Chapter 20
Small Emissions with Major Consequences: Specialized Malodorous Defenses in Birds

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20.1 Introduction

Nowadays, birds are among the most conspicuous living organisms on Earth. Their large size, often colorful plumage, breeding behavior, migration, as well as recognizable song and potential for domestication have made them probably the best studied group of vertebrates. Ornithologists, biologists, bird watchers, or simple amateurs have exhaustively studied their anatomy, physiology, distribution, ecology, behavior, and classification.

Nevertheless, it would be presumptuous to consider birds as a fully known territory. Much more remains to be studied among the nearly 10,000 avian species. Now, a fresh look at their intra- and interspecific interactions might be profitable, as old beliefs need to be revised. Largely underestimated, the avian sense of smell, as well

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as taste to some extent, belong to this category. For decades, this bias has negatively impacted potential observations and research on the importance of airborne signals in birds. The moment to catch up has arrived.

20.1.1 The Sense of Smell in Birds

If a complete review on avian olfactory abilities would be inappropriate, an overview is indispensable to place our work in context.

Until recently, most experts considered that birds made little, if any, use of olfaction. John James Audubon, the famous nineteenth century naturalist, was not the only scientist to make the argument, but he was particularly influential in arguing against the idea of a developed sense of smell in birds. His work on the turkey vulture (*Cathartes aura* L.), a scavenger from the New World feeding on carrion, suggested the absence of odorous attraction by rotten carcasses hidden in an open field. This became the central pillar of a sort of avian anosmia theory, which was cited regularly during the next 140 years (Audubon 1820). Among other points, it has been argued that the extreme diffusion of volatile compounds in the air makes the use of smell unreliable to localize food, prey, predators, or mating partners for any bird species. Even the fact that myriad other organisms (e.g. thousands of insect species) use volatile cues on a daily basis to cope with both complex life cycles and diverse environments did not modify such preconceived ideas. Furthermore, the exceptionally efficient sight and hearing capacities of birds were naturally mentioned as the major means to orientate and locate. All these elements explain why this "insensitive" theory dominated for so long, leading to consideration of the olfactory aptitudes of birds as anecdotal, and of little relevance.

Within the scientific community and beyond, there was real astonishment when diverse studies revealed a functional and well developed sense of smell in many unrelated avian species. In the 1960s, Kenneth Stager and Bernice Wenzel first broke this taboo. Stager tested again the olfactory responsiveness of the turkey vulture. He showed that odors emitted by fresh dead animals did in fact attract the vulture (Stager 1964). Further experiments on the same model proved its ability to find fresh cadavers without visual cues, relying mainly on the typical chemical components emitted naturally by dead animals in the early stages of decomposition (i.e. butanoic acid, ethanethiol, and trimethylamine). Later, monitoring of individual heart frequency and further bioassays revealed the limits of detection for those chemicals (Applegate 1990; Smith and Paselk 1986). Thus, Audubon's conclusions were incorrect, mainly because carcasses in an advanced state of decomposition are not the favored diet of the turkey vulture. Surprisingly, this discovery by Stager went almost unnoticed by scientific and public opinion. A few years later, Bernice Wenzel published multiple results on olfaction in kiwis (*Apteryx sp.*), pigeons (*Columba sp.*), and procellariiformes such as the Northern fulmar (*Fulmarus glacialis* L.) (Wenzel 1968, 1986; Wenzel and Rausch 1977). Her pioneering observations proved that unrelated bird species rely on olfactory information to navigate, to forage, or to interact socially. Since this challenge to the dogma, field observations, bioassays, anatomical and physiological studies, as well as modern genetic tools have been involved to restore the truth about the sense of smell in birds. Studies on procellariiform seabirds unite all these complementary aspects and propose a complete view of the role and importance of odors in this group. Albatrosses and petrels have in common interesting features such as colonial life, monogamy and long-term pairing, philopatry, limited reproductive capacities, and astonishing foraging skills. Pelagic seabirds localize directly and precisely fish banks kilometers away from their colonies along the shore. Olfactory navigation from nest to food resources has been observed in several albatross, petrel, and shearwater species (Grubb 1972, 1974; Nevitt et al. 2008). Bioassays confirmed the role of dimethyl sulfide (DMS), a foraging cue processed by procellariiform seabirds. Phytoplankton, if consumed by zooplankton or other small grazers, release dimethylsulfionopropionate (DMSP), which can be transformed into volatile DMS by aquatic microorganisms. Associative learning between DMS scent and areas offering abundant prey is frequent in these pelagic birds. Furthermore, fledglings of these species learn the importance of DMS before they have to forage themselves (Nevitt et al. 1995; Nevitt and Bonadonna 2005). During the same period, olfactory aptitudes in many non-procellariiform birds were observed, such as in the owl parrot or kakapo (*F. glacialis*, Gray 1845) which is endemic to New Zealand (Hagelin 2004).

On the morphological and functional side, complete olfactory systems including nasal cavities, tubular nasal passages, and olfactory bulbs have been studied in many species (Bang 1960; Wenzel 1971), and most extensively in procellariiformes (Bang and Cobb 1968; Bang and Wenzel 1985; Wenzel and Meisami 1987). Avian olfactory bulbs found close to the brain are responsible for the processing and integration of odorous volatiles. Their size and shape varies among species, with a positive correlation between a prominent bulb and a well-developed sense of smell. With a bulb proportionally larger than most of the other birds studied so far, the flightless kiwi is a perfect example of this morphological adaptation (Bang and Cobb 1968). In this species, chemoreception is crucial, with nostrils placed at the apex of a long beak used to “scent” earthworms and small arthropods in soil litter. On a physiological level, measurements of heart rate and electrical impulses in olfactory nerves have been used to identify some of the molecules that birds of diverse groups can smell (Clark et al. 1993). Finally, modern genetic tools have identified hundreds of functional olfactory receptor genes in birds (OR genes), with some species showing equivalent numbers of OR genes to other vertebrate species. Additionally, many of these avian OR genes are exclusive to this taxon, and they demonstrate a high degree of functionality, unlike in humans where 60 % of OR genes are not expressed. These results are indisputable, especially in kiwi and kakapo species with an estimated total number of OR genes close to 600 (Steiger et al. 2008). More surprisingly, even the common canary (*Serinus canaria* L.), described as a typical visual species, exhibits more than 150 OR genes. Finally, specific differences in genetic patterns in olfactory receptor genes have been observed between nocturnal and diurnal species, stressing again the existence of a fully functional and specialized avian sense of smell (Steiger et al. 2009).

