

Unconditional adoption rules out the need for parent–offspring recognition in a single-brooded colonial seabird

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Abstract

Parent–offspring recognition (POR) is fundamental in colonial birds when the potential intermingling of chicks is higher due to the large number and proximity of nests. In species with isolated nests, where chick presence in the nest is strong contextual evidence of kinship, there might be circumstances when the parent might doubt the identity of the chick, but not enough to reject it. Olfactory-based recognition of conspecifics and nest sites in birds has gained strong evidence suggesting a potential role of olfaction in POR. Despite that, there are no studies testing it. We used Scopoli's shearwater (*Calonectris diomedea*) as model colonial single-brooded species with a developed olfactory sense, usually breeding in well-spaced nests with low probability of chicks mixing. We tested the parent's ability to selectively respond to their own chick as opposed to a simpler rule of feeding any chick found in the nest by means of chick-fostering experiments. We designed two cross-fostering experiments using chicks of different ages to test whether the ability of parents to recognize a related chick develops over time, possibly after acquiring an own distinctive odour. Finally, we also manipulated nests' odour to disentangle the confounding effect of nest site recognition from POR when parents return at night. All experimental chicks were adopted by parents as the weight and bill growth of cross-fostered chicks did not differ significantly from the control group. We recorded a small difference in weight when foster chicks were inside an odour-manipulated nest; although we did not record weight loss in experimental chicks, only a steeper increase in weight was observed in control chicks. In conclusion, adoption in Scopoli's shearwater seems to follow the rule "if the young is in my nest, accept it" proposed by Beecher (1991) for species with spatially separated nests and low chick mobility.

KEYWORDS

cross-fostering, Kin recognition, Scopoli's shearwater

1 | INTRODUCTION

Natural selection favours individuals that support genetic relatives over individuals that give such aid indiscriminately (Hamilton, 1964). Parent–offspring recognition (POR)—, that is the ability to respond selectively to one's own eggs/chicks and parents (Hepper, 2005)—is thoroughly studied in avian brood parasitism co-evolutionary systems (Davies, 2000) and to some extent in colonial species where

POR is crucial to find and feed one's own offspring (Jouventin & Aubin, 2002; LeFevre et al., 1998; McCracken, 1984; McCracken & Gustin, 1987). In birds, hosts can reject natural or experimental parasitic chicks by nest desertion (Grim et al., 2003; Langmore et al., 2003), refusal to feed them (Lichtenstein, 2001; Payne et al., 2001) or by directly attacking, killing and/or ejecting them from the nest (Soler et al., 1999). The acceptance of an unfamiliar non-kin chick or egg is mainly due to two types of recognition error: perceptual

error and template error (Shizuka & Lyon, 2020). Perceptual errors occur because there are cognitive limits to an organism's ability to accurately discriminate between objects. Template errors are mistakes during the process of acquiring a recognition "template", that is a neural representation of the "correct" cues of their own eggs or chicks. Correct template acquisition can partially prevent brood parasitism by conspecifics, as in the case of the American coot (*Fulica americana*) (Shizuka & Lyon, 2020).

In seabirds, POR seems particularly important for colonial species where the potential intermingling of chicks is higher due to the large number and proximity of nests, as demonstrated in numerous species with highly mobile nestlings: penguins (Coffin et al., 2011; Davis & McCaffrey, 1989; Jouventin & Aubin, 2002), murrelets (LeFevre et al., 1998) and several gull species (Evans, 1970; Falls, 1982). On the contrary, when the nests are isolated by natural barriers (i.e. holes in a rock wall, burrows, etc.) or by long distances, discrimination is not always beneficial for the parent, like in Kittiwakes (*Rissa tridactyla*, Storey et al., 1992). There might be circumstances when the parent is reasonably certain that an individual in its nest is not its offspring, but not certain enough to take the risk of rejecting it. Therefore, recognition failure reflects conservative decision-making rather than perceptual inability. In many species with isolated nests, the presence of a nestling inside the nest is a strong contextual evidence that the young inside it is in fact the very parents' offspring. Consequently, the prior odds of a young being unrelated are negligible, often close to zero. In these circumstances, natural selection might favour a simple decision rule, such as "if the young is/are in my nest, accept it" (Beecher, 1991; Strickler, 2013), meaning that the role of nest recognition is crucial (Mínguez, 1997) for the recognition and provisioning of the offspring inside.

