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Can chicks smell their parents? No evidence of olfactory parent recognition in a shorebird

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In many taxa, young can recognize their parents using olfactory cues. Yet this possibility has been overlooked in birds, because they were long assumed to have a poor sense of smell. While evidence is growing that birds use odours to communicate, olfactory parent recognition has only been documented in two altricial bird species. Whether chicks of precocial species use olfaction to recognize parents is currently unknown. Parent recognition is particularly important in precocial species, as chicks leave the nest shortly after hatching, and may lose contact with their parents and encounter other conspecific adults. We conducted Y-maze trials in the wild to test whether chicks of a precocial shorebird, the white-fronted plover, *Anarhynchus marginatus*, can recognize parents via olfaction. We tested first whether chicks show a preference for the odour (preen oil) of an unfamiliar adult over a control (no odour), and second whether chicks show a preference for the odour of a parent over that of an unfamiliar adult. Plover chicks spent as much time with the odour of an unfamiliar adult as with the control, and as much time with the odour of a parent as with that of an unfamiliar adult. Therefore, we found no evidence that chicks react to the preen oil odour of a conspecific adult, nor that they can discriminate a parent using preen oil odours. It may be that chicks of this species can discriminate parental and foreign odours but that our experiment failed to detect it, that they rely on other (e.g. auditory) cues, or that they do not need to discriminate between parents and foreign conspecific adults.

Kin recognition (the ability to recognize close relatives) has evolved in many animal taxa (Hepper, 2011; Waldman, 1988). It allows individuals to cooperate with and care for relatives, and avoid mating or competing with them, thereby increasing their inclusive fitness (Hamilton, 1964; Waldman, 1988). One important context of kin recognition is parental care, where it is advantageous for parents and offspring to recognize one another (Hepper, 1986; Waldman, 1988). Indeed, parents should recognize their offspring (offspring recognition) to direct their parental care towards their offspring rather than nonkin young (Waldman, 1988). Offspring should also recognize their parents (parent recognition) to solicit parental care (e.g. begging) from their parents rather than nonkin adults (Jacot et al., 2010).

Parent recognition is likely to evolve in species where young can confuse their parents with nonkin conspecific adults, such as colonially breeding species (Aubin & Jouventin, 1998; Beecher et al., 1986) and precocial species (Mathevon et al., 2003; Scheiber et al., 2017). Precocial young are mature and mobile from the moment of hatching or birth (i.e. precocial) and can leave the nest shortly after (i.e. nidifugous). Thus, they are likely to lose contact with their parents and meet nonkin adults, from which soliciting care could have a cost. Indeed, chicks that solicit care from unrelated adults can be rejected (Beecher et al., 1981; Davis & McCaffrey, 1989) or attacked (Kalmbach et al., 2005; Öst & Bäck, 2003; Proffitt &

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McLean, 1990). In addition, the unsuccessful begging by the chicks may attract predators (Lima, 2009). However, we note that soliciting care from nonkin adults is not necessarily costly and may even be advantageous. For example, in cases where adults cannot discriminate between kin and nonkin young, young can take advantage of care provided by nonkin adults without risking rejection or aggression. Also, in cases where young have lost their parents, they may benefit from any care and should thus solicit care from other adults, even at the risk of eviction or aggression, or they may receive no care at all ('best of a bad job', Kalmbach, 2006). In such cases, parent recognition provides no (or only limited) selective advantage.

In birds, studies on parent–offspring recognition have focused on auditory and visual cues (Beecher, 1988; Jacot et al., 2010; Komdeur & Hatchwell, 1999), overlooking the potential role of olfactory cues. Yet, we now know that birds can use olfaction for intraspecific communication (reviewed in Caro et al., 2015; Grieves et al., 2022; Hagelin & Jones, 2007; Krause et al., 2018), including parent–offspring recognition. Indeed, adult birds can recognize the odour of their own nest (four petrel species, Bonadonna, Cunningham et al., 2003; Bonadonna, Hesters et al., 2003; two finch species, although only females, Krause & Caspers, 2012), eggs (zebra finch, *Taeniopygia guttata*, females, Golüke et al., 2016; blue petrel females, *Halobaena caerulea*, Leclaire, Bourret et al., 2017) and chicks (zebra finch, although only males, Golüke et al., 2021). However, female spotless starlings, *Sturnus unicolor*, do not discriminate between their own and other chicks using smell (Amo et al., 2014). Several studies have shown that young birds recognize and prefer familiar nest odours (domestic chicken, *Gallus gallus domesticus*, Burne & Rogers, 1995; Jones & Gentle, 1985; greylag goose, *Anser anser*, Würdinger, 1982; European storm petrel, *Hydrobates pelagicus*, Mínguez, 1997; Leach's storm petrel, *Oceanodroma leucorhoa*, O'Dwyer et al., 2008; zebra finch, Caspers et al., 2013, 2015; Caspers & Krause, 2011). In contrast, only two studies have investigated whether young birds can recognize parental odours.

A first study found that zebra finch hatchlings prefer (i.e. beg longer in response to) the odour of a familiar parent over that of an unfamiliar adult (Caspers et al., 2017). Moreover, zebra finch hatchlings prefer the odour of their genetic (unfamiliar) mother over that of their foster (nonkin familiar) mother (Caspers et al., 2017). In line with these results, a second study found that tree swallow nestlings, *Tachycineta bicolor*, begged longer and more intensely at the odour of a familiar adult (parent) than at the odour of an unfamiliar adult (Griebel & Dawson, 2020). Interestingly, these two species (zebra finches and tree swallows) are altricial, with chicks staying in the nest for an extended period after hatching (i.e. nidicolous), and may thus not need parent recognition, at least during the nestling phase (Scheiber et al., 2017). This begs the question whether chicks of precocial species, where selection pressure for parent recognition should be stronger, also show olfactory parent recognition.

