




Biological Sciences

Do chinstrap penguins use olfactory cues for partner recognition?

Luisa Amo^{1,2,3,4} , Miguel Ángel Rodríguez-Gironés³  and Andrés Barbosa² 

¹Area of Biodiversity and Conservation, Universidad Rey Juan Carlos, Móstoles, Spain; ²Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain; ³Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (CSIC), La Cañada de San Urbano, Almería, Spain and ⁴Instituto de Cambio Global, Universidad Rey Juan Carlos, Móstoles, Madrid, Spain

Abstract

Although there is increasing evidence that birds have individual chemical profiles that can be used in different social contexts, partner scent recognition has only been explored in procellariiform seabirds, a group of birds known for their highly developed olfactory system. However, olfaction is not restricted to Procellariiformes, and birds with smaller olfactory bulbs can also use chemical cues in different social contexts. More evidence from different bird groups is needed to disentangle whether olfaction plays a general role in partner recognition. We performed a choice experiment to examine whether chinstrap penguins *Pygoscelis antarcticus* can discriminate the scent of their partner from the scent of other conspecifics. Our results do not suggest a preference of penguins for the scent of their partners. Our results highlight the need to carry out additional studies to determine the mechanisms underlying partner recognition in penguins.

Keywords: Antarctic penguin; avian olfaction; partner scent recognition; *Pygoscelis antarcticus*

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Introduction

The size of the olfactory bulb, relative to brain size, has been proposed as an indicator of the ability of birds to detect and use chemical cues. The first studies on the olfactory capability of birds were performed with species with bigger olfactory bulb sizes, such as Procellariiformes (Bang & Cobb 1968). However, subsequent evidence suggests that birds with smaller bulbs, such as Passeriformes, can also detect odours in different contexts and with several functions (Avilés & Amo 2018). Today, a growing body of evidence shows that many bird species use chemical cues in their interactions with other species and their abiotic environment (for reviews, see Hagelin 2007a, Hagelin & Jones 2007, Caro & Balthazart 2010, Abankwah *et al.* 2020). Examples of the use of chemical cues by birds include, among others, the assessment of predation risk (Amo *et al.* 2008, 2011, Roth *et al.* 2008), the detection of the aromatic plants that some bird species introduce into their nests (Petit *et al.* 2002, Mennerat *et al.* 2005, Gwinner & Berger 2008) and orientation and navigation (Wallraff 2004, Mahr *et al.* 2022). Olfaction also seems to play an important role in foraging, from the acceptance of novel foods (Marples & Roper 1996, Kelly & Marples 2004) to food/prey location (e.g. Nevitt 2011, Amo *et al.* 2013a,b, Mrazova *et al.* 2019, Hernández *et al.* 2023). The results of a comparative study suggest that the olfactory capability of birds varies across bird species in relation to diet type and ecological conditions, suggesting that foraging mode has played an important role in the evolution of olfaction in birds (Avilés & Amo

2018). Furthermore, the olfactory capability of birds seems also to be related to their social complexity, with colonial species having relatively larger olfactory bulbs (i.e. greater olfactory abilities) than territorial breeders (Avilés & Amo 2018).

Therefore, olfaction seems to play an important role in social behaviour, although our knowledge regarding the importance of chemical cues in these intraspecific interactions is still far from what we have with regards to other taxa (Hagelin 2007a,b, Caro & Balthazart 2010, Abankwah *et al.* 2020). Birds have been shown to use chemical cues to identify their own nests (e.g. De León *et al.* 2003, Bonadonna *et al.* 2004, Caspers & Krause 2011, Krause & Caspers 2012). It has also been shown that chemical signals play a role in the social behaviour of crested auklets (Hagelin 2007b), and Hirao and collaborators (2009) found that mate preference of domestic cockerels involves olfactory responsiveness to the female's uropygial secretions. Psittaciformes (Zhang *et al.* 2010) and Passeriformes (Whittaker *et al.* 2011, Amo *et al.* 2012b) can discriminate the sex of conspecifics using chemical cues alone, and the source of scent that these birds are detecting is the uropygial gland secretion (Whittaker *et al.* 2011) that these birds spread on their feathers (Jacob & Zisweiler 1982). The activity of the uropygial gland as well as the composition of its secretion have been shown to vary not only between the sexes (e.g. Whittaker *et al.* 2011, Amo *et al.* 2012b, Gilles *et al.* 2024), but also among seasons (e.g. Reneerkens *et al.* 2002, Amo *et al.* 2012b, Grieves *et al.*, 2019a, 2022), age classes (Amo *et al.* 2012b), diets (e.g. Sandilands *et al.* 2004a,b), hormone levels (e.g. Whelan *et al.* 2010, Whittaker *et al.* 2018), levels of parasite infection (Pap *et al.* 2010, Grieves *et al.* 2018), body condition and immune status (Moreno-Rueda 2010, 2015), polymorphism (Tuttle *et al.* 2014), individuals (Mardon *et al.* 2010, Whittaker *et al.* 2010, Leclaire *et al.* 2011a) and even with genetic

Corresponding author: Luisa Amo; Email: luisa.amo@mncn.csic.es

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heterozygosity (Leclaire *et al.* 2011b, 2014, Strandh *et al.* 2012, Slade *et al.* 2016, Whittaker *et al.* 2019). Birds are even known to discriminate the immunological characteristics of potential partners by using chemical cues (Leclaire *et al.* 2017, Grieves *et al.* 2019b, but see Amo *et al.* 2022). Therefore, the chemical cues that birds emit may convey potentially useful information during social interactions (for reviews, see Campagna *et al.* 2012, Alves Soares *et al.* 2024), such as kin recognition (Coffin *et al.* 2011, Bonadonna & Sanz-Aguilar 2012, Krause *et al.* 2012, Leclaire *et al.* 2017), rival assessment (Amo *et al.* 2012a, Amo & López Rull 2024) and mate choice (Bonadonna & Sanz-Aguilar 2012, Grieves *et al.* 2019b).

