microsatellite genotypes were then analysed with the program Colony (Jones & Wang 2010) which uses a likelihood approach simultaneously to assign each chick a most likely mother and father and to reconstruct probable families. Default settings of the program were used, although individuals were masked in the analysis in such a way that each chick was only tested against two pairs of candidate parents: the host and foster chick's parents (see Appendix Tables A1 and A2 for details).

Data Analysis

We used a chi-square test to compare preferences of the foster chicks for the two odour stimuli: HNO versus nHNO. We also used a chi-square test to compare our results with those of a previous study in which chicks were fostered after hatching (Krause et al. 2012). The chi-square test was applied in the majority of cases in which the expected frequency was five or greater (Siegel & Castellan 1988), whereas the Fisher's exact test was used for lower expected frequencies. For the comparison of the amounts of time spent at certain stimuli, we used Mann–Whitney *U* tests. All tests were two tailed with a significance level (α) of 0.05.

Ethical Note

The experiments were conducted in accordance with the German laws for experimentation with animals. Breeding and housing at Bielefeld University were conducted with the permission of the Veterinäramt Bielefeld (No 530.421630-1, 18.4.02). Blood samples were taken with the permission of the LANUV NRW (No 84-02.05.20.12.283). All birds had ad libitum food and water. Birds and nestboxes were checked daily to verify that the individuals were healthy. All of the individuals were obtained from the Bielefeld University laboratory stock and remained in the laboratory stock after the experiments were completed.

RESULTS

Molecular Parentage Analysis

All of the individuals were genotyped at eight microsatellite loci carrying on average 8.6 alleles and with a mean observed heterozygosity of 0.85 (see Appendix Table A1). One locus deviated weakly from HWE ($P = 0.017$ after tablewide Bonferroni correction for multiple statistical tests) but did not show evidence of null alleles being present and was therefore retained in the parentage analysis (see Appendix Table A1). The program Colony assigned both maternity and paternity to every chick with a probability of 0.9654–1. For every host nest, a single chick was assigned to the donor parents and the remaining chicks were all assigned to the host parents. A total of 16 foster chicks and 43 host chicks (see Appendix Table A1) were successfully reared. On average ± SD, 2.69 ± 1.74 host chicks were present within each host nest.

Olfactory Preference Tests

Foster chicks

All 16 foster chicks were tested for their odour preference. The majority of individuals ($N = 11$) preferred the HNO, while three preferred the nHNO and two showed no preference (chi-square test: $\chi^2_1 = 4.571$, $P = 0.033$; Fig. 2a). Foster chicks spent much longer on average at the HNO than at the nHNO ($\text{median}_{\text{HNO}}$ 141 s, first quartile 0 s, third quartile 268.5 s; $\text{median}_{\text{nHNO}}$ 8.25 s, first quartile 0 s, third quartile 121.5 s). The absolute median difference

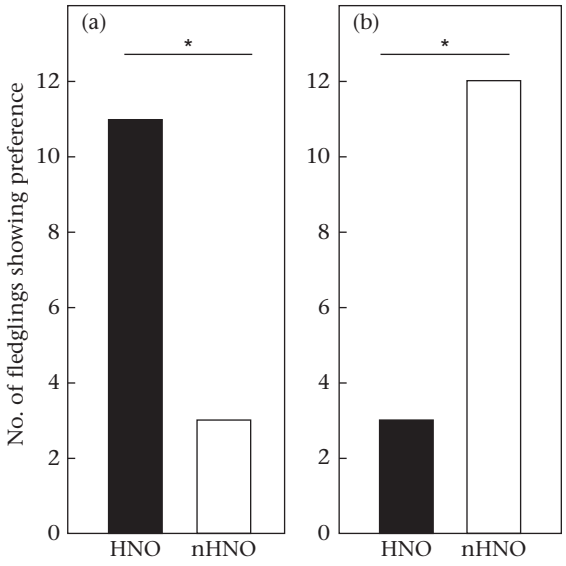

Figure 2. Number of zebra finch fledglings that showed a preference for the HNO (host nest odour) and the nHNO (nonhost nest odour) in (a) an egg-fostering experiment and (b) a previous chick-fostering experiment (Krause et al. 2012). *$P < 0.05$. Comparison of preference of chicks in the two experiments; $P < 0.01$.

in time that individuals spent in the preference zones was 72 s (first quartile 36.75 s, third quartile 285.75 s).

Nonfostered chicks

Nonfostered chicks showed no clear preference, with 19 individuals preferring the HNO, 16 the nHNO and eight making no choice (chi-square test: $\chi^2_1 = 0.26$, $P = 0.61$). We found the same pattern of behaviour at the brood level (chi-square test: $\chi^2_1 = 0.4$, $P = 0.53$). No significant differences were observed between the preference patterns of fostered and nonfostered chicks (Fisher's exact test: $P = 0.39$).