Nowadays, after 40 years of multidisciplinary scientific studies, all this evidence should convince the last skeptics that an olfactory sensibility in birds can no longer be denied. But as in other vertebrates, the avian sense of smell shows significant interspecific disparities.

20.1.2 Roles and Importance of Odors in Birds

With these new convictions in mind, the ornithological community has begun to carry out investigations into the roles and the importance of odors in bird behavior. Themes such as (1) navigation, (2) foraging, and (3) reproduction became the most familiar and well documented.

1. The influence of airborne signals for avian navigation gained real credibility with comprehensive studies on homing in pigeons, which add olfaction to other senses in order to orientate (Papi 1976; Wallraff 1982). In addition, procellariiformes brought new evidence that the localization of their colonies and nests may rely on odorous cues. In harsh and night conditions, Leach's storm petrels (*Oceanodroma leucorhoa*, Vieillot 1818) showed such ability (Grubb 1973), whereas other species were able to reach their nest burrows in very poor visibility (Bonadonna and Bretagnolle 2002). Furthermore, the global role of odors in navigation has been considered in many other species (Papi 1990; Jorge et al. 2009).
2. On the foraging side, albatrosses and other pelagic seabirds have been observed and tested meticulously. As described previously, captivating studies pointed out an essential olfactory assistance used to reach restricted nutritive resources in vast oceans (Hutchison and Wenzel 1980; Verheyden and Jouventin 1994; Nevitt et al. 1995).
3. As in other organisms, probable links between avian-produced odors and reproduction have been suspected in birds. Early research has proved that Leach's petrels use volatile indicators to join potential partners in precise places of reproduction (Grubb 1979), while diverse Antarctic seabirds rely on olfactory signatures to identify appropriate sexual partners (Bonadonna and Nevitt 2004; Jouventin et al. 2007). In 2003, Freeman-Gallant et al. studied the effect of similar or dissimilar major histocompatibility complexes (MHCs) on female mating fidelity in savannah sparrows (*Passerculus sandwichensis*, Gmelin 1789). MHCs present very diverse genes involved in immunity, and complementary genes brought by each parent should result in an optimal immunocompetency in their descendants. The classic hypothesis suggests that individual odors in vertebrates contain information related to this genetic assortment. Birds are not an exception (Zelano and Edwards 2002). If no precise odorants were identified in the aforementioned study, females in MHC-similar pairs were revealed to mate more regularly with extra-pair males, whereas breeding pairs showing MHC-dissimilarities exhibited higher fidelity, as expected (Freeman-Gallant et al. 2003). Likewise, specific odors released by different body parts and glands may

> serve as a perfect signaling tool to assess the status of a mating partner. In the preen oil of dark-eyed juncos (*Junco hyemalis* L.), the quantities of volatiles and semivolatiles have been correlated with hormonal variations, such as for testosterone. The resulting chemical signal may attest to the receptiveness of a potential mating partner during the breeding season (Whittaker et al. 2011). Going further, overall individual fitness and potential reproductive performance might be evaluated directly through perfumed messages emitted intentionally or unconsciously by both partners (Whittaker et al. 2013). Obviously, assessing this function is not an easy task because both the emission and perception of odors may vary considerably, among species, seasons, ages, migration areas, and populations (Clark and Smeraski 1990; Whittaker et al. 2010). Variability in uropygial gland secretions of budgerigars (*Melopsittacus undulates*, Gould 1840) (Zhang et al. 2010), gray catbirds (*Dumetella carolinensis* L.) (Shaw et al. 2011), and starlings (*Sturnus unicolor*, Temminck 1820) (Amo et al. 2012) have been investigated in this context. Linked with earlier observations, the existence of true pheromones in birds has also been debated (Balthazart and Schoffeniels 1979; Caro and Balthazart 2010), adding credit to the overall role of odors in bird reproduction (Lambrechts and Hossaert-McKey 2006).

In addition to the above areas, further hints support a major role of avian-produced volatile organic compounds (VOCs) in antagonist interactions as predation, parasitism, or microbial infections. To avoid or to repel those enemies is of the main importance for all avian species. Moreover, several birds are predators themselves, and regularly on other birds. In these circumstances, both sense of smell and production of VOCs act directly in various defensive or offensive avian interactions.

20.1.3 Chemical Defenses in Birds

Birds are among the most detectable inhabitants of most ecosystems, so they can represent a perfect target for predators. While the ability to fly is certainly the best strategy to flee from predators, some species are flightless, and the risk of predation can itself come from the sky. Moreover, both eggs and hatchlings show great vulnerability, with the greatest risks when the parents are foraging far from the nest. These risks might have led birds to evolve repulsive defenses, aiming to increase survival at any step of their life cycles. In this context, diverse avian defensive behaviors and strategies have been described in the literature, including some examples relying on chemical compounds. In the 1940s, Cott observed dead laughing doves (*Streptopelia senegalensis* L.) being consumed by scavenger hornets (*Vespa orientalis* L.), whilst the fresh carcass of pied kingfisher (*Ceryle rudis* L.) stayed intact because of likely unpalatable components contained in its tissues (Cott 1947). The same naturalist conducted experiments on 200 species from 57 families in order to assess the palatability of the eggs and meat for humans, hedgehogs, rats, ferrets, and cats.