In this study, we tested whether the precocial chicks of white-fronted plovers, *Anarhynchus marginatus* (formerly *Charadrius marginatus*), can recognize their parents via olfaction. White-fronted plover chicks leave the nest scrape shortly after hatching, and are attended and defended by their parents for an extended period of time (Safford & Hawkins, 2020; Zefania & Székely, 2022). Chicks can lose contact with their parents (e.g. after hiding from a threat or during territorial fights between adults) and, in places with high nesting densities, encounter foreign conspecific adults, which increases the necessity for parent recognition. Using a Y-maze in the field, we conducted two behavioural trials to investigate the responses of chicks to olfactory cues (preen oil) from adult conspecifics (unfamiliar adults and parents). In a first trial, chicks were exposed to the odour of an unfamiliar (and nonkin) adult on one side and a control (no odour) on the other side. If chicks identify the odour of the unfamiliar adult as a nonparent, and if there is a cost of soliciting care from an unfamiliar adult, we predicted that chicks would avoid it and spend more time with the control. Alternatively, if there is no cost of soliciting care from an unfamiliar adult, chicks may be attracted to the odour of an unfamiliar adult and thus spend more time with it. In a second trial, chicks were exposed to the odour of an unfamiliar (and nonkin) adult on one side and the odour of a parent on the other side. If chicks can discriminate the odour from their parents, we predicted them to show a preference for the odour of a parent, especially if there is a cost of soliciting care from an unfamiliar adult.

METHODS

Study Species and Subjects

We studied white-fronted plovers at Andavadoaka (22.02° S, 43.39° E) in southwest Madagascar in April–May 2022. At the study site, white-fronted plovers breed on salt marshes and sandy beaches (Jones et al., 2022). Nests are on average 250 m (SD = 170 m) apart but can be as close as 15 m apart (Zefania & Székély, 2019). Breeding occurs year round, but increases between February and June, after seasonal periods of heavy rainfall. White-fronted plovers are monogamous, with no extrapair mating (Maher et al., 2017). They exhibit biparental care, with both partners defending nest territories, incubating the eggs (one to four eggs, usually two) and caring for the chicks (one to four chicks, usually two, Eberhart-Phillips, 2019; Safford & Hawkins, 2020). Chicks are precocial (Fig. 1) and leave the nest shortly after hatching, but still need care from their parents until fledging (28–38 days), for example for protection against predators or thermoregulation (Safford & Hawkins, 2020). After losing contact with their parents (e.g. after hiding from a predator, or during territorial fights between adults from different families), chicks walk around in search of their parents and may encounter nonkin adults, especially in places with high nesting densities. As a result, broods can get mixed (chicks raised by unrelated adults), although rarely (Maher et al., 2017). It should be noted here that the occurrence of brood mixing does not imply the absence of recognition between parents and offspring. For example, Caspian terns, *Sterna caspia*, can adopt foreign young although they can discriminate between own and foreign young (Shugart, 1978). Young white-fronted plovers remain with their parents for 2–3 months (Safford & Hawkins, 2020).

When finding a family (i.e. at least one parent with at least one nonfledged chick), we first approached the chick(s) carefully and captured them by hand. We then placed the chick(s) under a sieve in a trap (spring or funnel trap) to attract and capture the parents (Székely et al., 2008). Chicks were captured to participate in odour preference trials (Fig. 1), whereas parents were captured to collect test odours for the trials. In total, we captured 44 chicks (from 33 families), all of which participated in odour preference trials. Chicks were between 1 and 23 days old, but most were less than 5 days old (average = 8 days, interquartile range = 12 days, age determined using tarsus length following Parra, 2015). The sex of the chicks was unknown during the trials and was determined after molecular sexing (19 females, 23 males, 2 chicks of unknown sex). For sexing, blood (25–50 μl) was sampled from the medial metatarsal (leg) vein (Székely et al., 2008) and stored in ethanol, DNA was extracted using a standard phenol–chloroform protocol and sex was determined using established molecular methods developed for *Charadrius* species (described in Jones et al., 2022).

Figure 1. Study subject and experimental set-up. (a) White-fronted plover chick released after participating in a behavioural trial in a (b) Y-maze in the wild in Madagascar. Photos: Marc Gilles.

Test Odours

As test odours, we used preen oil (secretion from the uropygial gland) swabs from adult white-fronted plovers collected during chick rearing (between 1 and 23 days after hatching). Preen oil is a major source of bird odour (Hagelin & Jones, 2007) and is commonly used as a proxy of body odour in behavioural trials (e.g. Grieves et al., 2019; Whittaker et al., 2011). We used preen oil swabs from chick-rearing birds only, because preen oil composition is known to change across breeding stages (Gilles et al., 2024; Reneerkens et al., 2002). In our odour preference trials, we used three types of test stimuli: parent odour (preen oil swab from a parent of the chick tested), unfamiliar adult odour (preen oil swab from an adult of another family than the chick tested) and no odour (swab with no preen oil). Because there is no extrapair paternity and only a low probability of intraspecific brood parasitism or brood mixing (<3.45%) in this species (Maher et al., 2017), familiarity and genetic relatedness were confounded. ‘Unfamiliar adults’ were most likely to be both unfamiliar and unrelated (nonkin) to the tested chick, while ‘parents’ were most likely to be both familiar and related (genetic parents) to the tested chick. For each family, we aimed to catch both parents but in most cases we caught only one parent, and in some cases no parent at all. From our experience, it was more difficult to capture parents with older chicks (more than 1 week old), as they came less close to the captured chicks.

We collected preen oil from adult birds by swabbing their uropygial gland with a cotton swab, wearing nitrile gloves. To standardize the quantity of preen oil collected, we systematically swabbed the uropygial gland 20 times. Preen oil swabs were stored in Teflon-capped 20 ml glass vials (Labsolute, Th. Geyer, Renningen, Germany), which were put in a fridge upon return to the field station at the end of the day and kept refrigerated until use in odour preference trials. In total, 34 preen oil swabs (from 34 individuals) were used in trials, and they were used on average in 2.4 ± 1.4 different trials. We systematically used the most recent preen oil swabs (sampled a maximum of 8 days before the trials). Owing to methodological constraints, preen oil swabs from unfamiliar adults were sampled on average 2.8 ± 2.3 days before use in trials, whereas preen oil swabs of parents were sampled shortly (less than 1 h) before use in trials. We controlled for this confounding effect by verifying that the freshness of the preen oil swabs had no effect in the analysis. As white-fronted plovers are sexually monomorphic (Zefania et al., 2010), we were blind to the sex of the birds sampled, which was revealed only after molecular analyses (same method as for chicks except that blood was sampled from the brachial vein, Jones et al., 2022; Székely et al., 2008). We controlled for the potential effect of the sex of the test odours (see Statistical Analyses), although we expected chicks to respond similarly to odours from females or males, because both sexes care for the chicks in this species (Eberhart-Phillips, 2019).