Detection of chemical cues during the breeding period may be useful in sexually monomorphic species, long-term monogamous species and those that breed in colonies. In these cases, chemical cues may allow birds to discriminate between individuals. To our knowledge, the only studies in which a recognition of the scent of partners has been examined have been performed with procellariiform seabirds, finding that Antarctic prions *Pachyptila desolata* (Bonadonna & Nevitt 2004), Wilson's storm petrels *Oceanites oceanicus* (Jouventin *et al.* 2007) and blue petrels *Halobaena caerulea* (Mardon & Bonadonna 2009) preferred the odour of their partner to the odour of another conspecific. Procellariiformes are known to have one of the most developed olfactory systems among birds (Bang & Cobb 1968), and it is also already known that they use olfaction for locating food (Nevitt 2008, 2011) and finding their burrows at night (e.g. Minguéz 1997, Bonadonna *et al.* 2003a,b, 2004, De León *et al.* 2003). While there is no reason to expect that all bird species use the same type of information in social contexts, recent evidence suggests that olfaction plays a role in intraspecific interactions in other groups apart from Procellariiformes (Coffin *et al.* 2011, Whittaker *et al.* 2011, Amo *et al.* 2012a, Krause *et al.* 2012, Grieves *et al.* 2019b), and therefore it is clearly necessary to increase the range of bird species in which chemical recognition of their partners is investigated.

In this context, we performed an experiment aimed at examining the ability of chinstrap penguins *Pygoscelis antarcticus* to discriminate the scent of their partners from the smell of other conspecifics. Although interindividual variation in the calls of chinstrap penguins (Bustamante & Marquez 1996) could allow acoustic communication to play a role in partner recognition, as has been observed in other penguin species (Clark *et al.* 2006), acoustic cues need not be the only ones involved in partner discrimination. Furthermore, non-acoustic cues may provide relevant information about the emitter, beyond its identity. For example, Humboldt penguins *Spheniscus humboldti* can use olfaction for kin recognition (Coffin *et al.* 2011). Therefore, we hypothesized that chinstrap penguins may be able to discriminate the scent of their partners from other conspecifics, even if partner recognition is not exclusively based on chemical cues. We offered wild chinstrap penguins the scents of two individuals, their partner and a conspecific, and noted their choice. We expected that chinstrap penguins would spend longer close to the scent of their partner than to that of a conspecific.

Materials and methods

Study area

We performed an experiment in natural conditions at a breeding rookery (20 000 breeding pairs; Lynch *et al.* 2012) of chinstrap penguins in the Vapour Col rookery on Deception Island, South Shet-

lands (63°00'S, 60°40'W) during the summer (January/February) of 2011. The experiment was performed from 11h00 to 17h00.

Experimental design

We performed the experiment when penguins were rearing ~20 day-old nestlings in order to minimize the disturbances on nestlings due to the capture of adults. During this late time of the guard phase, one of the parents would be in the nest taking care of nestlings while the other parent foraged at sea. Therefore, both parents spent only short periods of time together, when one parent returned from the sea and replaced the other in taking care of the nestlings. We observed penguins and located nests where both parents met. When one of the parents left the nest to go to the sea, we simultaneously captured with a long-handle net both the penguin that went to the sea (focal penguin) as well as the penguin that had arrived from the sea and would be taking care of the nestlings (partner). Another researcher observed the nestlings to monitor where they were and to prevent predation by skuas, as they remained alone during the capture of the adults. No chicks were lost during these captures. We placed the focal penguin in the habituation area of the experimental enclosure (see below). We obtained the scent of the partner by rubbing its body with absorbent paper for 1 min, focusing mainly on the feathers close to the uropygial gland to transfer its secretions from the feathers to the absorbent paper. After that, the penguin was released, and we ensured that it returned to the nestlings. All of the adults returned to take care of their nestlings. Simultaneously, we also captured a different penguin that was walking from the sea to the nest and obtained its scent using the same methodology. By selecting conspecific penguins that were walking from the sea to the colony we ensured that the papers containing conspecific scents were marked similarly to those containing the partner scent. After that, we took a blood sample from the conspecific penguin's foot vein using a needle and a heparinized capillary tube. A drop of blood was preserved in alcohol for molecular sexing following Ellegren (1996). The penguin was then immediately released at the point of capture, and we observed that it resumed its walk towards the colony.