Without any identification of putative repellent compounds, the results suggested a correlation between the visibility of a bird species and its unpalatability (Cott 1954; Müller-Schwarze 2012). Nevertheless, re-analysis of Cott's data questioned whether the criteria used to assess conspicuousness were appropriate. Indeed, some bias may have been introduced because mainly females with usually less bright plumages than related males were considered in the past (Götmark 1994). Almost 40 years after the publications of Cott, observations of the New Guinean pitohuis (fam. Oriolidae and Pachycephalidae), and especially the hooded pitohui (*Pitohui dichrous*, Bonaparte 1850), revealed the poisonous birds to the world (Dumbacher et al. 1992). Shortly after this initial discovery, the blue-capped ifrit (*Ifrita kowaldi*, De Vis 1890) was described as another toxic passerine (Dumbacher et al. 2000). Both studies highlighted the presence of batrachotoxin alkaloids (e.g. homobatrachotoxin) as defensive chemicals in these species. In all likelihood, these compounds are sequestered in the skin and feathers of noxious birds. The repellent chemicals are obtained by feeding on soft-wing flower beetles of the *Choresine* genus (Coleoptera: Melyridae) (Dumbacher et al. 2004). Aposematism is present in these bird genera in the form of warning coloration of the plumage. In the same way, but on other continent, the African spur-winged goose (*Plectropterus gambensis* L.) exhibits toxic properties when it eats blister beetles (Coleoptera: Meloidae). This time, cantharidin is the sequestered compound, which is a familiar toxin found in several insect species (Bartram and Boland 2001). All these observations prove that chemical defenses in birds might be more widespread than expected at first glance. Undoubtedly, toxins play a role in chemical protection of various bird species, whereas avian volatile-produced compounds identified recently open the door to a further question: are the odoriferous VOCs emitted by birds involved in defensive purposes?

20.1.4 Avian Odorous Defenses

The production and release of odors in birds has not suffered the same negative prejudice as their sense of smell. For centuries, it has been established that many species emit perfumes, with written scientific reports, popular books, or even sacred texts mentioning the malodorous hoopoe (*Upupa epops* L.). Scientific studies have rapidly shown that odors released by birds can contribute to their protection in many ways.

The scent of the predator itself may indicate its presence to avian prey. This has been documented both in Eurasian blue tits (*Cyanistes caeruleus* L.) and house finches (*Haemorhous mexicanus*, Müller 1776) exposed to mustelid odors and mammalian predator feces, respectively (Amo et al. 2008; Roth et al. 2008). Nevertheless, this aptitude might be scarce: untroubled Eastern bluebirds (*Sialia sialis* L.) build their nests close to the natural odors of their main predators (Godard et al. 2007), while both native New Zealand rifleman (*Acanthisitta chloris*, Sparrman

1787) and South Island robin (*Petroica australis*, Sparrman 1788) are unable to detect and to react appropriately toward odors from their introduced mammalian predators (Stanbury and Briskie 2015).

Otherwise, avian chemical emissions have been shown to keep away various ectoparasites. The crested auklet (*Aethia cristatella*, Pallas 1769) produces a strong tangerine-like odor based on two aldehydes with remarkable repulsive properties against ticks (Douglas et al. 2004; Douglas 2006). In seabirds, some of the VOCs produced by the colony deter mosquitoes (Douglas et al. 2005). Antiparasitic and antimicrobial properties might occur in nests perfumed with aromatic plants, as in the Eurasian blue tit (Petit et al. 2002). Many species exhibit obvious malodorous defenses against intruders. The fulmars and some other procellariiform birds spit stinking stomach oil on avian or mammalian invaders (Swennen 1974; Clarke and Prince 1976). Unsurprisingly, hatchlings are especially prompt to release such an unpleasant-smelling liquid in order to defend themselves. Still about the nests, eider ducks (*Somateria mollissima* L.) and shovelers (*Anas sp.*) have been observed using feces to protect their own (Swennen 1968), while insectivorous Eurasian roller nestlings (*Coracias garrulus* L.) emit an orange oral secretion as defense against potential predators (Parejo et al. 2013). Through olfaction, the same vomit can even inform the parents about recent attacks at their nests and modulate their parental cares (Parejo et al. 2012). Currently, the classic example of repulsive secretion in birds is found in hoopoes. Both adults and young rely on pungent odors and smelly substances to dissuade potential predators. In this species, extreme malodorous VOCs and other chemicals are produced in the uropygial gland, some through bacterial transformation of ubiquitous organic precursors (Ligon 2001). Multiple functions have been assessed or hypothesized for such secretions: repellent effect against predators of both adults and hatchlings (nests are covered with uropygial secretion by parents); direct attraction of small invertebrate prey (e.g. insects) for fledglings in the nest; and antimicrobial activity protecting young hoopoes against numerous infections (Martin-Platero et al. 2006; Martín-Vivaldi et al. 2010).

As suggested earlier, studies on odorous chemical defenses in birds are complex to carry out, as the studied volatiles may fluctuate considerably. Uropygial and other secretions show great variability, depending on several environmental and genetic parameters (Ruiz-Rodríguez et al. 2014). Comprehensive investigations are required to obtain better knowledge of the importance and use of odoriferous protections in birds. Axes of research may include juvenile-adult specificities, types of nests, seasonality, or migration behaviors. For instance, the possible development of aposematic colors linked to avian malodorous defensive abilities has only been recently investigated in four European Coraciiformes and Upupiformes species, suggesting that their colorful plumages do not reduce attacks by potential predators (Ruiz-Rodríguez et al. 2013). Finally, in-depth approaches are required to disentangle the respective roles of the same avian volatile. This remains a real challenge, because the same group of odors might be used in defense, intraspecific information, and reproduction. Such multiple functions have already been observed in the crested auklets (Hagelin and Jones 2007).