Y-Maze Apparatus

Odour preference trials were conducted directly in the field (Fig. 1) using a Y-maze consisting of one start arm and two test arms (three symmetrical arms, 20 × 15 × 15 cm angled at 120°, PVC material; Fig. 2, more details in Fig. A1). The floor of the maze was covered with a metal grid to allow chicks to walk without slipping. In the start arm, an acclimation chamber (15 × 15 × 15 cm) was covered with an opaque ceiling, and was separated by an opaque PVC door that could be slid open to allow the bird to explore the maze (Fig. 2). The bird was placed in the acclimation chamber using a sliding door made of perforated PVC, which allowed airflow but kept the acclimation chamber dark. The acclimation chamber was dark so that chicks could calm down after the stress of capture. The test arms were covered with semitransparent Plexiglas (Fig. A1), allowing video recording from above while limiting the effect of the environment from above the maze (e.g. clouds, trees). Chicks were therefore in the dark in the acclimation chamber, but not during the trial. Test odours (i.e. cotton swabs) were placed at the ends of the two test arms, separated by an opaque perforated PVC barrier, which allowed olfactory cues, but not visual cues, to be perceived from within the maze. Test odours were positioned vertically on a nail, with the cotton tip (containing preen oil, except for the ‘no odour’ stimulus where it contained no preen oil) reaching a height of 5 cm. To control the air flow coming from each test odour, we placed fans (Pure Wings 2, BeQuiet, Glinde, Germany) at the end of the test arms, which circulated air from the test odours towards the start arm. Trials were video recorded using a camera mounted on a tripod positioned above the maze. We set up the maze in the field at least 200 m from the territory of the family, to avoid any interference (e.g. auditory cues) from noncaptured parent(s). We placed the maze in the shade to limit the effect of sunlight. Also, we chose a place protected from the wind and orientated the maze with the start arm facing the wind to limit the effect of the wind.

Odour Preference Trials

Chicks participated in two successive odour preference trials in the Y-maze: (1) conspecific odour preference trial (odour of an unfamiliar adult versus no odour); (2) parent odour preference trial (odour of an unfamiliar adult versus odour of a parent).

We conducted the trials in this order, because we wanted to test first whether chicks react to (prefer or avoid) the odour of a conspecific adult (even if not their parent). In the second trial, we tested whether chicks show a preference for (and thus

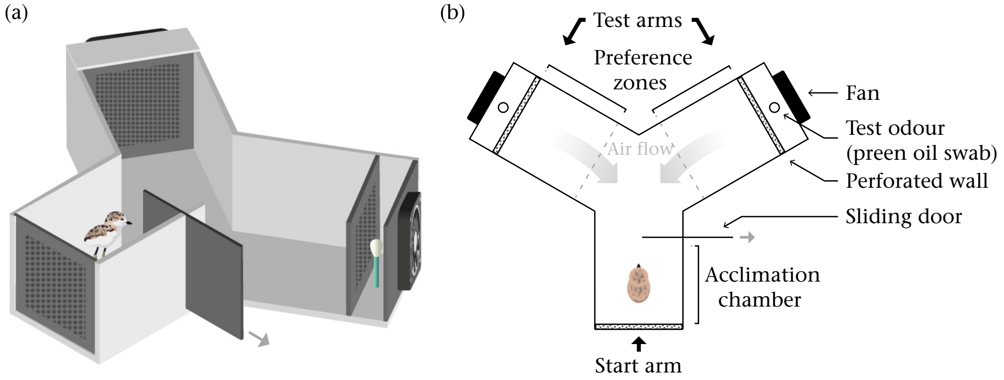

Figure 2. Schematic representation of the Y-maze (a) in 3D and (b) from above. The semitransparent ceiling and one opaque wall of the right arm are not displayed on the 3D representation for a better visualization of the inside of the Y-maze. At the start of a preference trial (i.e. when the door of the acclimation chamber was opened), the plover chick was allowed to explore the two test arms, from which came the odours, circulated by an air flow. To measure olfactory preferences, we recorded videos of the trials from above and measured the amount of time the chick spent with each test odour (i.e. in the preference zones) and which test odour it visited first.

discriminate) the odour of a parent over the odour of an unfamiliar adult. Using this fixed order, we reduced potential carryover effects (Bell, 2013), as chicks might have behaved differently in the second trial depending on whether they had been exposed to the odour of their parent in the first trial or not. The location (left or right arm of the Y-maze) of the test odours (parent odour, unfamiliar adult odour, absence of odour) was alternated systematically for each trial.

After capture, each chick was transported in a cotton bag to the Y-maze. The maze was washed with 96% ethanol and allowed to air dry before each trial to remove any odour residue. We placed the test odours at the end of the test arms and the chick in the acclimation chamber. When threatened, plover chicks hide and stay still for a while (from a few minutes to an hour) before going out to search for their parents. Thus, we decided on a 10 min acclimation period (in the dark acclimation chamber where chicks calmed down) to allow the chicks to feel confident enough to explore the Y-maze in search of their parents. After the acclimation period, we started video recording, turned on the fans and opened the door of the acclimation chamber to start the trial. The chick was allowed to explore the maze during a trial period of 15 min. If the chick did not leave the acclimation chamber, the trial was considered unsuccessful and was discarded. During the trial period, the chick could go in the test arms but also return to the start arm. In total, we recorded 44 conspecific odour preference trials (29 successful, 15 unsuccessful) and 30 parent odour preference trials (24 successful, 6 unsuccessful). Most chicks participated in both trials ($N = 30$ chicks), but some chicks participated only in the first trial (conspecific odour preference trial, $N = 14$ chicks), in those cases where no parent odour had been sampled. Chicks did not participate more than once in each trial. In successful trials, chicks did not necessarily make a single choice but rather explored the entire maze and often switched between arms. We scored the amount of time spent by the chick in each arm of the maze (up to 15 cm from the end of the arm, see ‘preference zones’ in Fig. 2) using the BORIS software (Friard & Gamba, 2016). Trials were scored blind with respect to the identity of the chick and the test odours. An example of a trial video is available in the Supplementary Material and at the repository PUB, Publications at Bielefeld University (https://pub.uni-bielefeld.de/record/2988559, https://doi.org/10.4119/unibi/2988559).