In Procellariiformes (albatrosses, petrels and shearwaters), the importance of olfactory cues in recognizing the nest, conspecifics and even one's own eggs has been investigated in several species, both on solitary and colonial breeders (e.g. Benvenuti et al., 1993; Bonadonna, 2009; Bonadonna & Nevitt, 2004; Cunningham et al., 2003; Gabirot et al., 2018; Leclaire et al., 2017a, 2017b; Wenzel, 1985). Furthermore, olfactory abilities might also be involved in social and familiar interactions as POR (Bonadonna & Sanz-Aguilar, 2012; Caspers et al., 2017), but there are no studies on petrels and shearwaters to date.

In this study, we investigated the existence of POR, the propensity for adoption and the role of olfaction in recognizing nests and chicks in breeding Scopoli's shearwaters (*Calonectris diomedea*). The Scopoli's shearwater is a single-brooded colonial seabird whose olfactory ability has been already investigated in various contexts such as homing and foraging behaviour (Benvenuti et al., 1993; Dell'Ariccia et al., 2014; Pollonara et al., 2015), thus representing an excellent model species to experimentally test whether olfaction is also involved in parent-offspring interactions. We assumed that nest identification (mediated by olfactory cues) can facilitate chick recognition, thus resulting in adopting (i.e. feeding) the nestling inside the burrow regardless of its genetic relatedness. Consequently, we hypothesized that the odour of an unfamiliar non-kin chick may

somehow change the propensity of parents to provision and adopt it. In particular, we expected that this propensity could change at older ages when chicks progressively develop the uropygial gland and its oil is distributed on the feathers while preening, likely producing an individual odour (Célérier et al., 2011; Wenzel, 1985). In addition, or alternatively, the propensity to adopt would change when chicks become more vagile and the probability of mixing with the others increases (Lengyel et al., 1998; Archuby et al., 2010).

Here, we designed three experimental settings to test (i) the effect of age on chick adoption and recognition (cross-fostering experiment at different ages), (ii) the effect of an unfamiliar odour on nest recognition by the parents (nest odour manipulation) and (iii) the effect of having an unfamiliar chick and a different nest odour (cross-fostering of chicks and nest odour manipulation) simultaneously. In the cross-fostering experiment, parents face the choice of feeding the unfamiliar non-kin chick either as their own, to feed it less or not to feed it at all. In the case of nest odour manipulation, parents from the treatment group experience their nest with a different scent, and misidentifying their nest could result in insufficient feeding of their own chick. Specifically, we predict that (1) the older the foster chick, the lesser the probability of being adopted and fed by foster parents; also (2) we expect a decrease in chick weight in nests treated with a different odour, determining the importance of the nest as the main guarantee of relatedness. Finally, (3) we expect an even stronger negative effect of both treatments (cross-fostering and nest odour manipulation) on provisioning and consequently on chick weight.

2 | MATERIALS AND METHODS

2.1 | Study site and species

The study was carried out in Linosa island (Pelagian Islands, Sicily Channel: 35°52' N, 12°52' E, 5.4 km²) from July 25 to September 10 of 2014. Linosa hosts the largest European colony of Scopoli's shearwaters (Massa & Lo Valvo, 1986), a colonial Procellariiform characterized by extended incubation (about 54 days) and rearing (about 90 days) periods of a single chick. Parental care is equally shared by partners during incubation and chick rearing by visiting nests only at night (Becciu et al., 2012). Adults seem to find their colony (Gagliardo et al., 2013; Pollonara et al., 2015) and nest in the darkness using both visual and olfactory cues (Benvenuti et al., 1993; Dall'Antonia et al., 1995). Chicks likely stimulate their parents with persistent begging calls (Quillfeldt et al., 2004; Träger et al., 2006) and are fed with highly energetic stomach oil (Warham, 1977).

