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Potential Semiochemical Molecules from Birds: A Practical and Comprehensive Compilation of the Last 20 Years Studies

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Abstract

During the past 2 decades, considerable progress has been made in the study of bird semiochemistry, and our goal was to review and evaluate this literature with particular emphasis on the volatile organic constituents. Indeed, since the importance of social chemosignaling in birds is becoming more and more apparent, the search for molecules involved in chemical communication is of critical interest. These molecules can be found in different sources that include uropygial gland secretions, feather-surface compounds, and molecules from feces and skin. Although many studies have examined the chemical substances secreted by birds, research on bird chemical communication is still at the start, so new strategies for collecting samples and development of new methods of analysis are urgently required. As a first step, we built a database that brings together potential semiochemicals, using a unique chemical nomenclature for comparing different bird species and also for referencing the different classes of substances that can be found in order to adapt future parameters of analysis. The most important patterns of the wax fraction of preen secretions are highlighted and organized in an ordered table. We also draw up a list of various combinations of sampling and analytical techniques, so that each method can be compared at a glance.

Key words: bird olfaction, chemical communication, feathers, feces, uropygial gland

Introduction

Avian olfactory communication is a poorly explored area of study, although it is now established that most birds possess a fully functional olfactory system. The number and diversity of avian genes coding for olfactory receptors and the presence of a proper olfactory bulb indicate that birds may use their smell more than previously thought (Steiger et al. 2008, 2009). Indeed, birds can use chemical signals from the environment for foraging (Hutchison and Wenzel 1980; Smith and Paselk 1986; Nevitt 2000), navigation (Papi 1991; Wallraff 2001, 2004; Gagliardo et al. 2009, 2011), nest material selection (Clark and Mason 1985, 1987; Clark and Smeraski 1990; Petit et al. 2002; Gwinner and Berger 2008; Mennerat 2008), homing (Minguez 1997; Bonadonna and Bretagnolle 2002; Bonadonna et al. 2003, 2004), and predator avoidance (Amo et al. 2008; Roth et al. 2008). Birds also have scent-producing organs (uropygial gland, cloacal gland, and epidermal cells) that could be involved, at least in some taxa, in social behavior via chemical communication (for review, see: Hagelin 2007).

Although birds apparently do not possess vomeronasal receptors, as neither the genes nor pseudogenes for such receptors are found in the chicken genome (Shi and Zhang 2007), they are still able to integrate olfactory information for social and reproductive behaviors. Some pheromonal responses can be mediated by the main olfactory system or possibly the septal organ. For example, some receptors from the main olfactory system have been associated with pheromone detection and belong to the trace-amine associated family of receptors (Liberles and Buck 2006), some members of which are present in the chicken genome (Lagerstrom et al. 2006; Hashiguchi and Nishida 2007; Mueller et al. 2008) and in other birds (Antarctic prion, blue and snow petrel unpublished results). The first study that linked olfaction to social behaviors was carried out in the late 70s on sexual behavior in mallards (Balthazart and Schoffeniels 1979). The role of chemosignals in the sexual behavior of birds was suggested by the difference in the chemical composition of the preen gland secretion between male and female ducks during the

reproductive season (Jacob et al. 1979). Furthermore, the sexual behavior of male domestic ducks (*Anas platyrhynchos*) was significantly disrupted when the birds were rendered anosmic through cutting their olfactory nerves, whereas neither their aggressive behaviors nor their plasma levels of pituitary–gonadal hormones were affected (Balthazart and Schoffeniels 1979). Following this early study, the role of avian olfaction was examined in different social contexts such as territoriality, parent-offspring recognition, environmental familiarity, and species recognition (Jones and Roper 1997; Roper 1999; Hagelin 2007; Hagelin and Jones 2007; Rajchard 2007, 2010; Balthazart and Taziaux 2009). Recent experimental evidence further suggested that olfaction influences mate choice in domestic chickens (*Gallus gallus domesticus*), in which the female's uropygial gland appears to act as a source of sexual chemosignals (Hirao et al. 2009).