Ethical Note

This study was approved by the ‘Direction des Aires Protégées, des Ressources Naturellement Renouvelables et des Ecosystèmes’ from Madagascar (permits no. 386/21 and 282/23/MEDD/SG/DGGE/DAPRNE/SCBE.Re). We attempted to minimize the stress of the birds at all stages of the study. Chicks were captured by hand after careful observation and approach. The chick(s) were then placed under a shaded sieve in a trap (spring trap with remote trigger or funnel trap) to attract and capture the parents (Székely et al., 2008). If the parents were not trapped after 20 min, we stopped the capture attempt. After capture, birds were held in opaque cloth bags to minimize stress. The birds, when held in the cloth bags or during trials in the Y-maze, were always kept in a warm place (to avoid overcooling) in the shade (to avoid overheating). We started the behavioural trials immediately after the 20 min of capture attempt if no parent could be captured, or immediately after sampling the preen oil of a parent if a parent could be captured. Chicks were transported to the Y-maze in opaque cloth bags and were placed in a dark acclimation chamber in the Y-maze for 10 min to reduce stress before the trial. Parents were sampled, measured and ringed during the trials to minimize the handling time. After the trial(s), chicks were measured, sampled and ringed. We collected a small blood sample from all adults (25–50 μl blood) and chicks (10–25 μl blood) for sexing. Chicks were then released together with their sibling (if two chicks of a family were captured) and their parents (if their parents were captured) at the place where they were captured (Székely et al., 2008). Upon release, we made sure that the parents reunited with their chick(s). For families breeding on beaches, we tried to synchronize the release of the birds with the low tide so that they could feed directly after release. In total, birds were held between 45 min (in cases where only one chick of a family was tested for the first trial only) and 2 h 15 min (in cases where two chicks of a family were tested for both trials).

Statistical Analyses

Statistical analyses were conducted using all successful trials ($N = 29$ conspecific odour preference trials, $N = 24$ parent odour preference trials). We used as a preference measure the proportion of time spent in the arm with the unfamiliar adult odour relative to the time spent in both test arms, with values >0.5 indicating a preference for the unfamiliar adult odour and values <0.5 indicating a preference for the other odour (no odour in the first trial, parent odour in the second trial). For each trial, we ran a one-sample *t* test to test whether the proportion of time spent with the unfamiliar adult odour differed from 0.5 (i.e. if chicks showed a preference for either odour). In addition, we recorded the odour that the chicks visited first, as their first choice may also indicate a preference. For each trial, we ran a two-tailed binomial test to test whether they consistently visited one type of odour first. Trials from sibling chicks (11 families where two siblings were tested) were considered independent, as we used different test odours (although the same parent odour had to be used for both chicks in the parent odour preference trial, if only one parent could be captured, $N = 5$ families) and in different locations (left or right arm of the Y-maze).

For each trial, we controlled for the potential effect of the sex and the freshness (number of days between sampling of the odour and use in the trial) of the test odours. For the proportion of time spent with the unfamiliar adult odour we ran a beta regression using the glmmTMB package (Brooks et al., 2017), and for the odour visited first we ran a generalized linear model (GLM) with binomial distribution, both with 'sex' and 'freshness' of test odour as fixed effects. For the parent odour discrimination trial, the sex of test odour included three levels (mother versus unfamiliar female, mother versus unfamiliar male, father versus unfamiliar male; coincidentally there was no trial with father versus unfamiliar female) to test whether chicks showed stronger preferences when using the odour of their mother or that of their father. Because the sex of one test odour was unknown, these models included one fewer trial ($N = 28$ conspecific odour preference trials, $N = 23$ parent odour preference trials). We also investigated potential side biases (left or right) using one-sample *t* tests for the proportion of time spent in the test arms, and binomial tests for the arm visited first.

In an exploratory analysis, we investigated the behavioural response of the chicks to their first exposure to the Y-maze (i.e. novel environment). We measured the probability and latency to leave the acclimation chamber in the first trial, and tested whether these measures were affected by the sex and age of the chicks. We ran a generalized linear mixed model (GLMM) with binomial distribution to test for differences in the probability to leave the chamber (all first trials with sexed chicks, one trial per chick, $N = 42$ trials), and with gamma distribution to test for differences in the latency to leave the chamber (only successful first trials with sexed chicks, one trial per chick, $N = 28$ trials) using the lme4 package (Bates et al., 2014). For both models, 'sex' and 'age' of the chicks were included as fixed effects, while 'brood' was included as a random effect to control for the nonindependence of sibling chicks.

Model assumptions were verified using the performance package (Lüdecke et al., 2021) and plots were created using the ggplot2 package (Wickham, 2016). We assessed the significance of our tests at $\alpha = 0.05$ by checking *P* values (significant if $P < 0.05$) for all tests, and 95% confidence intervals (significant if 95% CI does not contain 0) for the fixed effects of beta regressions, GLMs and GLMMs. The analysis was performed in R v4.2.2 (R Core Team, 2022).

RESULTS

Chicks showed no preference in the conspecific odour preference trial. They did not spend more time in the arm with the odour of an unfamiliar adult (average ± SD = 131 ± 102 s) than in the arm with no odour (average ± SD = 123 ± 106 s; one-sample *t* test: mean [95% CI] = 0.51 [0.42, 0.62], $t = -0.88$, $P = 0.71$; Fig. 3), nor did they show any preference in their first choice (binomial test: probability [95% CI] = 0.45 [0.26, 0.64], $P = 0.71$). Chicks also exhibited no preference in the parent odour preference trial. They spent as much time with the odour of an unfamiliar adult (average ± SD = 134 ± 123 s) as with that of their parent (average ± SD = 115 ± 81 s; one-sample *t* test: mean [95% CI] =