2.2 | Experiments

During the experimental period, chicks were measured every day in the evening from 18:00 to 20:00 h (local time GMT+2). The handling took about 2–3 min. Chicks used in the experiments were randomly

chosen from nests with a minimum inter-nest distance of 50 m among those usually monitored in the colony (more than 400 nests). It should be noted that during the experimental period there was some disturbance from nightclubs close to the shearwater colony, but the nests considered in this study were at least 500 m away from this and hopefully unaffected (Cianchetti-Benedetti et al., 2018a). The chosen chicks were split into experimental group (cross-fostered or nest odour manipulation) and control group (chicks remaining in their nest) (Table 1). Before the assignment to the experimental groups, we weighed the chicks and measured their bill length to use chicks of similar size for the experiments. Wilcoxon test showed that there is no difference in the median between the two groups for the first experiment (weight: $W = 90$, p -value = .73; bill: $W = 88$, p -value = .66) and for the second (weight: $W = 47$, p -value = .16; bill: $W = 78$, p -value = .75) (see Figures S1–S2). Also, we recorded their hatching date, so we could divide them into two age groups. The expected sex ratio after hatching should be 1:1 as previously found for this species (Genovart et al., 2005); therefore, we expect the ratio be maintained since the assignment of the chicks to the treatment and control groups was random, thus minimizing possible effects of sex in growth rate.

We performed two cross-fostering experiments to test the effect of chick age on parent recognition ability; in the first one, we switched 14.3 (SD: ± 1.8)-day-old chicks, whereas in the second experiment the average age of the chicks was 40.7 ± 3.89 days (mean \pm SD). After the cross-fostering, chicks remained in the adoptive nest for 10 and 13 days, respectively. Body mass and bill length (a measure of growth less sensitive to fluctuation) were systematically measured with a spring scale (Pesola[®], max 1000 g, precision 5 g) and a digital calliper (max 150 mm, precision 0.1 mm), respectively, at a three-day interval to limit the disturbance produced by the manipulation (see Carey, 2009, 2011). If chicks were not readily fed by the adoptive parents, we expected to find a decrease in body weight and the absence of bill length growth from Day1 of the experiment(s). Considering that chicks lose on average 10–30 g/day (Cianchetti-Benedetti et al., 2018a) when they are not fed and that in this period individual parents potentially return to their nests almost every day (Cianchetti-Benedetti et al., 2018b), a 10–13-day experimental period should have allowed us to observe any potential difference in weight change. At the end of the experiments (Day10 or Day13, after the last measurements were taken), the cross-fostered chicks

were returned to their native nest where they remained until they successfully fledged at the end of October. The nests and consequently the chicks used were different for each experiment.

We performed a nest odour experiment to test the potential effect of nest site (mediated by its specific odour) on chick provisioning and indirectly on chick recognition. We manipulated the natural nest odour introducing an unfamiliar odour of Citronella Essential Oil, Naissance[™] (United Kingdom)—hereafter CO—into each experimental nest (see Table 1). We selected this odour because it is commonly used in experiments with lab rodents due to its persistence and mild repellent effects (Singla & Kaur, 2014). The odour treatment included the placement of two plastic beakers filled with 20 ml of CO into each experiment day. The plastic beakers were filled with cotton and protected on top with a plastic mesh to prevent the intrusion of the birds' beak. The first beaker was placed at the nest entrance, and the second was hidden inside the nest. Ten chicks were assigned to the odour manipulation treatment with CO, and 12 chicks were monitored without any treatment (control group). The last experiment was conducted combining treatments from both experimental tests: we cross-fostered 10 chicks, and we treated their nests with CO as described above. We compared the treatment group with a control group of 18 chicks. The control group was treated with empty beakers, in order to account for the effect of the beakers' presence inside the nests. We measured the weight of the chicks every day from Day1 to Day4 in nests treated with CO and from Day1 to Day3 in nests with CO and cross-fostered chicks. In this case, the experimental period was shorter compared to the other two experiments because we expected to observe an immediate effect of CO odour on chick provisioning. The chicks in the last three experiments had similar starting weights, and their age ranged between 4 and 6 weeks.