The experiment was performed in a T-shaped mesh enclosure built using 50 cm-high chicken wire (mesh size 1.3 cm) and located in front of and 50 m away from the closest breeding sub-colony and 300 m away from the coast (Fig. 1). Both experimental arms of the enclosure were equally distant from the colony and the sea to avoid any confounding effects due to the possible attraction of penguins to such places. We used a mesh enclosure as chinstrap penguins are not burrow nesters. Both the 'vertical' and 'horizontal' segments of the T-shaped mesh enclosure were 150 × 50 cm corridors (Fig. 1). Just outside these arms, in the outer side of the experimental area (Fig. 1), we placed the two absorbent papers marked with the scents of the partner and the conspecific. The locations of the treatments in the enclosure were balanced between sides between trials (in nine trials the partner scent was located to the right and in nine trials the partner scent was located to the left). After each trial, the enclosure was cleaned with ethanol.

We captured 54 adult penguins (18 focal penguins and their partners and 18 conspecifics). After a brief habituation period of 10 min at the base of the central arm (habituation area; Fig. 1), focal penguins were released into the choice area, from which they could enter the left and right arms (experimental areas; Fig. 1) of the T-maze. The penguins moved continuously between both arms of the enclosure. Therefore, all penguins moved close to the

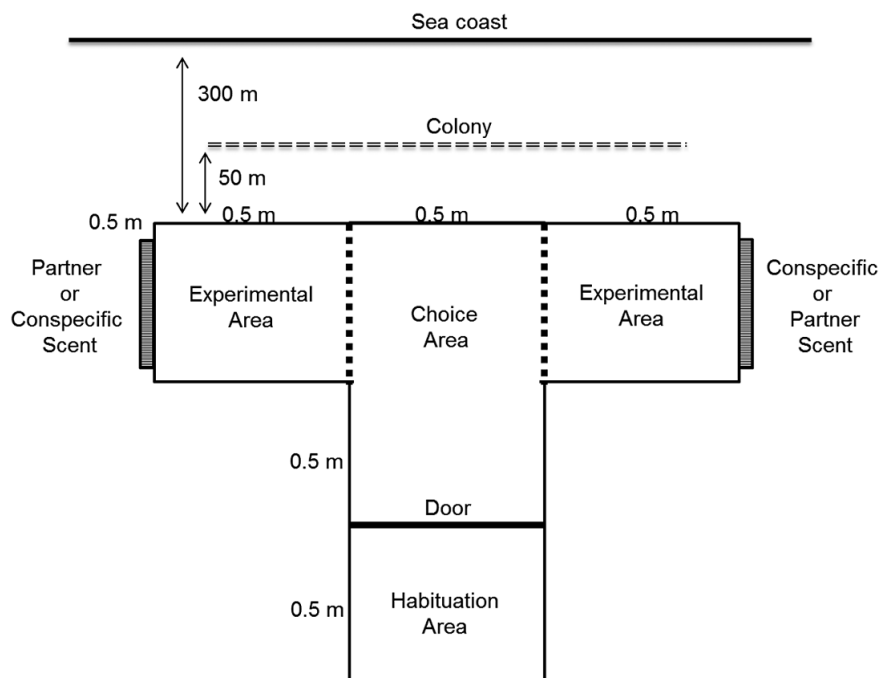


Figure 1. The enclosure where the experiment was carried out, with sizes indicated in metres. Grey boxes represent the absorbent papers soiled with the scent of a conspecific or a partner. The enclosure was located 50 m perpendicularly from the nearest sub-colony and 300 m from the coast. Dotted lines separating the choice and experimental areas do not represent physical barriers: penguins were free to move throughout the enclosure once the door of the habituation area was opened.

absorbent papers marked with the scents, and so they could detect these scents.

An observer situated 20 m from the enclosure recorded the times that penguins spent in each sector of the enclosure over a period of 10 min. Due to methodological restrictions, the observer was not blind to the treatments. After the trials, we took a blood sample (see above) from the experimental penguin, marked it with an indelible pen on one foot to avoid recapture and immediately released it in the exact place where it had been captured. Birds were kept in captivity for a maximum of 20 min. All of the birds showed normal behaviour after release (i.e. they continued on their way to the sea).

Data analysis

We compared the time that penguins spent close to their partner's scent and the time they spent close to the conspecific's scent by using two-tailed Wilcoxon matched pairs tests. The molecular analysis of sex determined that the focal birds consisted of 8 females and 10 males. Seven of the eight females were tested with their partner and the scent of a female conspecific, and only one was offered the choice between her partner scent and the scent of another male (see Table 1). By contrast, the sample was more balanced in the case of males, with six males choosing between their partner's scent and a conspecific male scent and four males choosing between their partner's scent and the scent of another conspecific female (see Table 1). Statistical analyses were performed with STATISTICA 8.0. We calculated the power of the statistical test with *G*Power* 3.1.9.7.

Results

Penguins did not spend more time close to their partner's scent than close to the conspecific's scent (Wilcoxon matched pairs test,

Table 1. Numbers of male and female focal penguins that were offered the choice between the scent of their partners and the scent of a male or a female conspecific.

		Focal penguin	
		Female	Male
Conspecific penguin	Male	1	6
	Female	7	4

$Z = 1.16$, $P = 0.25$, $n = 18$). This lack of preference for the scent of conspecifics was observed in males (Wilcoxon matched pairs test, $Z = 0.65$, $P = 0.51$, $n = 10$) as well as in females (Wilcoxon matched pairs test, $Z = 0.70$, $P = 0.48$, $n = 8$; Fig. 2).

With this sample size and fixing an alpha value of 0.1 (to minimize the probability of incurring a type II error), as well as a large effect size of 0.25 (to simulate the magnitude estimate of an effect of biological interest), the power of our test is 0.40. Furthermore, with a smaller effect size of 0.15, the power of our test is 0.25. Therefore, even with a large effect size, we may not be able to detect true choice differences.