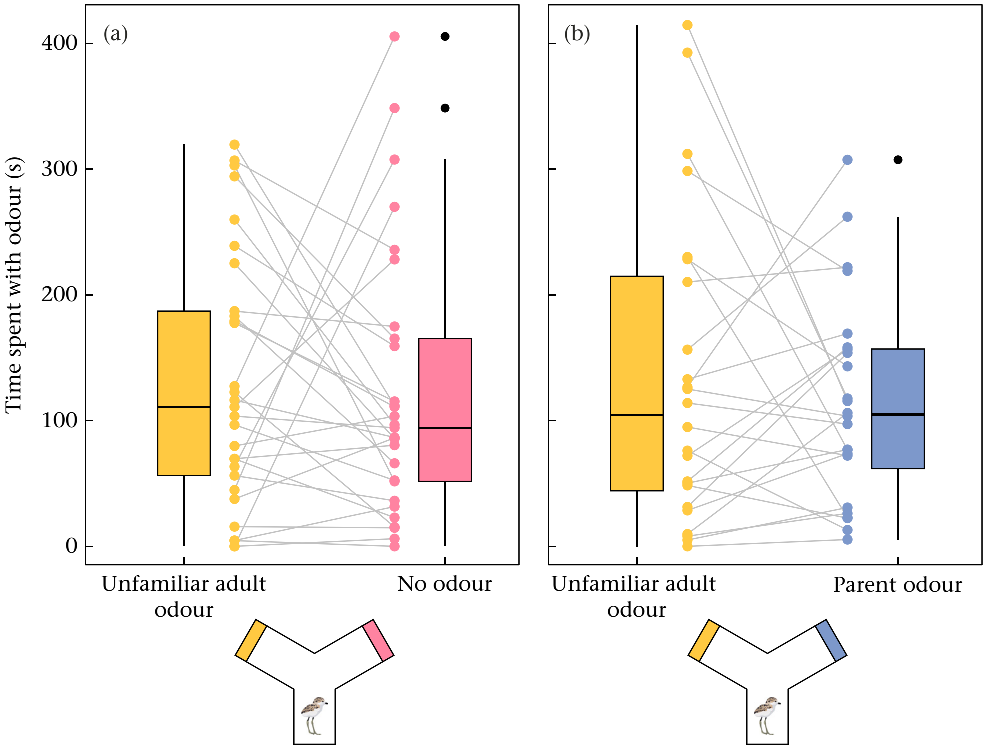

Figure 3. Time spent by plover chicks with (a) the odour of an unfamiliar adult versus no odour (conspecific odour discrimination trial, $N = 29$ trials) and with (b) the odour of an unfamiliar adult versus the odour of a parent (parent odour discrimination trial, $N = 24$ trials). Each grey line represents a chick in a trial. Trials lasted 15 min (900 s). Note that chicks could be in either test arm but also in the start arm. To test for chicks' preferences, we tested whether the proportion of time spent in the arm with the unfamiliar adult odour relative to the time spent in both test arms differed from 0.5 using one-sample *t* tests. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the black dots are outliers.

0.46 [0.35, 0.57], $t = -0.71$, $P = 0.48$; Fig. 3), and they did not visit first the odour of their parent (binomial test: probability [95% CI] = 0.56 [0.33, 0.74], $P = 0.83$). The preference measures (time spent with odour and odour visited first) were not affected by the sex or the freshness of the test odours (Tables A1, A2). The chicks showed no side bias in duration (one-sample t test: mean time spent in the left arm [95% CI] = 0.46 [0.36, 0.56], $t = -0.88$, $P = 0.38$) or their first choice (binomial test: probability of choosing the left side first [95% CI] = 0.48 [0.30, 0.67], $P = 1$).

The exploratory analysis revealed that the behavioural responses of the chicks to their first exposure to the Y-maze (novel environment) were affected by sex and age (Table A3). Males were less likely to leave the acclimation chamber than females (GLMM: odds ratio [95% CI] = 0.11 [0.02, 0.77], $P = 0.03$) and also waited longer than females before leaving the chamber (GLMM: estimate [95% CI] = 3.32 [1.05, 10.56], $P = 0.04$; Fig. 4). Older chicks were less likely to leave the chamber (GLMM: odds ratio [95% CI] = 0.83 [0.74, 0.93], $P = 0.002$) and waited longer before leaving the chamber (GLMM: estimate [95% CI] = 1.23 [1.08, 1.39], $P < 0.001$; Fig. 4). Because the model on the latency to leave the chamber included only chicks that left the chamber, and because older males were less likely to leave the chamber, the average age of males (3.6 days old) that left the chamber was lower than that of females (6.8 days old), although not significantly (t test: $t = 1.30$, $P = 0.21$).

DISCUSSION

Only recently have researchers started to study whether birds, as many other taxa, use olfactory cues for kin recognition. We tested for olfactory parent recognition in a precocial shorebird, where parent–offspring recognition should be important due to the high mobility of chicks and hence the high risk of brood mixing. Contrary to our predictions, we found neither a preference for the odour of an unfamiliar adult over a control (no odour) nor a preference for the odour of a parent over that of an unfamiliar adult. These results fit four mutually nonexclusive hypotheses.

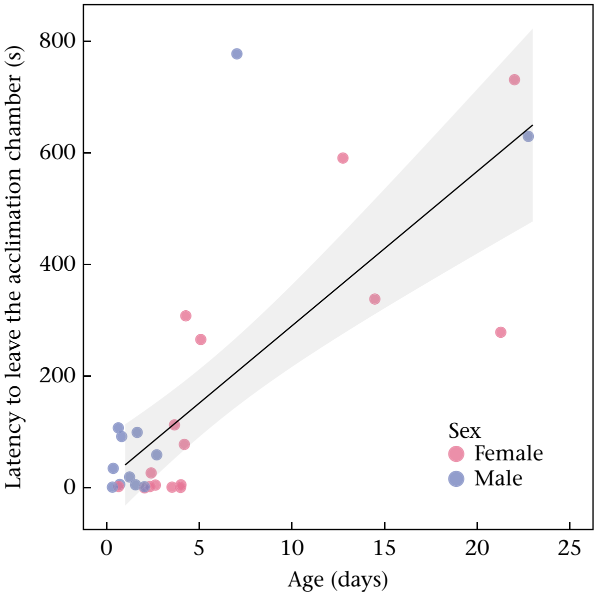

Figure 4. Sex and age differences in the latency of plover chicks to leave the acclimation chamber during their first trial in the Y-maze. The black line represents the linear regression, and the grey area the 95% confidence interval, of latency on age.

Ability to Smell

First, white-fronted plover chicks may not be able to perceive odours. Although we did not investigate the ability of chicks to smell (e.g. using a neurological approach), we think that this hypothesis is unlikely. Most of the bird species tested to date have been shown to have a functional sense of smell (Abankwah et al., 2020) and chicks of other bird species can discriminate odours shortly after hatching (Caspers et al., 2015, 2017; Porter et al., 1999). In fact, olfaction is among the first sensory systems to develop and is functional even before hatching (Bertin et al., 2010; Burne & Rogers, 1999; Lickliter, 2005). If olfactory parent recognition is acquired via associative learning (or imprinting), it may, however, be argued that chicks in our experiments were too young and did not have sufficient time to learn the odours from their parents. Indeed, associative learning seems to be the most common mechanism of parent recognition, and kin recognition in general (Komdeur & Hatchwell, 1999). Nevertheless, odour learning can start early during development, even in ovo, and very young chicks are able to recognize familiar odours (1-day-old and 4-day-old domestic chickens, Bertin et al., 2010; Burne & Rogers, 1999; 1-day-old and 2-day-old zebra finches, Caspers et al., 2015, 2017; 2-day-old tree swallows, Griebel & Dawson, 2020; 7-day-old blue tits, *Cyanistes caeruleus*, Rossi et al., 2017). On the contrary, we may even argue that chicks in our study were too old to respond to odours. Indeed, in some species, olfaction is mostly important during early life (i.e. shortly after birth or hatching) and becomes less important as visual and auditory senses develop (Lickliter, 2005). We hypothesize that, during the first days after hatching, altricial chicks may rely on odours more than precocial chicks, because their visual and auditory senses are less developed (e.g. closed eyes). This could explain why altricial chicks of zebra finches and tree swallows could discriminate parental odours (Caspers et al., 2017; Griebel & Dawson, 2020), while precocial plover chicks do not seem to. More studies on precocial species are needed to confirm this. In any case, we would rule out the possibility that white-fronted plover chicks are anosmic.