Although the importance of social chemosignaling in some bird taxa is becoming more and more apparent, the exact nature of the chemical cues involved remains largely undocumented. This is probably due to the difficulties of collecting body odor samples and/or extracting volatile molecules from biological samples for chromatographic analyses, as well as adequately processing these data. The exact identification of molecules emitted by avian secretory organs is, however, of critical importance for understanding the role of olfaction in the social life of birds. This review compiles information published in the last 20 years on avian chemical compounds in the form of a database that should prove particularly useful for colleagues, whether they study the chemical/chromatographic or behavioral aspects of chemical communication. In this compilation, the names of chemical compounds all use the International Union of Pure and Applied Chemistry (IUPAC) nomenclature to avoid the disparity observed in the literature that might lead to difficulties when comparing species. The most interesting patterns based on behavioral ecology and observed in the lipidic fraction of the uropygial secretion are organized in a separate table (Table 1). Furthermore, to compare data, we bring together details of various methods of the studies that we review (Table 5).

Molecules from the uropygial gland

The uropygial gland (or preen gland) in birds is located dorsally, above the last vertebrae of the pygostyle. The external morphology (size, shape, and proportions) of this holocrine secretory organ greatly varies among species but is usually relatively constant at the intraspecific level except among the Psittaciformes, Galliformes, and Anseriformes (Jacob and Ziswiler 1982; Johnston 1988). The gland can be completely absent or reduced as in the Struthionidae, Rheidae, Casuariidae, and Dromaiidae; and in a few species of Columbidae and Psittacidae (Johnston 1988). More anatomical and histological informations about this gland are available in other reviews (Haahti et al. 1964; Kolattukudy 1981; Jacob and Ziswiler 1982; Salibian and Montalti 2009). Because the gland produces a large amount of volatile and nonvolatile compounds that are spread on feathers, uropygial secretions are generally considered key sources of avian body scent. Moreover, the important variability of the chemical composition of these secretions across species (Jacob and Ziswiler 1982) suggests that the uropygial gland may be involved in a variety of functions (for review, see: Salibian and Montalti 2009; Rajchard 2010).

Large esters

The chemical composition of preen waxes from various birds has been extensively reviewed, mainly in the 70's and 80's (Haahti et al. 1964; Saito and Gamo 1972, 1973; Kolattukudy 1981; Jacob and Ziswiler 1982). The gland produces a greasy material that is mainly composed of unusual lipids that vary significantly from order to order (Jacob and Ziswiler 1982). Different factors have been shown to influence the content of the fatty acid fraction of the secretions such as age of the birds, that is, sexual maturity (Kolattukudy and Sawaya 1974; Sandilands et al. 2004), breeding stage (Kolattukudy et al. 1987; Piersma et al. 1999; Sinninghe Damste et al. 2000; Reneerkens et al. 2002; Reneerkens, Piersma, et al. 2007), sex (Zhang et al. 2009; Mardon et al. 2010), individuality (Zhang et al. 2009; Mardon et al. 2010), and diet (Thomas et al. 2010).

In adult birds, natural esters are made up of an extraordinary mixture of fatty acids and long-chain alcohols. The main components are usually monoester waxes made of fatty acids (nearly always saturated) with different degrees of methyl branching and long-chain monohydroxy fatty alcohols. In some groups of birds, diester waxes containing hydroxy fatty acids and/or alkanediols are also present. Other compounds such as alkanes, triglycerides, free fatty acids, and free alcohols may also be found (Jacob and Ziswiler 1982; Sweeney et al. 2004). At least some of these compounds might produce odors, considering their relatively high volatility.

The diversity of carbon chain lengths and substitution location observed in avian esters can lead to a mixture of hundreds of different compounds. Therefore, the structural identification of each original component is rarely achieved and most studies have focused on analyses of hydrolyzed or transesterified products of secretions. For the same reason, chromatographic data are often compared and treated in terms of qualitative profile without clearly identifying the compounds. Since the early reviews cited above, few new chemical data have been added, most of them focusing on the seasonal variability of secretions. These data are briefly described below, and the main patterns depending on behavioral contexts are summarized in Table 1.