Discussion

We found no preference of penguins for the scent of their partners. Chinstrap penguins are monogamous, and no extra-pair fertilizations have been observed in this species (Moreno *et al.* 2000). They do not renest if their nest is lost (Viñuela *et al.* 1995). Furthermore, the experiment was performed at the end of the breeding season, so we might not expect penguins to be interested in the scent of a conspecific in a context of mate searching. However, interpreting scent preferences in a choice experiment can be difficult because, even though the study was performed during the reproductive period of the species and we may expect a preference for the scent of their

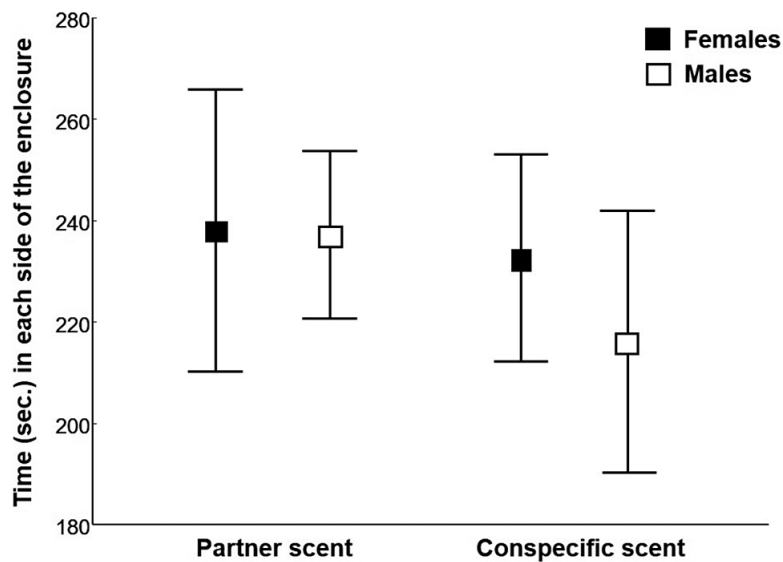


Figure 2. Mean time (\pm SE) in seconds that focal male (white squares, $n = 10$) and female (black squares, $n = 8$) penguins spent in the side of the enclosure containing the scent of their partner or the scent of a conspecific.

partners, odour preferences may be related to other behaviours that also take place during the reproductive period, such as territorial defence. Chinstrap penguins defend their nests against intruders (Müller-Schwarze 1984, Viñuela *et al.* 1995), and therefore, despite the recognition of their partner, they may also spend time close to a conspecific scent to evaluate their rival instead of remaining close to their partner's scent. These aggressive interactions have also been observed outside the territory and have been proposed to explain previous results in the case of sex discrimination in other bird species. For example, in both dark-eyed juncos *Junco hyemalis* (Whittaker *et al.* 2011) and spotted starlings *Sturnus unicolor* (Amo *et al.* 2012b) males were attracted to the scents of other males instead of female scents, probably because males may be more motivated to expel potential rivals than to search for a female. Our results do not show differences in the scent preferences of males and females, despite chinstrap penguin males being more aggressive than females, at least against human intruders (Viñuela *et al.* 1995). Therefore, our results suggest that chinstrap penguins do not use olfaction to recognize their partners, in contrast with previous results in procellariiform species such as Antarctic prions (Bonadonna & Nevitt 2004), Wilson's storm petrels (Jouventin *et al.* 2007) and blue petrels (Mardon & Bonadonna 2009).

This lack of preference of chinstrap penguins for the scent of their partners cannot be explained by the lack of olfactory capability of the species because results from a previous study showed that chinstrap penguins are able to use olfaction to detect dimethyl sulphide (Amo *et al.* 2013a), a molecule that signals high-productivity areas in the oceans (Nevitt 2011). In addition, it has been recently shown that other penguin species can use olfaction not only in foraging (African penguins; Cunningham *et al.* 2008, Wright *et al.* 2011), but also in social interactions such as kin recognition (Humboldt penguins; Coffin *et al.* 2011). However, despite previous evidence showing that chinstrap penguins have a functional olfactory apparatus, our results suggest that they do not use olfaction to recognize their partners, or at least that they do not exhibit a preference for the scent of their partners. Therefore, other senses may be responsible for partner recognition in this species. All penguin species studied to date can discriminate between con-

specific calls (Jouventin 1982), including discrimination of their partners from other conspecifics (e.g. Clark *et al.* 2006). Therefore, in chinstrap penguins, acoustic communication (Bustamante & Marquez 1996) may be sufficient for partner recognition, and they might not need to use olfaction in partner recognition. In contrast, although procellariiform species also use vocalizations in social communication, predation pressures and the lack of visual cues due to their nocturnal habits may have also favoured the use of chemical cues in their social life (Nevitt 2008, van Buskirk & Nevitt 2008).

The lack of partner scent preference might, in principle, be a methodological artefact if we had been unable to capture the penguin scents in the absorbent papers. The strong penguin smell detected by the human nose (L. Amo, pers. obs.) makes this explanation improbable. Furthermore, Coffin and collaborators (2011) used a similar methodology to show that Humboldt penguins can use scents to assess kinship. Therefore, we do not think that the lack of preference for a partner's scent can be attributed to a methodological artefact related to the scent source or the protocol of scent collection. We performed the experiment when penguins were rearing ~20 day-old nestlings in order to minimize the disturbances on nestlings due to the capture of the adults. Therefore, we also cannot exclude the possibility that penguins might behave differently at the start of the season, when partners are meeting again.