20.2 Foul-Smelling Defense of a Brood Parasitic Bird and Its Consequences

20.2.1 Avian Interspecific Brood Parasitism

Among all the various ecological interactions observable between birds, brood parasitism has drawn the attention of scientists for decades. Interspecific avian brood parasites lay eggs and leave their progeny in the nests of other species. Many but not all cuckoos (fam. Cuculidae) are commonly associated with typical brood parasites in birds. Usually, hosts raise the foreigner hatchling and undergo massive reduction of their own reproductive success. This failure can be due to either evicting parasites, which clear the nest of native eggs and offspring, or from non-evicting parasites, whose chicks can monopolize parental care and drive native offspring to starve to death (Spottiswoode et al. 2012). In evolutionary biology, the arms race between brood parasites and their hosts has been studied thoroughly. Host parents are known to harass parasitic adults in the proximity of the nest, or to remove parasitic eggs (Kilner and Langmore 2011). Generally, this leads to a costly waste of time and effort. In addition, harassment attempts present some risks, as adult parasites are often bigger and stronger than parasitized species. On the other side, many alien eggs imitate the legitimate ones in terms of size, shape, and color pattern, limiting efficient ejection by hosts, whereas under particular conditions some parasitic species can discourage their ejection with punitive actions against the entire host nest (the mafia hypothesis or mafia-like behavior) (Zahavi 1979). Despite this arms race, it has been hypothesized that the absence of defense might be seen between a brood parasite and its host, if: (1) interaction is too recent for there to have been the necessary time for defenses to evolve; (2) costs of defenses exceed their benefits; (3) presence of the parasite might be beneficial to its host, as suggested half a century ago (Smith 1968). This last counterintuitive possibility, tested successfully on giant cowbirds (*Molothrus oryzivorus*, Gmelin 1788) in the late 1960s, was never replicated (Davies 2000). Recently, our new observations in a non-evicting cuckoo-host system with the release of avian-produced volatile defense have revealed remarkable outcomes supporting the controversial Smith's hypothesis (Canestrari et al. 2014). More than an isolated case, these observations strengthen the crucial role and the importance of VOCs emitted by birds at various ecological levels.

20.2.2 Malodorous Secretion Produced by a Juvenile Brood Parasite Modifies Host–Parasite Interaction: A Concrete Case

For both avian connoisseurs and the population in general, cuckoos are infamous for their brood parasitic members. This label is partly wrongfully appropriated, the majority of the cuckoo species raising their own chicks like other birds. Among the parasitic

Pict. 20.1 An example of a non-evicting brood parasite that does not monopolize all crucial resources. In this nest, one great spotted cuckoo chick and three carrion crow fledglings are raised together successfully. This contributes to reduce the negative outcomes for the host. Courtesy of D. Canestrari and V. Baglione

cuckoos, more than 50 species are obligate brood parasites, laying their eggs in nests built by unrelated bird species. Few are non-obligate brood parasites, but occasionally place their eggs in the nests of other members of the same species (Payne 2005).

In southern Europe, the great spotted cuckoo (*Clamator glandarius* L.) is a common brood parasite of corvids, mainly magpies (*Pica pica* L.). This non-evicting cuckoo species frequently outcompetes magpie nestlings for food, and is therefore responsible for major reproductive failure in this host, which has evolved defensive strategies to discourage adult cuckoos from laying their eggs (Arías de Reyna 1998). As far as possible, parent magpies also try to remove cuckoo eggs (Soler et al. 1999a, b). In northern Spain, great spotted cuckoo chicks are also found in the nests of carrion crows (*Corvus corone corone* L.), which, unlike magpies, are larger than the parasite. In these nests, legitimate and parasitic hatchlings are frequently raised together (Pict. 20.1), and crows surprisingly do not show any defensive arsenal against their brood parasite (Canestrari et al. 2009). As in the controversial hypothesis of Smith, a beneficial brood parasite might explain the lack of host-parasite defenses observed in this system, opening the door to further investigations.

Those researches were carried by Daniela Canestrari and her colleagues during the last 16 years. During this period, intensive observations and monitoring on crow reproductive success in hundreds of nests ($n = 741$) and territories ($n = 109$) showed that parasitized and non-parasitized host nests produce, on average, an equivalent number of young crows annually (1.584 ± 0.149 vs. 1.379 ± 0.068, respectively; $z = 0.390$, $p = 0.694$, $n = 550$) (Canestrari et al. 2014). This unusual outcome derives from the combination of two counterbalancing effects: surprisingly, parasitized nests are more likely to successfully complete the reproductive cycle (i.e. are more likely to fledge at least one crow) compared with non-parasitized ones, whereas in successful nests fewer crow fledglings are produced if a cuckoo chick is present, as a consequence of competition for food among host and parasitic chicks (Canestrari et al. 2014). Experimental translocations of cuckoo hatchlings from parasitized to non-parasitized nests showed that nests where a cuckoo was added experienced an

Pict. 20.2 Upon harassment, a juvenile great spotted cuckoo releases its defensive foul-smelling secretion. The odors from this emission can repel most nest predators. Courtesy of D. Canestrari and V. Baglione

increased probability of fledging at least one crow chick compared to naturally non-parasitized nests, while nests where the cuckoo was removed failed more often than naturally parasitized nests. In a parallel control treatment, crow chicks were translocated among naturally non-parasitized nests, in order to exclude a possible confounding effect of brood size change (Canestrari et al. 2014). These results demonstrate that having a cuckoo chick in the nest is responsible for the advantageous effect on nest success, discarding the possibility that cuckoo adults defending the nest where they have laid eggs (Soler et al. 1999a, b) is the mechanism behind the patterns observed in the long-term dataset. The most plausible explanation for the positive effect of parasitism on crow nest success is increased nest protection against potential predators, through a copious, foul-smelling secretion released by juvenile cuckoo chicks when frightened by an intruder in the vicinity of the nest (Pict. 20.2). Interestingly, only nestlings produce such secretion in this species, adults being unable to emit this mixture even when threatened. The supposed repulsiveness of this pungent emission and its beneficial effect were tested in several ways: (1) gas chromatography and mass spectrometry (GC-MS) were used to identify and quantify the volatile blend from the cuckoo secretion; (2) an artificial transparent solution mimicking the odor of juvenile cuckoo excretion was synthetized in order to assess the exact role of volatiles in repulsiveness; (3) deterring tests of both natural secretion and artificial solution were carried out on representative nest predator species (Canestrari et al. 2014; Röder et al. 2014).