One of the first of the rare studies that achieved a full structural identification of intact wax esters was carried on preen oils from captive red knots (*Calidris canutus*, a shorebird) using gas chromatography-mass spectrometry (GC-MS) and GC-MS-MS (Dekker et al. 2000). The lipids from the uropygial gland secretion collected out of the breeding

Table 1 Characteristics of the lipid fraction from of uropygial secretions observed in different species and studies

Biological and environmental factors		Bird species	Pattern	Main compounds
Season	Captive birds, nonbreeding season[a]	Red-knot shorebird	Monoesters waxes	C_{21}–C_{32} monoesters: *odd carbon-numbered esters composed of even carbon-numbered n-alcohols (C_{14}, C_{16}, and C_{18}) esterified mainly with odd carbon-numbered 2-methyl fatty acids (C_7, C_9, C_{11}, and C_{13}). *complex even carbon numbered waxes.
Season	Captive and free-living birds, before migration to breeding grounds[b,c,d]	Red-knot shorebird	Shift from monoesters to diesters	C_{32}–C_{46} diesters: C_8–C_{18} straight-chain fatty acids esterified with C_{12}–C_{18} alkane-1,2-diols.[b]
Season	Breeding season[e]	Bar-tailed gotwit, Gray plover and Pacific golden plover	Shift from monoesters to diesters	C_{32}–C_{48} diesters: C_{10}–C_{18} β-hydroxy fatty acids esterified with C_8–C_{18} fatty acids and C_{12}–C_{18} fatty alcohols.
Season	Breeding season Comparison of species with: A) Uniparental incubation[d] B) Biparental incubation[d]	A) Curlew sandpiper, Ruff, Buff-breasted sandpiper, and Red phalarope B) Red-knot, Western sandpiper, and Temminck's stint	A) Shift from monoesters to diesters for the incubating sex only B) Shift from monoesters to diesters for both sexes except for males and females Temminck's stint that secreted only diesters	A and B) C_{34}–C_{50} diesters: Mainly 1,2-diols esterified with straight-chain fatty acids at both positions.
Season	Collection of samples at different times of the year[f]	Species of passerine	Unimodal distribution of monoesters except for Northern mockingbirds	C_{23}–C_{40} monoesters (C_{29}–C_{36} mainly): Straight chain alcohols esterified with * 3-methyl branched acids * 2-methyl branched and small quantities of straight acids (Blue jay)
Season	Nonbreeding season[g]	Rock dove	Mostly unsaturated fatty acids with no differences between male and female	C_{14}–C_{20} fatty acids (approximately 58% unsaturated): $C_{18:1}$ is the most prevalent unsaturated fatty acids (37%)C_{16} is the most prevalent saturated fatty acids (31%)
Habitat	Tropical and temperate habitats[h]	A) Thamnophilidae family: Dusky, Chestnut-backed, and White bellied antbirds B) Formicaridae family: Black-faced antthrush C) Pipridae family: White-ruffed manakin D) Dendrocolaptidae family: Spotted and Streak-headed wood creepers E) Tyrannidae family: White-throated spadebill	Esters of higher molecular weight in some tropical birds compared with temperate birds. Presence of monounsaturated and tri-unsaturated esters in some species.	A) Triterpenoids, free fatty alcohols and acids, and small quantities of esters (C_{12}–C_{20} saturated alcohols esterified with C_{19}–C_{28} saturated acids) B) Squalene and isoprenyl derivatives made up of sester, tri and tetra terpenes, with the triterpene squalene being the major product C) Esters with C_{18}–C_{25} saturated acids D) Esters with saturated C_{13}–C_{22} and monounsaturated $C_{32:1}$–$C_{42:1}$ acids combined with mono-alcohols E) Long chain of saturated, mono and tri-unsaturated esters with mono and di-ols