2.3 | Ethical note

All experiments were performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes and in accordance with ASAB/ABS guidelines. The study was conducted under a permit issued by the Regione Siciliana and Assessorato Risorse Agricole e Alimentari.

TABLE 1 Summary information of the experiments

Experiment	N (control)	N (experimental)	Duration (days)	Measures	Sampling interval
Cross-fostering age 1	14	14	10	Weight, bill length	Every 3 days (D1, D4, D7, D10)
Cross-fostering age 2	12	12 ^a	13	Weight, bill length	Every 3 days (D1, D4, D7, D10, D13)
Nest odour manipulation	12	10	4	Weight	Everyday (D1–D4)
Cross-fostering + Nest odour manipulation	18	10	3	Weight	Everyday (D1–D3)

^aTwo chicks were found predated (probably by cats) during the experimental period between D4 and D7; we excluded them from the analysis.

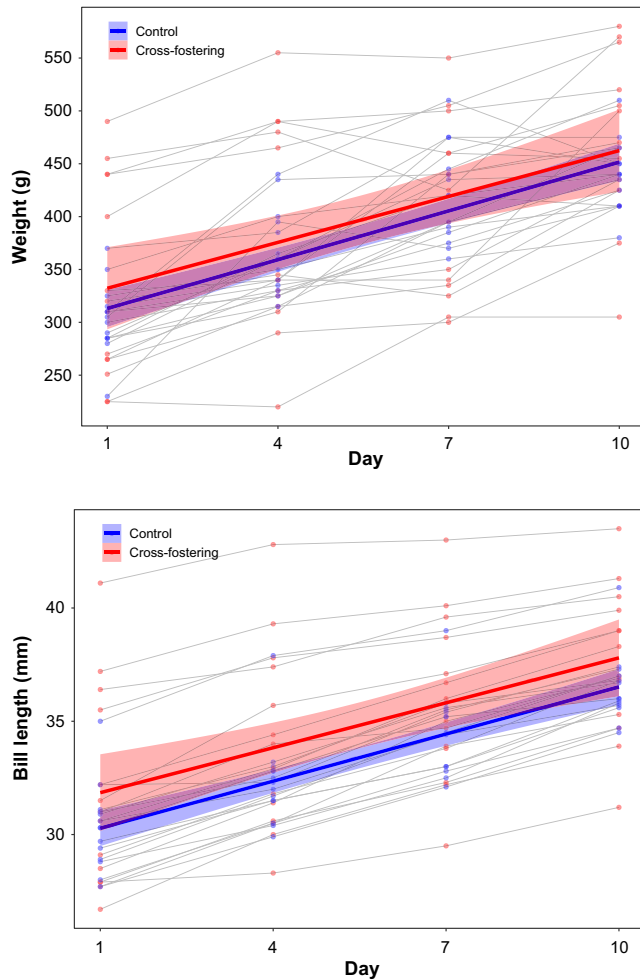


FIGURE 1 Body weight (top) and bill length (bottom) of cross-fostered and control chicks at starting age of 14.3 ± 1.76 days. Measurements were taken every 3 days. Dots represent individual values with grey lines connecting them. Regression lines are represented with 95% C.I. [Colour figure can be viewed at wileyonlinelibrary.com]

Disturbance to the study species was low because of the short duration of manipulation and the few visits to each nest. Both the cross-fostering or nest odour manipulation procedures took less than 5 min. As previously mentioned, there was no evidence of any effect on fledging success.