1. First of all, VOCs released by the juvenile parasite secretion were trapped with the solid phase microextraction (SPME) technique and analyzed with GC-MS (Röder et al. 2014). The results revealed a caustic mixture of malodorous organic volatiles, which must deter most of the usual mammalian and avian nest predators (Fig. 20.1). Several short-chain fatty acids (e.g. propanoic, butyric, valeric acid, etc.), organosulfur compounds (dimethyl disulfide, dimethyl trisulfide, etc.), phenolic compounds (e.g. *p*-cresol), and indoles (e.g. indole and scatole) were

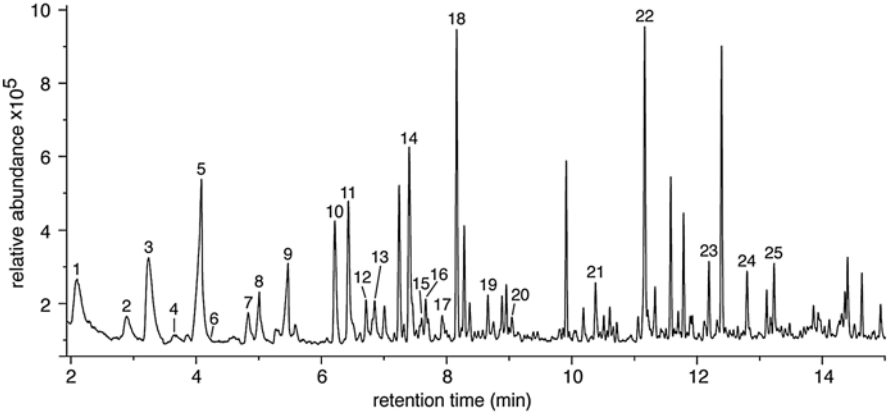


Fig. 20.1 Representative chromatographic profile of the volatiles found in defensive excretion of the great spotted cuckoo hatchling. The volatiles were analyzed by various methods (Canestrari et al. 2014), including the SPME method shown here. The major compounds are: 1, acetic acid; 2, propanoic acid; 3, dimethyl disulfide; 4, isobutyric acid; 5, butyric acid; 6, pivalic acid; 7, isovaleric acid; 8, 2-methylbutanoic acid; 9, valeric acid; 10, α-pinene; 11, dimethyl trisulfide; 12, phenol; 13, caproic acid; 14, 3-carene; 15, 2-ethylhexanol; 16, limonene; 17, acetophenone; 18, *p*-cresol; 19, nonanal; 20, camphor; 21, dimethyl tetrasulfide, 22, indole; 23, skatole; 24, longicyclene; 25, longifolene

well represented in this emission and create rancid and rotten perfumes, known to repel predators such as coyotes, dogs, or wolverines (Lehner et al. 1976; Landa and Tømmerås 1997).

2. In the overall repellent effect of the secretion, an evaluation of the efficiency of volatiles alone was not possible, as the natural secretion is dark tinted and sticky. To disentangle these traits, a liquid synthetic blend that mimicked the odor of juvenile cuckoo secretion was obtained by mixing together the 22 pure standards of the dominating volatile compounds found in the natural emission. In this solution, the ratios between the 22 compounds were based on the analytical results for four different defensive secretions of young great spotted cuckoos (Röder et al. 2014).
3. Finally, repellent properties of the juvenile cuckoo secretion were tested in wild, semi-captive and captive mammals and birds used as models of potential predators of crow nests. As expected, both natural secretion and artificial solution caused a clear deterrence in *quasi* feral cats that usually hunt in the neighborhood, carrion crows which show intraspecific predation, and hand-raised raptor birds (*Falco sp.*) (Table 20.1) (Canestrari et al. 2014; Röder et al. 2014). In artificial solution trials, one exception has to be mentioned regarding the carrion crows: they consumed the same amount of treated and control chicken baits. In this species, visual cues might play a role in repulsiveness, whilst a non-repellent effect by the odor of the secretion alone would be logical in terms of feeding habits (carrion feeders), as well as the care at the nest that adoptive crow parents must offer even after a cuckoo hatchling has released the secretion.

Table 20.1 Repellant effects against potential nest predators

Repellent effect of *natural* secretion		
Mammals (*quasi* feral cats)	Corvids (captive crows)	Raptors (captive raptors)
$n = 17$	$n = 7$	$n = 7$
Ten pieces of chicken meat, treated or control	Six pieces, one at a time, three treated and three control	Six pieces, one at a time, three treated and three control
Strongly avoided; $p = 0.01$	Strongly avoided; $p = 0.008$	Strongly avoided; $p = 0.001$
Repellent effect of *artificial* blend		
$n = 6$	$n = 7$	$n = 7$
Ten pieces of chicken meat, treated or control	Six pieces, one at a time, three treated and three control	Six pieces, one at a time, three treated and three control
Strongly avoided; $p = 0.014$	Consumption equivalent; $p = 0.755$	Strongly avoided; $p = 0.008$

Both natural defensive secretion of juvenile great spotted cuckoo and synthetic solution mimicking its pungent odors were applied on chicken baits. Fisher's Exact tests were used for statistical interpretation. Complete experiments are described in Canestrari et al. (2014) and Röder et al. (2014)

> These recent findings offer a significant breakthrough, being one of the first studies to identify and test exhaustively avian-produced volatiles and their repellent effects on potential predators. Furthermore, they confirm that juvenile great spotted cuckoo use such preventive emissions for protection, and by extension the entire crow nest against intruders. The annual outcome of crow/cuckoo interaction is context-dependent. As the presence of cuckoos reduces nest failure due to predation, raising a cuckoo chick conveys a net benefit in terms of annual reproductive success for crow foster parents only in years with high predator pressure, while in years with low predation, parasitized crows produce, on average, fewer young and the net effect of parasitism is negative. Additional records on laying date, dependency period, annual adult survival, effort to raise a cuckoo chick, the condition of crow fledglings growing alongside cuckoos, or subsequent reproductive success of parasitized parents indicate that the costs of raising a parasitic chick in terms of adult provisioning effort do not erode the net benefit on crow reproductive success in years of high predation, because raising a cuckoo requires significantly less effort than a crow chick, due to the smaller size and shorter dependence period of the parasite (Canestrari et al. 2014). Annually, all these parameters lead to a fluctuation from parasitic to mutualistic interaction in this system. Because the abundance and composition of the predator community varies annually and geographically within the same host, and also differs among host species, the effect of the presence of a great spotted cuckoo chick on nest success is likely to vary with space and time within the same host, and among different host species.