Table 1 Continued

Biological and environmental factors		Bird species	Pattern	Main compounds
Age	From one day old to 15 weeks of age[i]	Domestic chicken	Modification of the proportion of some saturated fatty acids	Changes in C_{12}, C_{13}, C_{19}, and C_{24} fatty acids
Sex		Blue petrels[j]	Higher occurrence of some esters in females Difference in the position of methyl substitution	C_{23}–C_{28} esterified acids 4-methyl substitution in all female-associated compounds, whereas 2-methyl substitution dominated the male associated ones
Species	Procellariidae birds from different genera[j]	Blue petrels and Antarctic prions	Divergence in the type of ester methyl-substitution	4-methyl substituted esters mainly in Blue petrel instead of 3-methyl substituted esters in Antarctic prion
Species	Passeriformes birds from different families[k]	Estrildidae family: Bengalese finch and Zebra finch Emberizidae family: Yellow-browed bunting Corvidae family: Rook	Some family-specific and some genus-specific esters	Diethyl hexanedioate and 3 unidentified diesters found only in estrildidae.Hexadecyl heptanoate and one unidentified diester found only Bengalese finch but not in Zebra finch.
Individual identity		Blue petrels[j]	Differences in the relative abundances of compounds.	No individually specific compounds.

[a]Dekker et al. (2000).
[b]Piersma et al. (1999).
[c]Sinninghe Damste et al. (2000).
[d]Reneerkens, Almeida, et al. (2007).
[e]Rijpstra et al. (2007).
[f]Haribal et al. (2005).
[g]Montalti et al. (2005).
[h]Haribal et al. (2009).
[i]Sandilands et al. (2004).
[j]Mardon et al. (2010).
[k]Zhang et al. (2010).

season are dominated by monoesters waxes (Table 1). The problem in identifying intact wax esters was overcome by using GC-MS-MS once the building blocks (fatty acids and alcohols) were identified by traditional analysis, that is, after hydrolysis and derivatization of each monoester fraction. The odd carbon-numbered esters are predominantly composed of even carbon-numbered *n*-alcohols esterified predominantly with odd carbon-numbered 2-methyl fatty acids. The distribution of even numbered carbon waxes is much more complex. In this case, odd and even numbered carbon alcohols are approximately equal in amount, and the presence of various isomers of dimethyl branched fatty acids is observed when the molecular weights increase. Interestingly, this characterization of intact wax esters shows that the biosynthesis of such complex molecules might be controlled, rather than being a random combination of fatty acids and alcohols available although the reasons remain unclear (Dekker et al. 2000).

Just before spring migration to breeding ground, the preen wax composition of red knots shifts from monoesters (described above) to less usual diester waxes (Piersma et al. 1999; Sinninghe Damste et al. 2000) (Table 1). The presence of diester waxes was not reported before in the order Charadriiformes, but they are particularly prevalent in Galliformes (Haahti and Fales 1967). Moreover, although a similar change from monoester to diester waxes has been previously reported for wild-type and domesticated mallard (*A. platyrhynchos*) females during courtship and incubation (Jacob et al. 1979; Kolattukudy et al. 1987), so abrupt a shift has not been found in the family Scolopacidae. In this group, the GC analysis of uropygial secretions from captive and free-living birds revealed that the diesters are composed of straight chain fatty acids esterified with alkane-1,2-diols (Piersma et al. 1999). The distribution in the diesters is dominated by C_{12} to C_{16} diols esterified with octanoic, decanoic, and dodecanoic acid at one position and even-numbered carbon fatty acids at the other position in the carbon chain (Sinninghe Damste et al. 2000).

Another type of diester was detected in the preen waxes of 3 other shorebirds (*Limosa lapponica*, *Pluvialis squatarola*, and *Pluvialis fulva*) during the incubation period (Table 1). These diesters are composed predominantly of fatty acids

esterified with a fatty acid at the β-hydroxy position and with fatty alcohols at the carboxyl group. A small amount of diester waxes based on C_{16}–C_{20} alkan-1,2-diols is also found (Rijpstra et al. 2007).