Need for Parent Recognition

Second, white-fronted plover chicks may not need parent recognition. Because white-fronted plovers are precocial, chicks are likely to encounter nonparent adults, from which they should not solicit parental care in order to avoid unnecessary energy expenditure, brood mixing, aggression or increased exposure to predators (Beecher et al., 1981; Davis & McCaffrey, 1989; Kalmbach et al., 2005; Lima, 2009). However, even at high nesting densities, white-fronted plover chicks will not encounter hundreds of conspecific adults, as is the case in colonially breeding species (Aubin & Jouventin, 1998). In addition, the costs of misidentification of parents may not be high. In fact, soliciting care from unrelated adults may bear no cost at all for the chicks, and may even be beneficial (Kalmbach, 2006). For example, adults may respond favourably to any begging chick (e.g. if they are unable to discriminate between kin and nonkin offspring, or if there is a low risk of misidentification combined with a low cost of caring for unrelated chick) and chicks may therefore safely and successfully beg towards unrelated adults (Beecher, 1988). This is for example the case in pied avocets, *Recurvirostra avosetta*, where chicks seem to benefit from joining other families (Lengyel, 2002). In conclusion, the selection pressure in this species may not be strong enough for parent–offspring recognition to evolve.

Alternatively, if the selection pressure for parent–offspring recognition is only moderate, unidirectional recognition might be sufficient (Knörnschild & von Helversen, 2008): chicks may not recognize their parents but their parents may recognize them. This way, chicks could simply respond to any adult providing care to them. If this is the case (i.e. offspring recognition only), we can question whether isolated chicks actually search for their parents actively (i.e. in a goal-oriented way, responding to parental cues), which was an assumption of this study, or whether they randomly move around to maximize the chance that their parents will find them. Interestingly, in ungulate species in which young hide between nursing periods (‘hider’ species), parent–offspring recognition is often unidirectional (either offspring recognition only or parent recognition only), and this has been assumed to be an antipredator adaptation (limiting the emission of cues on which predators could eavesdrop, Torriani et al., 2006). In plovers, chicks have a similar ‘hider’ antipredator strategy, and we can speculate whether this shaped a similar unidirectional parent–offspring recognition (offspring recognition only). To investigate this further, we should first test whether parent plovers can discriminate between their own chicks and foreign chicks (e.g. by auditory cues, olfactory cues or contextual cues like spatial cues or the size of the chicks). In such a scenario, where chicks should hide from olfactorily searching predators, we can also hypothesize that chicks would have a reduced odour to be olfactorily cryptic (Grieves et al., 2022).

Note that olfactory parent recognition has been reported in two altricial species (zebra finches and tree swallows, Caspers et al., 2017; Griebel & Dawson, 2020), where parent–offspring recognition is presumably not highly beneficial (Scheiber et al., 2017). Indeed, in altricial species, parents can locate their offspring simply by locating their nests, as chicks do not switch between nests, and discriminating between own and foreign nest would be sufficient (Becciu et al., 2021).

Finally, parent–offspring recognition can be beneficial not only during parental care, but also during subsequent breeding when offspring have reached sexual maturity. Indeed, parents and offspring should recognize each other during mate choice to avoid inbreeding (Bonadonna & Sanz-Aguilar, 2012), notably in philopatric species (regardless of altricial or precocial development). For example, in the philopatric European storm petrels, parents and their past offspring seem to discriminate and avoid each other (also based on olfactory cues) during mate choice (Bonadonna & Sanz-Aguilar, 2012). To summarize, (1) parent recognition may not be highly beneficial in this species, and it would be interesting to investigate olfactory parent recognition in a species with higher risk of intermingling between families (e.g. colonially nesting species with precocial chicks); (2) parent–offspring recognition may be unidirectional in this species, so we should test for olfactory offspring recognition in adults.

Need for Olfactory Cues

Third, chicks may use other cues than odours to recognize their parents. Chicks from other Charadriiformes species (i.e. shorebirds, gulls, auks and allies) seem to rely on auditory cues for parent recognition (e.g. laughing gull, *Larus atricilla*, Beer, 1969; thick-billed murre, *Uria lomvia*, Lefevre et al., 1998; although more evidence is needed for shorebirds, Johnson et al., 2008). A hint that acoustic parent–offspring recognition occurs in white-fronted plovers is that both adults and chicks were calling when they were reuniting after the behavioural trials (M. Gilles, personal observations). It would be interesting to investigate whether white-fronted plover chicks recognize parents based on their calls. None the less, even if Charadriiformes species (including white-fronted plovers) use calls for recognition, they may use odours in addition (multimodal communication, Higham & Hebets, 2013). Indeed, in several species, parent recognition is not based only on calls, but on a combination of sensory cues. For example, in domestic sheep, *Ovis aries*, young use auditory and visual cues to recognize their mother over long distances, and olfactory cues at a closer range (Lindsay & Fletcher, 1968). Following this hypothesis, it could be that odours alone (not in combination with calls) are not sufficient for chicks to recognize their parents. To our knowledge, our study is the first to investigate olfactory parent recognition in a Charadriiformes species (in fact in any other avian order than Passeriformes). The absence of evidence reported in this study should not discourage researchers from studying olfactory communication in these species. Quite the contrary, olfactory communication has already been reported in some Charadriiformes species (crested auklet, *Aethia cristatella*, Hagelin, 2007; black-legged kittiwake, *Rissa tridactyla*, Pineaux et al., 2023) and more research is needed to establish whether there is olfactory parent–offspring recognition in this order.