To summarize, chinstrap penguins do not exhibit a preference for the scent of their partners over a conspecific's scent, at least under the experimental conditions tested. However, a potential explanation of the lack of partner scent preference found in our study could be that our study had low statistical power. Thus, with a sample size of 18 penguins and fixing an alpha value of 0.1, we might have not detected even large differences in preference (i.e. effect size: 0.25; power: 0.40). This low statistical power calls into question whether our results are conclusive, and these results should be interpreted with caution. Therefore, our study highlights the need for carrying out further experiments to disentangle the possible role of olfaction in partner recognition and other social relationships in penguins.

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Author contributions. LA, MAR-G and AB conceived the study and performed the experiments, the data analysis and the interpretation of results. LA prepared the first version of the manuscript.

References

- ABANKWAH, V., DEEMING, D. & PIKE, T. 2020. Avian olfaction: a review of the recent literature. *Comparative Cognition & Behavior Reviews*, **15**, 10.3819/CCBR.2020.150005.
- ALVES SOARES, T., CASPERS, B.A. & LOOS, H.M. 2024. Volatile organic compounds in preen oil and feathers - a review. *Biological Reviews*, **99**, 10.1111/brv.13059.
- AMO, L. & LÓPEZ-RULL, I. 2024. Zebra finch females avoided the scent of males with greater body condition. *Birds*, **5**, 10.3390/birds5010009.
- AMO, L., RODRÍGUEZ-GIRONÉS, M.A. & BARBOSA, A. 2013a. Olfactory detection of dimethyl sulphide in a krill-eating Antarctic penguin. *Marine Ecology Progress Series*, **474**, 10.3354/meps10081.
- AMO, L., VISSER, M.E. & VAN OERS, K. 2011. Smelling out predators is innate in birds. *Ardea*, **99**, 10.5253/078.099.0207.
- AMO, L., AMO DE PAZ, G., KABBERT, J. & MACHORDOM, A. 2022. House sparrows do not exhibit a preference for the scent of potential partners with different MHC-I diversity and genetic distances. *PLoS One*, **17**, 10.1371/journal.pone.0278892.
- AMO, L., GALVÁN, I., TOMÁS, G. & SANZ, J.J. 2008. Predator odour recognition and avoidance in a songbird. *Functional Ecology*, **22**, 10.1111/j.1365-2435.2007.01361.x.
- AMO, L., JANSEN, J.J., VAN DAM, N.M., DICKE, M. & VISSER, M.E. 2013b. Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecology Letters*, **16**, 10.1111/ele.12177.
- AMO, L., LÓPEZ-RULL, I., PAGÁN, I. & MACÍAS GARCÍA, C. 2012a. Male quality and conspecific scent preferences in the house finch *Carpodacus mexicanus*. *Animal Behaviour*, **84**, 10.1016/j.anbehav.2012.09.021.
- AMO, L., AVILÉS, J.M., PAREJO, D., PEÑA, A., RODRÍGUEZ, J. & TOMÁS, G. 2012b. Sex recognition by odour and variation in the uropygial gland secretion in starlings. *Journal of Animal Ecology*, **81**, 10.1111/j.1365-2656.2011.01940.x.
- AVILÉS, J.M. & AMO, L. 2018. The evolution of olfactory capabilities in wild birds: a comparative study. *Evolutionary Biology*, **45**, 10.1007/s11692-017-9427-6.
- BANG, B.G. & COBB, S. 1968. The size of the olfactory bulb in 108 species of birds. *Auk*, **85**, 10.2307/4083624.
- BONADONNA, F. & NEVITT, G.A. 2004. Partner-specific odour recognition in an Antarctic seabird. *Science*, **306**, 10.1126/science.1103001.
- BONADONNA, F. & SANZ-AGUILAR, A. 2012. Kin recognition and inbreeding avoidance in wild birds: the first evidence for individual kin-related odour recognition. *Animal Behaviour*, **84**, 10.1016/j.anbehav.2012.06.014.
- BONADONNA, F., HESTERS, F. & JOUVENTIN, P. 2003a. Scent of a nest: discrimination of own-nest odours in Antarctic prions, *Pachyptila desolata*. *Behavioral Ecology and Sociobiology*, **54**, 10.1007/s00265-003-0610-7.
- BONADONNA, F., CUNNINGHAM, G.B., JOUVENTIN, P., HESTERS, F. & NEVITT, G.A. 2003b. Evidence for nest-odour recognition in two species of diving petrel. *Journal of Experimental Biology*, **206**, 10.1242/jeb.00610.
- BONADONNA, F., VILLAFANE, M., BAJZAK, C. & JOUVENTIN, P. 2004. Recognition of burrow's 'olfactory signature' in blue petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark. *Animal Behaviour*, **67**, 10.1016/j.anbehav.2003.08.013.
- BUSTAMANTE, J. & MARQUEZ, R. 1996. Vocalizations of the chinstrap penguin *Pygoscelis antarctica*. *Colonial Waterbirds*, **19**, 10.2307/1521812.