It may be argued that alternative mechanisms, such as the "farming" and "mafia" hypotheses, which suggest a role of adult cuckoos as potential predators of non-parasitized nests ("farming") or of parasitized nests where cuckoo eggs or chicks have been tossed out by host parents ("mafia") in order to force hosts to re-lay, may explain the increased success of crow nests with cuckoos (Zahavi 1979; Soler et al. 1995; Arcese et al. 1996). However, both hypotheses can be discarded (Canestrari et al. 2014). A “farming strategy” is not consistent with the patterns found in the long-term dataset, where failure rate of non-parasitized nests was higher at the hatching stage but not at the egg stage, when crows are more likely to re-lay upon failure and thus adult cuckoos are expected to destroy host clutches. Furthermore, annual failure rate of non-parasitized nests did not increase with annual parasitism pressure (which is expected under the “farming hypothesis” scenario). Theoretically, a “mafia tactic” by adult cuckoos may be responsible only for the increased failure rate of experimental nests where cuckoo chicks were removed (as crows do not toss out alien eggs or chicks from the nest), but it cannot explain why nests where cuckoos were added experienced an increased success.

Based on our long-term field observations, carrion crow parents are not monopolized if they raise a foreigner cuckoo chick in their nests, suppressing the likely development of costly but useless defenses. The simple chemical signals produced by this juvenile brood parasite species illustrates the role and the importance that avian odors and sense of smell can have in precise ecological interspecific interactions. The system offers a significant advance in brood parasitism, as well as in research considering the importance of volatile cues in vertebrates.

20.3 New Perspectives in Malodorous Avian Chemical Defenses

Pioneering studies carried out on great spotted cuckoos and their carrion crow hosts have brought as many questions as answers. This opens new perspectives of research in avian chemical ecology. In many circumstances, both interspecific and intraspecific interactions are of ecological importance. In the paradoxical interactions between a brood parasitic bird and its host, what might be the various consequences when VOCs are emitted by one species cohabiting with another? Most of the brood parasite–host interactions have been well studied and documented, but never from the point of view of ecological effects ruled by odorants released from parasites or hosts. Based on the great spotted cuckoo—carrion crow system, many questions are currently being evaluated: (1) In the great spotted cuckoo, is the specialized secretion very different from characteristic excrements? (2) Which anatomical structure(s) is/are responsible for the production of the mixture? (3) Is the secretion based on metabolic byproducts or biosynthesized by symbiotic bacterial strains? (4) Can an equivalent secretion be found in other brood parasitic bird species, and what is its effect? (5) Is the production and the efficiency of such malodorous excretion correlated with a specific pattern of brood parasitism (e.g. evicting or non-evicting avian parasites; only in juvenile or at different ages; sedentary or migrant habits; host–parasite size ratio, etc.)? Further experiments will explore these paths. In the meantime, our recent investigations provide some hint of answers:

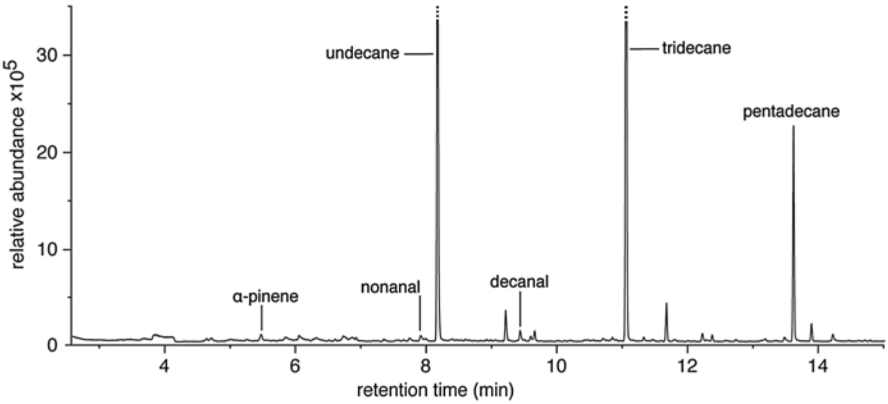


Fig. 20.2 This chromatographic profile of the VOCs emitted by excrements of great spotted cuckoo chicks was obtained by the SPME method. Comparison with Fig. 20.1 underlines the drastic differences between the foul-smelling volatiles of the defensive secretion and the less odoriferous compounds found in the feces

1. After initial batches of VOCs analysis carried out on the secretion produced by juvenile great spotted cuckoo, it has been necessary to test whether the defensive emission was a special excretion or a sort of natural excrements. New repulsive secretions of the great spotted cuckoo chicks were analyzed at the University of Neuchâtel (Switzerland). In addition, samples of excrements from each protagonist involved in this brood parasite–host system were added. All the different vials of fresh secretions and feces were sent from Spain in a frozen container at −20 °C. Immediately after arrival, volatile components were trapped with a solid phase microextraction (SPME) technique and analyzed with GC-MS, exactly as described in Röder et al. 2014. The odors found in these secretions were then compared with those found in excrements of juvenile great spotted cuckoos, carrion crow hatchlings, and parental carrion crows (Fig. 20.1). The comparison of the odorant profiles showed evident differences both in composition and quantity, as illustrated in Fig. 20.2. This chromatogram presents the volatiles trapped from the excrements of juvenile great spotted cuckoo. For a human nose, the repulsive secretion produced by cuckoo chicks is undoubtedly the worst smelling. Various vomit and rancid perfumes are issued by carboxylic acids whilst remarkable amounts of *p*-cresol or skatole are responsible for the standard odors of mammalian dirty hair and feces, respectively. On the other hand, excrements produced by birds showed diverse odorous profiles, but with few volatile compounds and limited malodorous properties. After exhaustive data processing with MSD ChemStation Enhanced Data Analysis (Agilent), XCMS online (Scripps Center for Metabolomics), and MassLynx Mass Spectrometry Software (Waters), a principal component analysis (PCA) based on the constitutive ions of VOCs linked with GC-MS retention time attest the dissimilarities between