Methodological Limitations

Fourth, the absence of preferences in our experiments might be due to methodological limitations. First and foremost, we acknowledge that this study lacks a positive control, that is, evidence that the experimental set-up can elicit preferences in plover chicks. To validate the methodology, we could have run preference trials using stimuli that chicks are expected to prefer (e.g. warmth versus cold, food versus no food). However, our methodology should be valid, because we followed methods from other studies (Y-maze set-up, odour stimuli, duration of habituation and test periods, scoring of preferences) that successfully detected odour preferences in adults of various bird species, both in captivity (13 songbird species and one parrot species, Grieves et al., 2019; Krause et al., 2023; Van Huynh & Rice, 2019; Whittaker et al., 2011; Zhang et al., 2010; Zhang et al., 2013) and in the wild (three seabird species, Bonadonna & Mardon, 2010; Bonadonna & Sanz-Aguilar, 2012; Leclaire, Bourret, et al., 2017; Leclaire, Strandh, et al., 2017; Mardon & Bonadonna, 2009). In addition, studies also detected olfactory preferences in chicks, using similar two-choice experiments in the wild (European storm petrel chicks, Mínguez, 1997; Leach's storm petrel chicks, O'Dwyer et al., 2008). We note that the studies performed in the wild were all conducted on burrowing seabirds, for which the Y-maze may be less stressful. It is possible that the chicks were too agitated (e.g. because of the isolation or the apparatus) during the trials to exhibit any preference. Yet we believe that our trials are ecologically relevant, because we investigated parent recognition in the context of chicks losing contact with their parents (e.g. after hiding from a predator), which is also stressful. To overcome the possible hindering effect of the agitation of the chicks, we would need to capture complete families and keep them in captivity for a few days to habituate the chicks, before sampling parental odours and conducting trials with habituated chicks.

Second, we used preen oil swabs from adult birds as odour stimuli. Although preen oil is an important source of avian body odour (Mardon et al., 2011), it is not the only one (e.g. plumage, skin or faeces, Hagelin & Jones, 2007). Furthermore, preen oil substances may be altered once spread onto the plumage (e.g. by feather microbiota, Jacob et al., 2014), and as a result plumage and overall body odour may differ from preen oil odour (e.g. Alves Soares et al., 2024; Leclaire et al., 2019). In contrast to our study, the two previous studies on parent recognition in zebra finches (Caspers et al., 2017) and tree swallows (Griebel & Dawson, 2020) used overall body odours as odour stimuli. Thus, we cannot rule out the possibility that chicks in our study can recognize their parents by smell, but not based on preen oil odours only. However, dark-eyed juncos, *Junco hyemalis*, and song sparrows, *Melospiza* *melodia*, responded to preen oil odours in similar Y-maze trials (Grieves et al., 2019; Whittaker et al., 2011).

Third, it might be possible that the test odours have faded after sampling and were not strong enough to be perceived by the chicks. This is unlikely, however, as chicks did not respond to parent odours, which were sampled right before the trial, and we found no effect of the freshness of the test odours (number of days between sampling of the odour and use in the trial) on the behaviour of the chicks.

Fourth, it is possible is that the chicks could discriminate between the odours but, as they could not find any adult bird in the Y-maze, they ceased searching after a while. This was probably not the case, however, since we also found no preference at the beginning of trials (i.e. first odour visited).

Finally, it could be that there was no preference in the second trial (unfamiliar adult odour versus parent odour) because of the simultaneous presentation of odours, which can hamper preferences (Krause & Caspers, 2012). However, this is unlikely as an explanation here since the chicks also showed no preference in the first trial (unfamiliar adult odour versus no odour), where only one odour was presented at a time.

Sex and Age Differences in Behaviour

Although this was not part of our initial study questions, we found sex and age differences in the behavioural response of chicks to a novel environment. During their first trial in the Y-maze, females were more likely (and took less time) to leave the acclimation chamber than males, and younger chicks were more likely (and took less time) to leave the acclimation chamber than older chicks. These differences in movement in a novel environment may reflect differences in exploration, risk taking, boldness or proactivity (Réale et al., 2007; Verbeek et al., 1994). The age effect was expected from our field observations, as young chicks did not stay still as long as older chicks during capture attempts, which facilitated their capture. This may be explained by the fact that younger chicks need more brooding from their parents (Colwell et al., 2007; M. Gilles, personal observations) and may thus be more motivated (or more quickly motivated) to search for them. The sex effect, however, is an exciting finding. Indeed, early sex differences in behaviour were unexpected and may have long-term consequences (e.g. behaviour at adulthood, survival, dispersal). Indeed, in the same white-fronted plover population, it was found that females have a higher apparent survival during their first year than males (Eberhart-Phillips et al., 2018). This female-biased survival may be explained by early sex differences in behaviour (e.g. if more explorative female chicks are more efficient at foraging, Verbeek et al., 1994, but see Bijleveld et al., 2014), but may also be explained by demographic causes (e.g. male-biased dispersal, Eberhart-Phillips et al., 2018). In any case, these preliminary results should be considered with caution, as the study was not designed to test for personality (a single trait measured only once per individual, Beckmann & Biro, 2013; Réale et al., 2007). Nevertheless, this interesting result warrants further research on interindividual differences in behaviour in this species.

Conclusion

Although parent–offspring recognition can be mediated by odour cues in birds, and although parent–offspring recognition should be important in this precocial species, we found no evidence of olfactory parent recognition in white-fronted plover chicks. It may be that plover chicks do not need to discriminate between parents and foreign adults, or that they rely on other (e.g. auditory) cues. It is also possible that chicks can discriminate parental and conspecific odours but that our experiment failed to detect it. More research is needed to understand how common and important olfaction is for parent recognition in birds. Precocial species are well suited to address this question, as (1) they probably need parent–offspring recognition, and (2) Y-maze trials can easily be conducted on mobile chicks. Finally, our study revealed that female and male chicks may differ in their behaviour, which calls for more research on individual differences in behaviour in this species.

Author Contributions

Marc Gilles: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sama Zefania:** Writing – review & editing, Project administration, Investigation. **Tafitasoa J. Mijoro:** Investigation. **Innes C. Cuthill:** Writing – review & editing, Funding acquisition, Conceptualization. **Tamás Székely:** Resources, Methodology, Conceptualization. **Barbara A. Caspers:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

Data and R code used in the analyses are available in the Supplementary Material and at the repository PUB, Publications at Bielefeld University (https://pub.uni-bielefeld.de/record/2988559, https://doi.org/10.4119/unibi/2988559).

Declaration of Interest

The authors declare there are no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.08.007.