2.4 | Statistical analysis

To test the difference in chicks' growth rate (i.e. weight and bill length) among treatments, we ran a linear mixed-effect model (LMM) for each experiment with day of treatment (Day), group (Control or Experimental) and their interaction as a fixed structure, with the chick's ID as random intercept. For each model, we focused primarily on the interaction term to evaluate the slope differences between the groups during the experimental days. Statistical analyses and graphs were done using packages "lme4" (Bates et al., 2015)

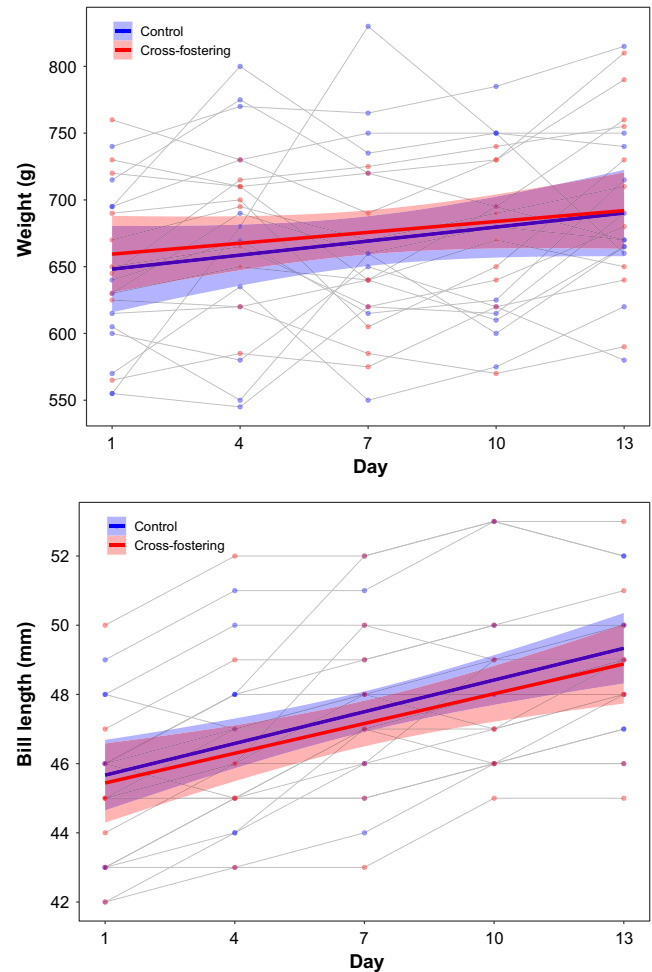


FIGURE 2 Body weight (top) and bill length (bottom) of cross-fostered and control chicks at starting age of 40.7 ± 3.89 days. Measurements were taken every 3 days. Dots represent individual values with grey lines connecting them. Regression lines are represented with 95% C.I. [Colour figure can be viewed at wileyonlinelibrary.com]

and "ggplot2" (Wickham, 2016), respectively, in R 4.0.2 (R Core Team, 2020).

3 | RESULTS

The cross-fostering treatment of chicks at different ages did not cause any significant change in chick weight and bill length between fostered and control individuals (Figures 1 and 2). The nest odour manipulation experiment showed that unfamiliar CO odour did not influence the behaviour of breeding birds to feed their offspring, in fact chick weight in nests treated with CO was similar to that of control nests during the treatment period (Figure 3). In contrast, the cross-fostering +nest odour manipulation experiment highlighted a weight difference between groups (estimate = -19.69 , lower C.I. 95% = -30.41 , upper C.I. 95% = -8.98 , $t = -3.6$, $p < .001$; Figure 4). Since the confidence interval is quite large, the result must be taken

cautiously, but indeed the control chicks on average increased in weight by 16 g/day, whereas chicks switched to treated nests remained at nearly the same weight. Full model results are reported in Supplementary Materials.