The switch from monoesters to diesters during the breeding period was also investigated in 7 different shorebirds (Reneerkens, Almeida, et al. 2007) (Table 1). The switch appears to be mainly restricted to the incubating sex in species with uniparental incubation (Curlew sandpiper, ruff, buff-breasted sandpiper, and red phalarope; *Calidris ferruginea*, *Philomachus pugnax*, *Tryngites subruficollis*, and *Phalaropus fulicarius*, respectively). But it occurs in both sexes in species with biparental incubation (red knot and Western sandpiper; *C. canutus* and *Calidris mauri*). Some exceptions, however, were observed as for Temminck's Stints (*Calidris temminckii*) in which both males and females secreted only pure diester preen waxes. Some nonincubating males from curlew sandpiper and buff-breasted sandpiper species also displayed diesters in their preen wax but at very low amounts. The authors proposed as a possible explanation that the diester secretion in this case is a remnant of an evolutionary past when both males and females shared incubation. In all species investigated in this study, the secreted diesters range between C_{34} and C_{50} with small amounts of C_{30}–C_{32} in red knot, ruff and curlew, and some C_{52} in Temminck's stints. The majority of the diesters are made of 1,2-diols esterified with straight-chain fatty acids at both positions (Table 1). Interestingly, the preen wax composition of captive female ruff presents the same shift from monoesters to diesters in the spring despite the fact that no incubation took place suggesting that circannual rhythms may trigger this shift, as previously observed with captive red knots (Reneerkens, Piersma, et al. 2007).

However, although the switch from monoesters to diesters during the mating season is observed for several bird species, the biochemical processes underlying this phenomenon are still poorly known. A study carried out at the physiological level in mallard ducks (*A. platyrhynchos*) indicated a role for hormonal induction (Bohnet et al. 1991). Indeed, the injection of thyroxine with estradiol induces the diester synthesis even in male mallards that do not normally produce these compounds. Moreover, the hormonal treatment also induces the proliferation of peroxisomes specifically in the uropygial gland and peroxisomes appear to be a compartment that specializes in the synthesis of diesters.

Seasonal differences were also observed by analyzing the wax components extracted from the uropygial gland of 11 different passerines species from diverse microhabitats and with diverse ecologies (Haribal et al. 2005) (Table 1). Although the order Passeriformes includes the majority of bird species, the exact composition of secretions of this order has been poorly explored. The preen secretions from the same species but collected at different times of the year showed both quantitative and qualitative variations in their contents. The lipid secretions are made of homologous monoesters of varying chain lengths. Only Northern Mockingbirds (*Mimus polyglottos*) have a more complex chemical profile with more compounds. Most of the fringillids, icterids, and emberyzids exhibit monomethyl 3-methyl and some further branched acids while the Blue Jay (*Cyanocitta cristata*) has mostly 2-methyl branched acids and small quantities of straight chain components. Interestingly, monoesters of similar molecular weight are formed through different combinations of acids and alcohols, which are characteristic of each individual species (Haribal et al. 2005).

The composition of the uropygial secretions can be affected by environmental factors, as demonstrated by tropical birds (Haribal et al. 2009) (Table 1). For example, the esters of antbirds and manakins are composed of higher molecular weight components compared with temperate birds. The presence of monounsaturated and tri-unsaturated esters is also detected in the secretion of tropical birds from the Dendrocolaptidae and Tyrannidae families. Although monounsaturated esters have been previously reported in few species, such as kiwis (Apteriformes) and Galliformes (Jacob 1982), Haribal et al. (2009) is the first to report the presence of tri-unsaturated esters of mono- and di-ols in preen secretions. Some tropical birds do not display esters in their secretions, as birds from the Formicaridae family (black-faced antthrush, *Formicarius analis*) exclusively secrete terpenoids, especially squalene and its derivatives. Other terpenoids such as cholesterol are found in the secretions of antbirds of the Thamnophilidae family (Dusky, chestnut-backed and white bellied antbirds; *Cercomacra tyrannina*, *Myrmeciza exsul*, and *Myrmeciza longipes*, respectively).

The analysis of the uropygial secretion is sometimes also used as a tool in reinvestigating the systematic status of a bird. The Hume's ground jay (*Pseudopodoces humili*) was traditionally placed by taxonomists next to ground jays of the genus *Podoces*. Genomic and other data indicated that the species is a member of the Paridae. The monoester waxes were then analyzed; after hydrolysis, the alcohols and fatty acids profiles revealed the exclusive presence of 2-ethyl substituted fatty acids as well as unbranched (76.8%) and monomethyl branched (23.2%) alkanols (Gebauer et al. 2004). By comparison with the data from Corvidae and Paridae, it is obvious that the composition of the preen secretions places *P. humilis* with the parids rather than corvids, although behavioral attributes of this bird are more typical of corvids (Gebauer et al. 2004). However, the use of the chemical composition of preen secretions as taxonomic tool should be considered with care, as it can be influenced by a variety of environmental, hormonal, and physiological factors (Levy and Strain 1982).