Effect of fostering time

Comparison of the preferences of birds fostered as eggs (this study) with those fostered as chicks in a previous experiment (Krause et al. 2012) revealed a highly significant difference in odour preference (chi-square test: $\chi^2_1 = 9.95$, $P = 0.002$; Fig. 2a, b). Both studies found that fostered chicks preferred the odour of the nest they were born in, although this was the nongenetic nest odour in the present study. Moreover, fostered fledglings from the chick-fostering experiment (Krause et al. 2012) spent significantly more time (median 241.5 s, first quartile 19.5 s, third quartile 298.5 s) at the nHNO than fostered fledglings from the egg-fostering experiment (Mann–Whitney U test: $Z = -2.48$, $P = 0.012$). The median total amount of time individuals spent in either preference zone did not differ significantly between fledglings from the two experiments (egg-fostering experiment: 283.5 s; chick-fostering experiment: 298.5 s; Mann–Whitney U test: $Z = -1.01$, $P = 0.33$).

DISCUSSION

Through a combination of egg switching, genetic analysis and a comparison with a previous chick-fostering study, we have shown that zebra finches acquire olfactory information about the nest through olfactory imprinting around the time of hatching. A simple rule can explain our results: birds prefer, and probably build a template from, the nest that they smell at or around the time of hatching.

Imprinting requires individuals to learn about specific characteristics, for example of their parents and/or other family members, usually during a specific sensitive phase during development (Hudson 1999). Our results, taken together with those of Krause et al. (2012), suggest that the sensitive phase for olfactory imprinting of the nest odour in zebra finches is short, extending no further than 48 h after hatching. This is because hatchlings fostered either on their first day (i.e. 1–12 h posthatching) or the fourth day (i.e. 72–80 h posthatching), showed contrasting preferences to hatchlings from our egg-fostering experiment. When fostered posthatching, fledglings showed a clear preference for their genetic nest odour.

We cannot discount the possibility that imprinting could have occurred prior to hatching because the eggs were switched up to 6 days before hatching. Moreover, previous studies have shown that certain bird species are able to perceive chemical cues as embryos (e.g. Tolhurst & Vince 1976; Sneddon et al. 1998; Burne & Rogers 1999; Bertin et al. 2010). However, in contrast to our experiment, these studies were conducted with precocial bird species and used artificial flavours. It remains unclear whether nest or other natural odours could be strong enough to elicit similar responses prehatching.

Zebra finch fledglings in the wild often return to their natal nest during the first few days after fledging (Immelmann 1962, 1970) and are fed in the nest during this time by their parents (Immelmann 1962). Thus, olfactory imprinting shortly after hatching is likely to be adaptive because individuals need to be able to recognize and return to their own nest after fledging in order to be fed by their parents. However, it is also possible that this information about the family nest odour could be used later in life to recognize kinship. It is already known that female zebra finches prefer males that sing or look like their fathers, implying the use of acoustic and visual cues in mate choice (Oetting & Bischof 1996; Witte & Caspers 2006). However, using each of these cues alone runs the risk of mating with close relatives, which could lead to inbreeding depression (Hemmings et al. 2012). The latter appears to be avoided, at least in an experimental setting (Arct et al. 2010), suggesting that an interesting avenue for future research could be to investigate whether odour could also contribute to mate choice decisions.

The short, early time window we identified (probably between hatching and 48 h of age), could be beneficial for the accuracy of imprinting (Caspers & Krause 2013) since very young altricial hatchlings are immobile. The sensitive phases of sexual imprinting based on visual and acoustic cues are substantially later at around 15–40 days (Zann 1996; Oetting & Bischof 1996; Brainard & Doupe 2002; Witte & Caspers 2006). These alternative modalities could be potentially influenced by individuals encountered outside the home nest and within the wider colony, since both overlap with the average fledging date (around day 19, see Introduction). Hence early olfactory imprinting could potentially be more accurate than either visual or acoustic imprinting for kin recognition later in life.

Our analysis of the nonfostered chicks also provides tentative support for our conclusions based on the fostered birds. Both experienced a similar nest environment, but some of the nonfostered chicks will have hatched before the foster chick hatched, whereas others will have hatched after the foster chick. This could potentially have confounded the choice of the nonfostered chicks in two ways: (1) nonfostered chicks hatching before the foster chick experienced the pure HNO at hatching but were asked to choose between a contaminated HNO and the nHNO; (2) nonfostered chicks hatching after the foster chick experienced a contaminated HNO. Either or both of these possibilities could potentially influence the preference of nonfostered chicks. In contrast, hatching order is unlikely to have been of importance for the foster chicks because all of these individuals hatched into pure host nests. To understand better how hatching order can influence odour preference, it would be

interesting to conduct further studies aimed directly at manipulating hatching order and/or host nest composition.