- CAMPAGNA, S., MARDON, J.A., CELERIER, A. & BONADONNA, F. 2012. Potential semiochemical molecules from birds: a practical and comprehensive compilation of the last 20 years studies. *Chemical Senses*, **37**, 10.1093/chemse/bjr067.
- CARO, S.P. & BALTHAZART, J. 2010. Pheromones in birds: myth or reality? *Journal of Comparative Physiology A*, **196**, 10.1007/s00359-010-0534-4.
- CASPERS, B.A. & KRAUSE, E.T. 2011. Odour-based natal nest recognition in the zebra finch (*Taeniopygia guttata*), a colony-breeding songbird. *Biology Letters*, **7**, 10.1098/rsbl.2010.0775.
- CLARK, J.A., BOERSMA, P.D. & OLMSTED, D.M. 2006. Name that tune: call discrimination and individual recognition in Magellanic penguins. *Animal Behaviour*, **72**, 10.1016/j.anbehav.2006.04.002.
- COFFIN, H., WATTERS, J. & MATEO, J. 2011. Odor-based recognition of familiar and related conspecifics: a first test conducted on captive Humboldt penguins (*Spheniscus humboldti*). *PLoS One*, **6**, 10.1371/journal.pone.0025002.
- CUNNINGHAM, G.B., STRAUSS, V. & RYAN, P.G. 2008. African penguins (*Spheniscus demersus*) can detect dimethyl sulphide, a prey-related odour. *Journal of Experimental Biology*, **211**, 10.1242/jeb.058230.
- DE LEÓN, A., MÍNGUEZ, E. & BELLURE, B. 2003. Self-odour recognition in European storm-petrel chicks. *Behaviour*, **140**, 10.1163/156853903770238382.
- ELLEGREN, H. 1996. First gene on the avian W chromosome (*CHD*) provides a tag for universal sexing of non-ratite birds. *Proceedings of the Royal Society of London, Series B*, **263**, 10.1098/rspb.1996.0239.
- GILLES, M., FOKKEMA, R.W., KORSTEN, P., CASPERS, B.A. & SCHMOLL, T. 2024. Preen oil composition of pied flycatchers is similar between partners but differs between sexes and breeding stages. *Ibis*, **166**, 10.1111/ibi.13246.
- GRIEVES, L.A., BERNARDS, M.A. & MACDOUGALL-SHACKLETON, E.A. 2019a. Wax ester composition of songbird preen oil varies seasonally and differs between sexes, ages, and populations. *Journal of Chemical Ecology*, **45**, 10.1007/s10886-018-1033-2.
- GRIEVES, L.A., GLOOR, G.B., BERNARDS, M.A. & MACDOUGALL-SHACKLETON, E.A. 2019b. Songbirds show odour-based discrimination of similarity and diversity at the major histocompatibility complex. *Animal Behaviour*, **158**, 10.1016/j.anbehav.2019.10.005.
- GRIEVES, L.A., KELLY, T.R., BERNARDS, M.A. & MACDOUGALL-SHACKLETON, E.A. 2018. Malarial infection alters wax ester composition of preen oil in songbirds: results of an experimental study. *Auk*, **135**, 10.1642/AUK-17-242.1.
- GRIEVES, L.A., GILLES, M., CUTHILL, I.C., SZÉKELY, T., MACDOUGALL-SHACKLETON, E.A. & CASPERS, B.A. 2022. Olfactory camouflage and communication in birds. *Biological Reviews*, **97**, 10.1111/brv.12837.
- GWINNER, H. & BERGER, S. 2008. Starling males select green nest material by olfaction using experience-independent and experience-dependent cues. *Animal Behaviour*, **75**, 10.1016/j.anbehav.2007.08.008.
- HAGELIN, J.C. 2007a. Odors and chemical signaling. In JAMIESON, B.G.M., ed., *Reproductive biology and phylogeny of birds*. Enfield, NH: Science Publishers, 75–120.
- HAGELIN, J.C. 2007b. The citrus-like scent of crested auklets: reviewing the evidence for an avian olfactory ornament. *Journal of Ornithology*, **148**, 10.1007/s10336-007-0185-6.
- HAGELIN, J.C. & JONES, I.L. 2007. Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? *Auk*, **124**, 10.1093/auk/124.3.741.
- HERNÁNDEZ, M.C., VILLADA, A.M. & BARJA, I. 2023. Onto the sense of smell in macaws, amazons and toucans: can they use volatile cues of fruits to make foraging decisions? *Integrative Zoology*, **18**, 10.1111/1749-4877.12694.
- HIRAO, A., AOYAMA, M. & SUGITA, S. 2009. The role of uropygial gland on sexual behavior in domestic chicken *Gallus gallus domesticus*. *Behavioural Processes*, **80**, 10.1016/j.beproc.2008.10.006.
- JACOB, J. & ZISWEILER, V. 1982. The uropygial gland. In FARNER, D.S., KING, J.R. & PARKES, K.C., eds, *Avian biology*, vol. 6. New York, NY: Academic Press, 199–314.
- JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. *Advances in Ethology*, **24**, 10.1002/iroh.3510680523.
- JOUVENTIN, P., MOURET, V. & BONADONNA, F. 2007. Wilson's storm petrels *Oceanites oceanicus* recognise the olfactory signature of their mate. *Ethology*, **113**, 10.1111/j.1439-0310.2007.01444.x.