4 | DISCUSSION

In this study, we used two experimental approaches, a manipulation of the nest odour and a cross-fostering procedure, separately and combined, to test the propensity of breeding Scopoli's shearwaters to adopt a non-kin chick. The cross-fostering was intended to modify the cues associated with the chick, while the odour manipulation served to modify the cues associated with the nest. Our results showed that neither the novel odour added to the nest nor the cross-fostering of chicks at different ages, when used separately, affected adoption by the adult breeders. When the two conditions were used in combination there was a difference in body mass between the control and the cross-fostered chicks. However, the fostered chicks did not lose weight. If chicks had not been fed, they should have lost between 10 and 30 g/day (Cianchetti-Benedetti et al., 2018a), but since their weight remained stable, there has likely been an initial reluctance of the adults to feed non-kin chicks but then adoption progressed. Other possible reasons for this small difference in weight could be that foster chicks begged in a different way or were stressed by being in a different nest and/or having an unfamiliar odour in the nest.

The results of our manipulations also did not support the prediction that propensity to adopt a foster chick varied with the age of the chick and that older chicks had lower probability to be adopted by foster parents than younger chicks. The lack of a significant between-group difference in both cross-fostering experiments can be explained by the fact that we used chicks up to ca. 54 days old

(fledging is at ca. 90 days), which probably had not yet fully developed their preen gland and consequently their individual smell.

We expected a possible rejection of older chicks which we related to the development of an individual odour occurring later during the development, similarly to that found in blue petrels (*Halobaena caerulea*) where the chicks develop their own odour just before fledging, coinciding with full development of the preen gland (C  lerier et al., 2011). However, this was not the case in our study. In fact, adoption occurred during the initial phase of the chick rearing period (2 weeks old), as well as when chicks were older (6 weeks old). Taken together these results prove that breeding Scopoli's shearwaters adopt and feed a non-kin chick as their own at various stages of its development and that continue to attend their nest even when confounded by an unusual novel odour. This behaviour seems to be the result of a strong attachment to the nest and an extraordinary motivation to fulfil the reproductive duties across all phases of the breeding season. The nest represents the only place where the parents can meet, and it is defended by both partners from their first arrival to the colony in February, after winter migration, until their departure for post-breeding migration eight months later at the end of October. Every year, parental investment is condensed in the production of one single egg. The incubation period is one of the longest among birds of similar size (51 days on average in our study population), and when the birds are in the phase of chick rearing, they have already invested so much in time and effort that they would not take the risk of any failure. Therefore, they are so determined to carry on achieving the breeding success that adoption represents a compulsory behavioural response to any chick or egg in their nest. Opportunistic field observations made in a colony of Cory's shearwater (*Calonectris borealis*), a species closely related to our study model, revealed that two ca. 10-day-old chicks (one being an outsider) can live together in the same nest and can be fed

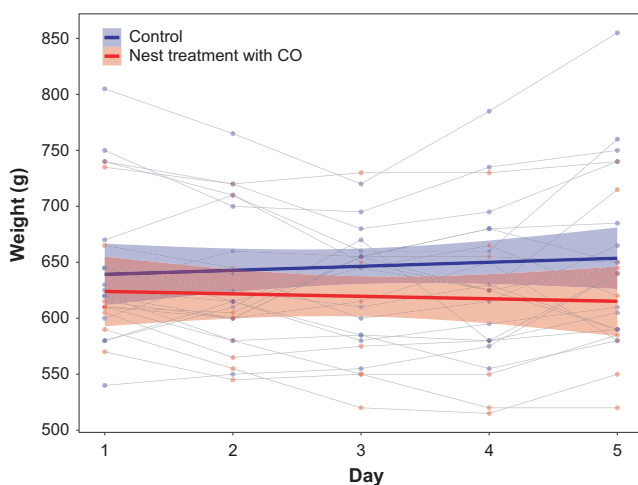


FIGURE 3 Body weight of chicks in nests treated with Citronella Essential Oil (CO) and control ones during the experimental period. Measurements were taken every day. Dots represent individual values with grey lines connecting them. Regression lines are represented with 95% C.I. [Colour figure can be viewed at wileyonlinelibrary.com]