Our finding that nest odours are acquired early in life also suggests that the avian brain may be capable of processing olfactory information at this time. In the zebra finch brain, the volume of the nucleus taeniae of the amygdala grows rapidly in comparison with the rest of the telencephalon, especially during the first week after hatching (Ikebuchi et al. 2013). This predates the growth of the song control nuclei and could be due to direct afference from the olfactory bulb (Ikebuchi et al. 2013). Whether the nucleus taeniae of the amygdala or other specific brain regions are involved in the process of olfactory imprinting could be addressed in future studies of olfaction-deprived or anosmic birds.

In conclusion, we have shown that zebra finches imprint on the odour of their nest at or around hatching. Whether individuals are able to use the same cues later in life to avoid inbreeding is unclear, but this offers a fertile avenue for future research.

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APPENDIX

Table A1
Polymorphism characteristics of the eight microsatellite loci employed in this study

Locus	No. of alleles	H_{obs}	H_{exp}	HWE *P*
Indigo41	9	0.88	0.81	0.999
Tgu1	9	0.83	0.76	1.000
Tgu3	9	0.88	0.82	0.801
Tgu4	8	0.74	0.72	0.082
Tgu5	7	0.87	0.81	1.000
Tgu8	11	0.90	0.81	0.017
Tgu09	9	0.83	0.80	0.962
Tgu12	7	0.85	0.81	0.946
Average	8.63	0.85	0.79	NA

Allele number and observed and expected heterozygosity (H_{obs} and H_{exp}, respectively) were calculated based on all individuals whereas HWE *P* values were calculated using only adult zebra finches. Bonferroni correction was applied to the latter to control for multiple statistical testing.

Table A2
Pair IDs of the parents of each chick, inferred using genetic analysis

Chick ID	Nest ID where chick hatched	Pair ID of inferred father	Pair ID of inferred mother	Probability	Foster or host chick?
o929	51	52	52	1.000	Foster
o977	52	51	51	1.000	Foster
o957	53	60	60	1.000	Foster
o934	56	65	65	1.000	Foster
o973	57	58	58	0.999	Foster
o941	58	57	57	0.999	Foster
o937	59	67	67	1.000	Foster
o961	61	63	63	1.000	Foster
o948	64	Failed	55	1.000	Foster
o985	67	59	59	1.000	Foster
o983	68	56	56	1.000	Foster
gr304	60	53	53	1.000	Foster
gr302	55	PK02	PK02	1.000	Foster
gr494	PK24	PK21	PK21	1.000	Foster
gr489	PK02	PK23	PK23	1.000	Foster
gr500	PK 03	PK20	PK20	1.000*	Foster
o930	51	51	51	1.000	Host
o976	52	52	52	1.000	Host
o978	52	52	52	1.000	Host
o979	52	52	52	1.000	Host
o980	52	52	52	1.000	Host
o981	52	52	52	1.000	Host
o958	53	53	53	1.000	Host
o959	53	53	53	1.000	Host
o960	53	53	53	1.000	Host
o971	53	53	53	1.000	Host
o972	53	53	53	1.000	Host
o935	56	56	56	1.000	Host
o974	57	57	57	0.999	Host
o975	57	57	57	0.999	Host
o939	58	58	58	0.999	Host
o940	58	58	58	0.999	Host
o942	58	58	58	0.999	Host
o943	58	58	58	0.999	Host
o938	59	59	59	1.000	Host
o936	59	59	59	1.000	Host
o953	61	61	61	1.000	Host
o954	61	61	61	1.000	Host
o956	61	61	61	1.000	Host
o955	61	61	61	1.000	Host
o949	64	64	64	1.000	Host
o950	64	64	64	1.000	Host
o951	64	64	64	1.000	Host
o952	64	64	64	1.000	Host
o987	67	67	67	1.000	Host
o988	67	67	67	1.000	Host
o991	67	67	67	1.000	Host
o986	67	67	67	1.000	Host
o990	67	67	67	1.000	Host
o982	68	55	68	1.000	Host
o984	68	55	68	1.000	Host
hbl60	60	60	60	1.000	Host
gr309	60	60	60	1.000	Host
gr301	55	Failed	55	1.000	Host
gr303	55	Failed	55	1.000	Host
gr495	PK02	PK02	PK02	1.000	Host
gr497	PK02	PK02	PK02	1.000	Host
gr496	PK02	PK02	PK02	1.000	Host
gr499	PK02	PK02	PK02	1.000	Host

* Based on observation, since only the fostered egg was successfully incubated.