The effect of different variables on the uropygial gland secretions were also studied by focusing only on fatty acids profiles after hydrolyzing the ester bonds. In domestic chickens, the preen secretions contain fatty acids ranging from C_{10} to C_{24} whose relative composition differs with age and with whether or not feathers were pecked by conspecific

individuals (Sandilands et al. 2004). The changes, occurring with bird age and significantly affecting the proportion of some saturated fatty acids, were most likely related to sexual maturity. Indeed, the changes were observed during the sampling periods corresponding to the onset of lay where hormonal state is modified as visualized by the increase in circulating hormones. Differences in fatty acid compositions are also detected between feather pecked and non-feather pecked bird's involving 4 saturated fatty acids (C_{12}, C_{13}, C_{14}, and C_{20}). The study suggests that the changes in preen oil composition may influence whether or not a bird is targeted for feather pecking by affecting the odor of the plumage and thus its attractiveness to other birds (Sandilands et al. 2004). Another study on fatty acid composition from preen gland waxes was carried out on rock dove (*Columba livia*), during the nonbreeding season (Montalti et al. 2005). The lipid content of the gland is constituted of fatty acids ranging from C_{14} to C_{20}, most of them being unsaturated (Table 1). The fatty acid profile is different than that of the food given to the birds. No differences are observed between male and female, although this can be due to the fact that analyses were carried out during the nonbreeding period (Montalti et al. 2005). Interestingly, although the uropygial gland of rock dove is very small (0.022% related to the body mass), the secretion represents 32% of its mass. Thus, the physiological role of the gland may depend upon the quantities of its secretion rather than upon its mass per se (Montalti and Salibian 2000).

Some intact wax esters were also identified in recent studies focusing on sex, individual, and species information coded by the uropygial gland secretions in domesticated Bengalese finch (*Lonchura striata*) and in 3 sympatric passerine species, that is, Zebra finch (*Taeniopygia guttata*), Yellow-browed bunting (*Emberiza chrysophrys*), and Rook (*Corvus frugilegus*) (Zhang et al. 2009) (Table 1). Six ester molecules are found in the uropygial gland secretions of male and female Bengalese finches, but they are not detected in the secretions from Yellow-browed buntings and Rooks. In male Zebra finches, the same esters are present except for one unidentified diester and hexadecyl heptanoate and 4 additional long-chain monoesters. The interspecific differences observed in the esters and particularly the presence of some esters found only in Zebra finches might separate different genera of the Estrildidae family (Zhang et al. 2009). A search of social chemosignals was also carried out on preen secretions in birds from the Procellariiform order, Blue petrels (*Halobaena caerulea*), and Antarctic prions (*Pachyptila desolata*) in particular, which led to the identification of several intact esters (Mardon et al. 2010). As expected, a chemical similarity is observed in the secretions of the 2 closely related species, but a strong species-specific chemical signal is also detected. The type of ester methyl substitution is divergent with a high level of 4-methyl substituted esters in the Blue petrel's secretion, whereas Antarctic prion' secretion has more 3-methyl substituted esters (Table 1). This species-specific signal is proposed as a possible example of divergence caused by strong interspecific competition for burrows. At the intraspecific level, an individual signal is detected, although the signature is not made up of individually specific compounds but rather by differences in the relative proportions of a large number of compounds shared by all individuals. An intraspecific sex signal is also found within the uropygial secretions of Blue petrels: esterified acids between C_{23} and C_{28} occur more often in females than in males. This indicates that the sex signal may be female derived. The type of methyl substitution also diverges with 4-methyl substitution making up all "female-associated" compounds, whereas 2-methyl substitution dominates the "male-associated" ones. The female-specific nature of the chemical sexual dimorphism is unusual compared with other vertebrates in which males often display secondary sexual characteristics. In female ducks, a similar phenomenon was described with male secretions remaining constant, whereas female secretions exhibited qualitative and quantitative variations (Jacob et al. 1979). The preen secretions of Blue petrels also display a significant interannual variation for the 2 sampling years (2008 and 2009), with 48 analytes present only in 2008 and 1 analyte present only in 2009. This could be explained by environmental fluctuations that could affect metabolism and diet and/or a degradation process during the breakdown of the cold chain between the field and the laboratory in 2008 (Mardon et al. 2010).