- KELLY, D.J. & MARPLES, N.M. 2004. The effects of novel odour and colour cues on food acceptance by the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, **68**, 10.1016/j.anbehav.2004.07.001.
- KRAUSE, E.T. & CASPERS, B.A. 2012. Are olfactory cues involved in nest recognition in two social species of Estrildid finches? *PLoS One*, **7**, 10.1371/journal.pone.0036615.
- KRAUSE, E.T., KRÜGER, O., KOHLMEIER, P. & CASPERS, B.A. 2012. Olfactory kin recognition in a songbird. *Biology Letters*, **8**, 10.1098/rsbl.2011.1093.
- LECLAIRE, S., STRANDH, M., MARDON, J., WESTERDAHL, H. & BONADONNA, F. 2017. Odour-based discrimination of similarity at the major histocompatibility complex in birds. *Proceedings of the Royal Society of London B*, **284**, 10.1098/rspb.2016.2466 PMID: 28077776.
- LECLAIRE, S., MERKLING, T., RAYNAUD, C., GIACINTI, G., BESSIÈRE, J.M., HATCH, S.A. & DANCHIN, E. 2011a. An individual and a sex odor signature in kittiwakes? Study of the semiochemical composition of preen secretion and preen down feathers. *Naturwissenschaften*, **98**, 10.1007/s00114-011-0809-9.
- LECLAIRE, S., MERKLING, T., RAYNAUD, C., MULARD, H., BESSIÈRE, J.M., LHUILIER, E., *et al.* 2011b. Semiochemical compounds of preen secretion reflect genetic make-up in a seabird species. *Proceeding of the Royal Society of London B*, **279**, 10.1098/rspb.2011.1611.
- LECLAIRE, S., VAN DONGEN, W.F.D., VOCCIA, S., MERKLING, T., DUCAMP, C., HATCH, S.A., *et al.* 2014. Preen secretions encode information on MHC similarity in certain sex-dyads in a monogamous seabird. *Scientific Reports*, **4**, 10.1038/srep06920.
- LYNCH, H.J., WHITE, R., BLACK, A.D. & NAVEEN, R. 2012. Detection, differentiation and abundance estimation of penguin species by high-resolution satellite imagery. *Polar Biology*, **35**, 10.1007/s00300-011-1138-3.
- MAHR, K., NOWACK, L., KNAUER, F. & HOI, H. 2022. Songbirds use scent cues to relocate to feeding sites after displacement: an experiment in great tits (*Parus major*). *Frontiers in Ecology and Evolution*, **10**, 10.3389/fevo.2022.858981.
- MARDON, J. & BONADONNA, F. 2009. Atypical homing or self-odour avoidance? Blue petrels (*Halobaena caerulea*) are attracted to their mate's odour but avoid their own. *Behavioural Ecology and Sociobiology*, **63**, 10.1007/s00265-008-0688-z.
- MARDON, J., SAUNDERS, S.M., ANDERSON, M.J., COUCHOUX, C. & BONADONNA, F. 2010. Species, gender, and identity: cracking petrels' sociochemical code. *Chemical Senses*, **35**, 10.1093/chemse/bjq021.
- MARPLES, N.M. & ROPER, T.J. 1996. Effects of novel colour and smell on the response of naive chicks towards food and water. *Animal Behaviour*, **51**, 10.1006/anbe.1996.0145.
- MENNERAT, A., BONADONNA, F., PERRET, P. & LAMBRECHTS, M. M. 2005. Olfactory conditioning experiments in a food-searching passerine bird in semi-natural conditions. *Behavioural Processes*, **70**, 10.1016/j.beproc.2005.07.005.
- MINGUEZ, E. 1997. Olfactory recognition by British storm-petrel chicks. *Animal Behaviour*, **53**, 10.1006/anbe.1996.0308.
- MORENO, J., BOTO, J., FARGALLO, J.A. & POTTI, J. 2000. Absence of extra-pair fertilisations in the chinstrap penguin *Pygoscelis antarctica*. *Journal of Avian Biology*, **31**, 10.1034/j.1600-048X.2000.1310418.x.
- MORENO-RUEDA, G. 2010. Uropygial gland size correlates with feather holes, body condition and wingbar size in the house sparrow *Passer domesticus*. *Journal of Avian Biology*, **41**, 10.1111/j.1600-048X.2009.04859.x.
- MORENO-RUEDA, G. 2015. Body-mass-dependent trade-off between immune response and uropygial gland size in house sparrows *Passer domesticus*. *Journal of Avian Biology*, **46**, 10.1111/jav.00358.
- MRAZOVA, A., SAM, K. & AMO, L. 2019. What do we know about birds' use of plant volatile cues in tritrophic interactions? *Current Opinion in Insect Science*, **32**, 10.1016/j.cois.2019.02.004.
- MÜLLER-SCHWARZE, D. 1984. *The behavior of penguins: adapted to ice and tropics*. Albany, NY: State University of New York Press, 193 pp.
- NEVITT, G.A. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology*, **211**, 10.1242/jeb.015412.
- NEVITT, G.A. 2011. The neuroecology of dimethyl sulfide: a global-climate regulator turned marine infochemical. *Integrative and Comparative Biology*, **51**, 10.1093/icb/ucr093.