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Appendix

Table A1

Effect of the sex and freshness of the test odours (preen oil) on the preference of chicks in conspecific odour trials (unfamiliar adult odour versus no odour)

Fixed effects	β estimate	95% CI	*P*
Response: proportion of time spent with unfamiliar adult odour			
Intercept	−0.23	[−1.28, 0.81]	0.66
Odour sex (male)	0.25	[−0.67, 1.17]	0.59
Odour freshness	0.02	[−0.18, 0.22]	0.84
Response: odour visited first			
Intercept	−2.52	[−6.47, 0.02]	0.11
Odour sex (male)	2.06	[−0.09, 5.16]	0.10
Odour freshness	0.32	[−0.15, 0.94]	0.23

Results from beta regression (proportion of time spent with unfamiliar adult odour relative to the time spent in both test arms) and binomial linear regression (odour visited first). Odour freshness is the number of days between the sampling of the unfamiliar adult odour and the trial. $N = 28$ trials. CI: confidence interval.

Table A2
Effect of the sex and freshness of the test odours (preen oil) on the preference of chicks in the parent odour trials (unfamiliar adult odour versus parent odour)

Fixed effects	β estimate	95% CI	*P*
Response: proportion of time spent with unfamiliar adult odour			
Intercept	−0.31	[−1.00, 0.37]	0.37
Odour sex (unfamiliar male vs mother)	0.81	[−0.24, 1.88]	0.13
Odour sex (unfamiliar male vs father)	0.54	[−0.28, 1.35]	0.20
Odour freshness	0.09	[−0.25, 0.08]	0.30
Response: odour visited first			
Intercept	−0.69	[−2.50, 0.88]	0.41
Odour sex (mother vs unfamiliar male)	1.62	[−0.83, 4.86]	0.23
Odour sex (father vs unfamiliar male)	1.16	[−0.69, 3.22]	0.23
Odour freshness	0.11	[−0.28, 0.57]	0.57

Results from beta regression (proportion of time spent with unfamiliar adult odour relative to the time spent in both test arms) and binomial linear regression (odour visited first). The reference level of odour sex is unfamiliar female versus mother. There was no trial with odours from unfamiliar female versus father. Odour freshness is the number of days between the sampling of the unfamiliar adult odour and the trial (the parental odour was always sampled on the day of the trial). $N = 23$ trials. CI: confidence interval.

Table A3
Effect of the sex and age of plover chicks on their probability and latency to leave the acclimation chamber during their first trial (conspecific odour preference trial)

Effects	Type	β estimate	95% CI	*P*	Variance	SD
Response: probability of leaving the chamber						
Intercept	Fixed	3.76	[1.57, 5.96]	**<0.001**	–	–
Sex (male)	Fixed	−2.22	[−4.18, −0.26]	**0.027**	–	–
Age	Fixed	−0.18	[−0.30, −0.07]	**0.002**	–	–
Brood ID	Random	–	–	–	0	0
Response: latency to leave the chamber (s)						
Intercept	Fixed	1.68	[0.31, 3.06]	**0.016**	–	–
Sex (male)	Fixed	1.20	[0.05, 2.36]	**0.041**	–	–
Age	Fixed	0.21	[0.08, 0.33]	**<0.001**	–	–
Brood ID	Random	–	–	–	3.26	1.81

Results from generalized linear mixed models (GLMMs) with binomial distribution (probability of leaving the chamber) and gamma distribution (latency to leave the chamber). Probability of leaving the chamber was recorded for all chicks that participated in the trial ($N = 42$ chicks from 32 broods), while latency to leave the chamber was measured only in chicks that left the chamber ($N = 28$ chicks from 21 broods). Estimates of probability of leaving the chamber are log-odds and should be exponentiated to obtain odds ratios. $P < 0.05$ indicated in bold. CI: confidence interval.

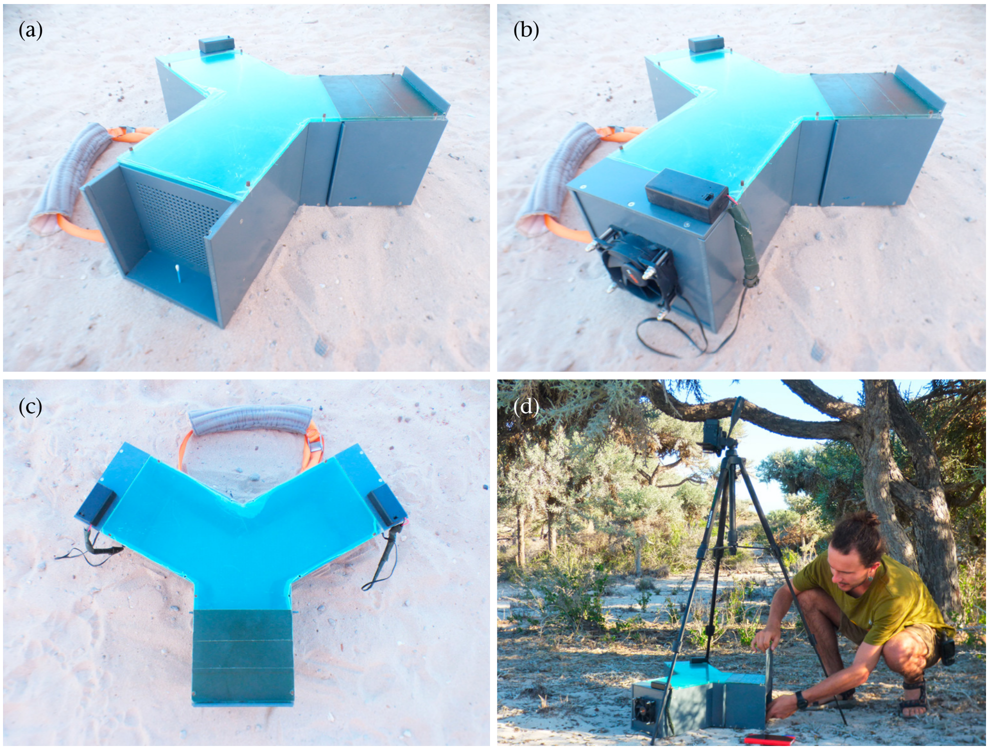

Figure A1. Y-maze apparatus used to conduct olfactory preference trials on plover chicks in the field. The Y-maze consisted of one start arm (with opaque cover) and two test arms (with semitransparent cover). At the end of each of the two test arms, we placed (a) a test odour (cotton swab with or without preen oil) and (b) an electric fan powered by a battery, which circulated air from the test odour towards the inside of the maze through a perforated wall. We recorded the preference trials (c) from above, (d) using a camera mounted on a tripod, directly in the field.