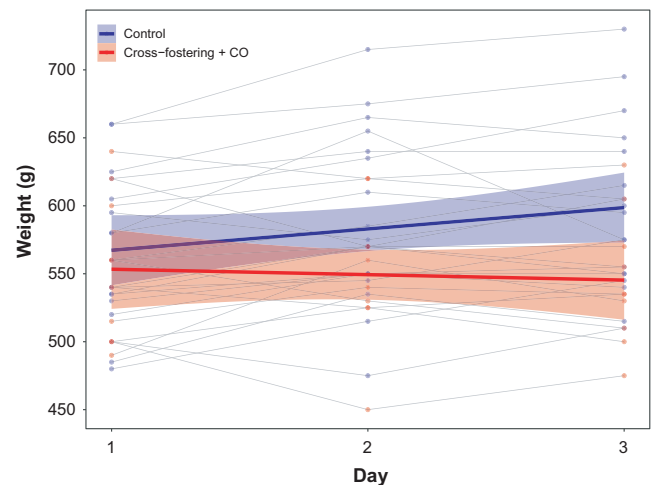


FIGURE 4 Body weight of experimental chicks (cross-fostered in a nest treated with Citronella Essential Oil (CO) and control chicks during the experimental period. Measurements were taken every day. Dots represent individual values with grey lines connecting them. Regression lines are represented with 95% C.I. [Colour figure can be viewed at wileyonlinelibrary.com]

by the same pair of parents for at least a week, thus supporting the fact that in the early developmental stage breeding shearwaters can even adopt a non-kin chick in the presence of their own chick (Romero J. and Campioni L. pers. obs., see Table S7). Given these considerations, there seems not to be a need for POR in shearwaters.

The possibility that POR is absent in altricial species like shearwaters has been already suggested by Beecher (1988) who argued that there is no obvious necessity for it, in contrast to nidifugous species. In addition, the low probability of intermingling of chicks in shearwaters likely promotes no selection on recognition of non-familiar nestlings and facilitates adoption. This is the case also for other seabirds, such as thick-billed murre (*Uria lomvia*) and kittiwakes (*R. tridactyla*), in which fostered chicks were adopted until the age of ca. 15–18 days from hatching. After that age, they received less food from the adoptive parents, but they were not abandoned (LeFevre et al., 1998; Storey et al., 1992). A similar situation also occurred in species such as the colonial cave swallow (*Petrochelidon fulva*; Strickler, 2013), suggesting that this kind of behaviour is common in colonial breeding species which in spite of living in different environments experience similar breeding conditions.

In Procellariiformes, the sense of smell has been suggested to enable birds to locate their nest in the colony at night (Bonadonna, 2009; Bonadonna et al., 2004; Wenzel, 1985) and for storm petrel chicks in recognizing their nest (Dell'Ariccia et al., 2015). The existence of a chemically unique scent label (Celerier et al., 2011; Mardon et al., 2010), the capacity to distinguish the scent of genetically related individuals which have been documented in European storm petrels (*Hydrobates pelagicus*; Bonadonna & Sanz-Aguilar, 2012) and the fact that nests are concentrated in the same caves (Minguez, 1996) point to the existence of POR. On the one hand, surprisingly, in this species adults breeding in a cave identify their nest not by olfaction but by using other proprioceptive cues (Dell'Ariccia et al., 2015), and parents do not discriminate between their own offspring and their neighbours (Minguez, 1997). On the other hand, storm petrel chicks can wander among neighbouring nests and do not get lost; in fact, they can recognize the scent of their nest and find it at night and in total darkness (Minguez, 1997) and distinguish their own odour and the parents' scent (De Leon et al., 2003). In addition, chicks can chase away an intruder chick when it approaches their nest (Minguez, 1997).