- PAP, P.L., VÁGÁSI, C.I., OSVÁTH, G., MUREÇAN, C. & BARTA, Z. 2010. Seasonality in the uropygial gland size and feather mite abundance in house sparrows *Passer domesticus*: natural covariation and an experiment. *Journal of Avian Biology*, **41**, 10.1111/j.1600-048X.2010.05146.x.
- PETIT, C., HOSSAERT-MCKEY, M., PERRET, P., BLONDEL, J. & LAMBRECHTS, M.M. 2002. Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecology Letters*, **5**, 10.1046/j.1461-0248.2002.00361.x.
- RENEERKENS, J., PIERSMA, T. & SINNINGHE DAMSTÉ, J.S. 2002. Sandpipers (Scolopacidae) switch from monoester to diester preen waxes during courtship and incubation, but why? *Proceedings of the Royal Society of London B*, **269**, 10.1098/rspb.2002.2132.
- ROTH, T.C. II, COX, J.G. & LIMA, S.L. 2008. Can foraging birds assess predation risk by scent? *Animal Behaviour*, **76**, 10.1016/j.anbehav.2008.08.022.
- SANDILANDS, V., SAVORY, J. & POWELL, K. 2004a. Preen gland function in layer fowls: factors affecting morphology and feather lipid levels. *Comparative Biochemistry and Physiology A*, **137**, 10.1016/j.cbpb.2003.10.004.
- SANDILANDS, V., POWELL, K., KEELING, L. & SAVORY, C.J. 2004b. Preen gland function in layer fowls: factors affecting preen oil fatty acid composition. *British Poultry Science*, **45**, 10.1080/00071660410001668932.
- SLADE, J.W.G., WATSON, M.J., KELLY, T.R., GLOOR, G.B., BERNARDS, M.A. & MACDOUGALL-SHACKLETON, E.A. 2016. Chemical composition of preen wax reflects major histocompatibility complex similarity in songbirds. *Proceedings of the Royal Society of London B*, **283**, 10.1098/rspb.2016.1966.
- STRANDH, M., WESTERDAHL, H., PONTARÉ, M., CANBÄCK, B., DUBOIS, M.P., MIQUEL, C., *et al.* 2012. Major histocompatibility complex class II compatibility, but not class I, predicts mate choice in a bird with highly developed olfaction. *Proceedings of the Royal Society of London B*, **279**, 10.1098/rspb.2012.1562.
- TUTTLE, E.M., SEBASTIAN, P.J., POSTO, A.L., SOINI, H.A., NOVOTNY, M.V. & GONSER, R.A. 2014. Variation in preen oil composition pertaining to season, sex, and genotype in the polymorphic white-throated sparrow. *Journal of Chemical Ecology*, **40**, 10.1007/s10886-014-0493-2.
- VAN BUSKIRK, R.W. & NEVITT, G.A. 2008. The influence of developmental environment on the evolution of olfactory foraging behaviour in procellariiform seabirds. *Journal of Evolutionary Biology*, **21**, 10.1111/j.1420-9101.2007.01465.x.
- VIÑUELA, J., AMAT, J.A. & FERRER, M. 1995. Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology*, **99**, 10.1111/j.1439-0310.1995.tb00906.x.
- WALLRAFF, H.G. 2004. Avian olfactory navigation: its empirical foundation and conceptual state. *Animal Behaviour*, **67**, 10.1016/j.anbehav.2003.06.007.
- WHELAN, R.J., LEVIN, T.C., OWEN, J.C. & GARVIN, M.C. 2010. Short-chain carboxylic acids from gray catbird (*Dumetella carolinensis*) uropygial secretions vary with testosterone levels and photoperiod. *Comparative Biochemistry Physiology B*, **156**, 10.1016/j.cbpb.2010.03.005.
- WHITTAKER, D.J., ROSVALL, K.A., SŁOWINSKI, S.P., SOINI, H.A., NOVOTNY, M.V. & KETTERSON, E.D. 2018. Songbird chemical signals reflect uropygial gland androgen sensitivity and predict aggression: implications for the role of the periphery in chemosignaling. *Journal of Comparative Physiology A*, **204**, 10.1007/s00359-017-1221-5.
- WHITTAKER, D.J., SOINI, H.A., ATWELL, J.W., HOLLARS, C., NOVOTNY, M.V. & KETTERSON, E.D. 2010. Songbird chemosignals: volatile compounds in preen gland secretions vary among individuals, sexes, and populations. *Behavioral Ecology*, **21**, 10.1093/beheco/arq033.
- WHITTAKER, D.J., RICHMOND, K.M., MILLER, A.K., KILEY, R., BURNS, C.B., ATWELL, J.W. & KETTERSON, E.D. 2011. Intraspecific preen oil odor preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology*, **22**, 10.1093/beheco/arr122.
- WHITTAKER, D.J., SŁOWINSKI, S.P., GREENBERG, J.M., ALIAN, O., WINTERS, A.D., AHMAD, M.M., *et al.* 2019. Experimental evidence that symbiotic bacteria produce chemical cues in a songbird. *Journal of Experimental Biology*, **222**, 10.1242/jeb.202978.
- WRIGHT, K.L.B., PICHEGRU, L. & RYAN, P.G. 2011. Penguins are attracted to dimethyl sulphide at sea. *Journal of Experimental Biology*, **214**, 10.1242/jeb.058230.
- ZHANG, J.X., WEI, W., ZHANG, J.H. & YANG, W.H. 2010. Uropygial gland-secreted alkanols contribute to olfactory sex signals in budgerigars. *Chemical Senses*, **35**, 10.1093/chemse/bjq025.