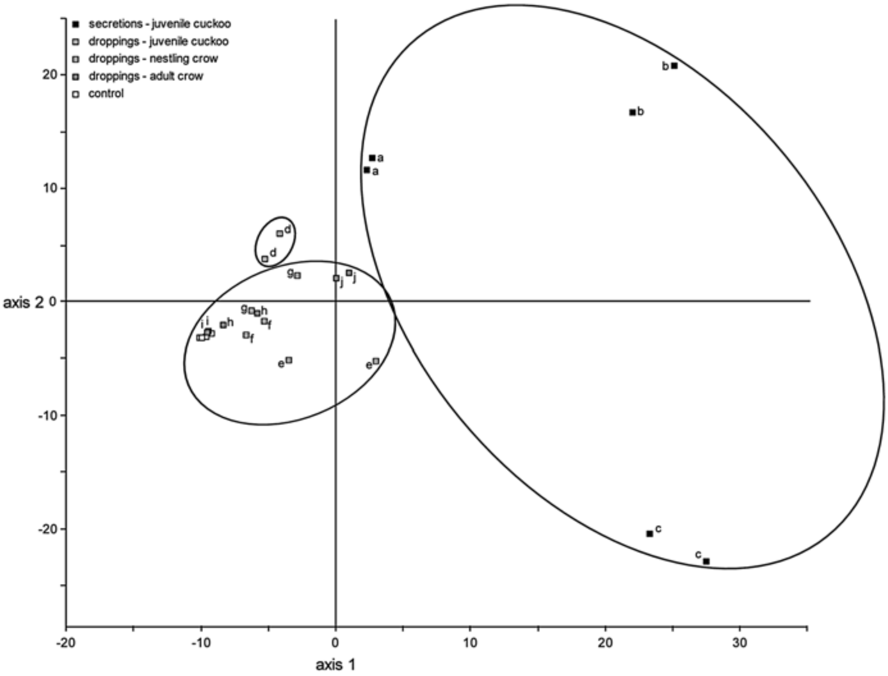


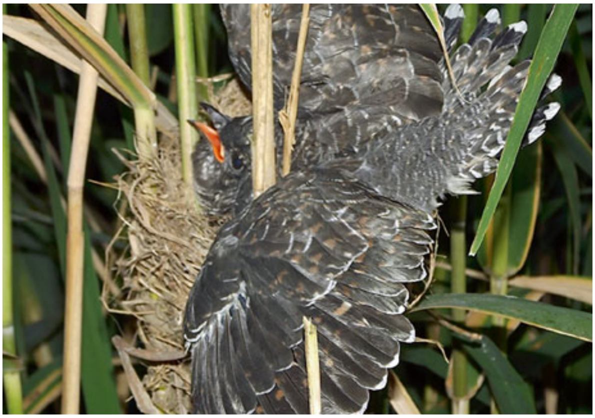
Fig. 20.3 Unsupervised principal component analysis (PCA) based on aligned features (ions) obtained with GC-MS analysis carried out on three great spotted cuckoo chick defensive secretions, seven excrements (1 juvenile cuckoos—3 young crows—3 adult crows), and five control samples. Each sample has been split in two parts and analyzed individually (same letter in the graphic). The more a sample is close to the controls (*white squares*), the less it smells. Variability exists in defensive secretion of the juvenile great spotted cuckoo but cannot be mistaken for any other classic droppings

specialized repulsive emissions of the great spotted cuckoo chicks, and the feces produced by both cuckoos and carrion crows (Fig. 20.3). Identical lettering in this PCA shows that two different portions of each sample were analyzed separately to assess the homogeneity of such production. Finally, five corresponding control analyses were run aiming to exclude ghost peaks and to determine which of the chemicals were not of avian origin (Fig. 20.3). Without further analysis, our results prove that the defensive secretion emitted by the great spotted cuckoo chicks is special, and distinct from the usual excrements. This trait supports the defensive function of this secretion produced only in great spotted cuckoo nestlings.

2. Until now, avian-produced malodorous volatiles have been mainly associated with uropygial glands, as in hoopoes (Cramp 1998), or with oils expelled from digestive organs, as in procellariiformes (Swennen 1974; Clarke and Prince 1976) and nestlings of Eurasian rollers (Parejo et al. 2013). Interestingly, these two common origins are not the source of the defensive secretion of cuckoo nestlings. In

the great spotted cuckoo, the exact place of production for this mixture is not yet known. We can expect that with a sudden ejection of more than 10 ml, the responsible gland or structure will be easily identified and described soon. The avian anal gland, cloacal gland, or cecum are the best candidates to assume this function. Birds typically have paired ceca hosting numerous bacteria, which help in the digestion of various nutriments. Presently, this organ seems to show all the required traits to produce this foul-smelling secretion.