The absence of POR emerged from our study using odours rules out the involvement of other communication cues, like vocalizations. In fact, even if we did not control for acoustic cues and the fostered chicks might have emitted begging calls of different intensity and frequency than the control chicks, acoustic cues *per se* had no effect on deterring adoption of the foster chicks. In line with this, a study on thin-billed prions (*Pachyptila belcheri*) shows that vocalization varies largely among chicks and does not indicate the "level of hunger" of the chick (Quillfeldt et al., 2010). On the contrary, a study on Cory's shearwater found that begging behaviour changes with body condition and adults can modulate their rate of feeding, increasing

it when chicks are begging more and have poorer body condition (Granadeiro et al., 1999).

One important consideration must be made: the absence of POR based on olfactory cues emerged from our manipulations does not exclude the existence of olfactory discrimination abilities in this species. In particular, an individual scent based on a bouquet of a few lipid compounds that are present in different combinations has been reported to provide a unique olfactory signature (Bonadonna, 2009; Bonadonna & Mardon, 2013; Célérier et al., 2011; Strandh et al., 2012). The typical Procellariiform odour is produced by the lipid secretion of the uropygial and other exocrine glands (Wenzel, 1985) and is spread on the body when the birds preen. The odour signature probably emerges with the development of the preen gland around fledging (Célérier et al., 2011).

One clear-cut conclusion we can draw from our experiments is that there could be no selection mechanisms to favour POR in a species with low probability of mixing chicks, such as the Scopoli's shearwater or at least not until the age of approximately 54 days. Furthermore, several studies on non-marine species (Beecher, 1991; Beecher et al., 1981, 1985; Strickler, 2013) underline the importance of the social context for POR, showing that it is well developed in three colonial species, but it is absent or weak in two solitary nesters (Beecher, 1991; Beecher et al., 1981, 1985) and one colonial species with separated nests, without probability of mixing chicks (Strickler, 2013). In species that breed in colonies, with close nests, it is important to recognize one's own nest among the others. Feeding the chick inside the nest is a direct consequence of successful nest recognition (Strickler, 2013). This is supported also by observation of albatrosses feeding their chicks only when they are in the nest cup (P. A. Prince, personal communication, cited in Minguez, 1997) and, when chicks stay outside the nest, they hurry back to their nests as soon as the parent reappears (Richdale, 1952, cited in Warham, 1990). In addition, we must say that so far our nest odour manipulation protocol (i.e. use of disruptive odour) has worked on Manx shearwaters (*Puffinus puffinus*; James, 1986) but was unsuccessful in several other attempts, which failed to be published due to negative results. In those experiments, lavender oil and toilet deodorants were used in nests of blue petrels and Antarctic prions (*Pachyptila desolata*) that were still able to find their nests despite added odours (F. Bonadonna, unpublished data).

In conclusion, in this study we found that Scopoli's shearwater breeding adults adopt and feed any chick up to 54 days old in their nest as their own offspring. The birds seem to follow the rule "if the young is in my nest, accept it" as proposed by Beecher (1991) for species with separated nests and low chick mobility. The adoption is confirmed by the continuous feeding of the chicks regardless of all experimental manipulations, and probably such an unconditional behavioural response is related to high parental investment ruling out POR.

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AUTHOR CONTRIBUTIONS

PB and GD conceived the study and designed the experiments. PB collected the data, performed the analyses, interpreted the results and made the graphics. GD and LC fundamentally contributed to the interpretation of data and drafting of the manuscript. BM substantially contributed to conception and design of the study. All authors have been involved in drafting the manuscript and revising it critically for important intellectual content. All authors gave their final approval of the manuscript to be published.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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