3. The constitutive compounds of the secretion produced by the juvenile great spotted cuckoo have a biochemical origin which remains unclear. The cecum and glands contain a rich bacterial fauna, which is commonly associated with the production of malodorous volatiles. Hence, a bacterial biotransformation of metabolic precursors is a logical explanation, as described in the uropygial gland of hoopoes and red-billed woodhoopoe (*Phoeniculus purpureus*, Miller 1784). In hoopoe, the production of odoriferous excretion requires the presence of *Enterococcus faecalis* (Martín-Vivaldi et al. 2010), whereas the uropygial gland of the red-billed woodhoopoe houses *Enterococcus phoeniculicola* among others (Law-Brown and Meyers 2003). As we can imagine, the bacterial strains present in an uropygial gland may vary under several parameters, adding diversity and variability in avian-produced volatiles (Lucas and Heeb 2005). In the secretion of *C. glandarius*, high production of scatole (i.e. 3-methylindole), indole, and other unpleasant odorants supposes a comparable bacterial transformation, especially because avian excrements do not emit such compounds. Within bacterial communities, the enterobacteria (e.g. *Enterobacter cloacae*) are known to generate such molecules (Jensen et al. 1995). More interestingly, our previous repellence tests revealed an optimal protection against mammals. Here, we can hypothesize that evolution has developed an ideal odoriferous protection for great spotted cuckoo chicks. Indeed, predators remain strongly repelled by their own excrements, mainly to avoid disease and intoxication. Therefore, a juvenile cuckoo smelling like their own dung surely deters most mammals. It would not be a surprise if classic mammalian fecal bacteria would be present in the avian structure producing the defensive secretion, corroborating the expected bacterial origin of this protection.
4. Interspecific parasitic cuckoo chicks cannot rely on their own parents for protection. Usually, smaller and weaker host parents raise them. For a juvenile cuckoo, the development of efficient defenses might be a plus. Although the young great spotted cuckoos exhibit such malodorous defense, nothing is known in other parasitic bird species. Is the secretion of the great spotted cuckoo unique, or is there any equivalence in other species? Currently, this question is being evaluated by comparison with the common cuckoo (*Cuculus canorus* L.), whose nestlings also produce a sticky secretion upon harassment (Pict. 20.3). Preliminary volatile analyses have been carried out on the secretion produced by young common cuckoos. As previously described, GC-MS was used to obtain chromatographic descriptions of both the likely new defensive secretion and classic excrements of juvenile common cuckoo chicks. The final publication is in preparation, but some informative results can be presented here. The unlabeled chro-



Pict. 20.3 A common cuckoo fledgling in defensive posture, before the emission of its foul-smelling secretion. Courtesy of A. Trnka

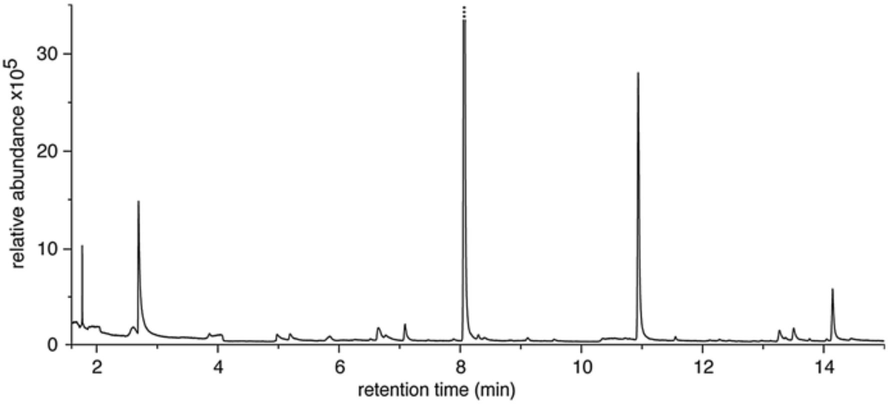


Fig. 20.4 Another defensive secretion in a brood parasite: Preliminary chromatographic results of the volatiles released by juvenile common cuckoo upon threat. Visually, the secretion produced by common cuckoo hatchling looks like the one of the great spotted cuckoo chick, but chemically the constitution is very different. This odorant profile was obtained by the SPME method

matographic profile shows the odorants found in the secretion released by young common cuckoos (Fig. 20.4). It suggests that odors are far from identical with those emitted by *C. glandarius*. Compared with this species (see Fig. 20.1), the main malodorous volatiles are absent or very weak in the common cuckoo hatchlings. This highlights the great variability of such secretions, and suggests variation in the effectiveness of defense. The common cuckoo is an evicting brood parasite, which reduces strongly the reproductive success of its hosts. Compared with the great spotted cuckoo, both the strategy and needs are different. Consequently, we can expect that being alone in the nest with full parental care might have led to the evolution of different traits, including less fetid secretion ensuring that host parents will stay after emission. Obviously, the evolution of these defensive secretions might be under many selective parameters, and may have diversified as a function of the main brood parasitic strategies.

5. Finally, an extensive study of odorous defensive secretions in parasitic cuckoos may reveal a correlation of various types of secretions with particular ecological patterns. In our studied organisms, only juvenile great spotted and common cuckoos are able to produce and release a specialized secretion against intruders. Is this true for all other parasitic cuckoo species, in which adults would be unable to use any malodorous defense? As described previously, the different strategies between evicting and non-evicting cuckoos may have consequences for the production of odoriferous defenses. Moreover, many brood parasitic adults are migrant species, which may have an impact on the production, use, and efficiency of likely smelly protections. With many other future questions, all these current interrogations are waiting for answers. These new perspectives will surely lead to new captivating findings in the field of avian-produced volatile defenses.

20.4 Conclusion

Clearly, birds represent a group in which chemical signals are numerous, diverse, and essential. Today, the main types of olfactory communication and behaviors initially observed in mammals have been documented in one or another avian species. In some very specific ecological interactions, such as host–brood parasitism, avian odors can play an unsuspected but crucial role. In attempting to understand the relations between individuals, species, and their biotopes, VOCs should no longer be excluded. Here, we have showed that the extreme precariousness of interspecific brood parasite–host interactions might be strongly influenced by a few volatile molecules. A small emission of individual odorants may have serious ecological consequences for an entire system. For researchers and ornithologists, this constitutes a great challenge, as well as some fantastic opportunities to work with emblematic systems and species, but with a new approach. Chemical ecology in birds is surely at the dawn of major discoveries.

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