Compounds other than esters

In addition to wax esters, it appears that preen secretions contain many volatile and semivolatile molecules that could constitute relevant cues for biological functions and for behavioral assays. Surprisingly, relatively few studies have reported the composition of the volatile fraction of uropygial secretions, underscoring the disregard for bird chemical communications until recent years.

The hoopoes (Upupidae) and woodhoopoes (Phoeniculidae) are particularly interesting cases because uropygial secretions in these 2 closely related bird families are dark and pungent (Burger et al. 2004; Martin-Vivaldi et al. 2009, 2010). This unusual odorous secretion is only produced by nestlings and breeding females in European hoopoes (Martin-Vivaldi et al. 2009), whereas the secretion is very similar in all individuals throughout the life cycle in woodhoopoes (Burger et al. 2004). The study of the volatile compounds from the preen oil of green woodhoopoes (*Phoeniculus purpureus*) was carried out using solid phase microextraction (SPME) or dichloromethane extraction (Burger et al. 2004) (Table 5). GC-MS analyses of solvent extracts show the presence of wax esters (not analyzed) with high retention times, given the conditions of the study. These compounds are not found in total ion traces of SPME extracts from the headspace of the secretion because of their low volatility. No consistent variation is found between males and females. In the volatile fraction, different class of compounds

Table 2 Molecules other than esters from the uropygial secretions collected on different birds

Chemical compound (IUPAC name)	Bird species	CAS number	Molecular formula
Alkanes			
Undecane	DJ[1]	1120-21-4	$C_{11}H_{24}$
Tridecane	DJ[1], GW	629-50-5	$C_{13}H_{28}$
Pentadecane	GW	629-62-9	$C_{15}H_{32}$
Hexadecane	GW	544-76-3	$C_{16}H_{34}$
2-methylhexadecane	GW	1560-92-5	$C_{17}H_{36}$
Heptadecane	BP[2], DJ[1], GW	629-78-7	$C_{17}H_{36}$
3-methylheptadecane	GW	6418-44-6	$C_{18}H_{38}$
Octadecane	BP[2], GW	593-45-3	$C_{18}H_{38}$
Nonadecane	BP[2], GW	629-92-5	$C_{19}H_{40}$
5-methylnonadecane	GW	55193-47-0	$C_{20}H_{42}$
Icosane	GW	112-95-8	$C_{20}H_{42}$
Henicosane	GW	629-94-7	$C_{21}H_{44}$
Docosane	GW	629-97-0	$C_{22}H_{46}$
Tricosane	GW	638-67-5	$C_{23}H_{48}$
Tetracosane	GW	646-31-1	$C_{24}H_{50}$
Alkenes			
(Z)-Heptadec-7-ene	GW	54290-12-9	$C_{17}H_{34}$
(Z)-Heptadec-9-ene	GW	n.a.	$C_{17}H_{34}$
Octadec-1-ene	DJ[1]	112-88-9	$C_{18}H_{36}$
(Z)-Nonadec-7-ene	GW	n.a.	$C_{19}H_{38}$
(Z)-Nonadec-9-ene	GW	n.a.	$C_{19}H_{38}$
(Z)-Icos-9-ene	GW	n.a.	$C_{20}H_{40}$
(Z)-Henicos-7-ene	GW	n.a.	$C_{21}H_{42}$
(Z)-Henicos-9-ene	GW	n.a.	$C_{21}H_{42}$
(Z)-Docos-7-ene	GW	n.a.	$C_{22}H_{44}$
(Z)-Docos-9-ene	GW	n.a.	$C_{22}H_{44}$
(Z)-Tricos-7-ene	GW	52078-57-6	$C_{23}H_{46}$
(Z)-Tricos-9-ene	GW	52078-48-5	$C_{23}H_{46}$
(Z)-Tetracos-7-ene	GW	n.a.	$C_{24}H_{48}$
(Z)-Tetracos-9-ene	GW	n.a.	$C_{24}H_{48}$
(Z)-Pentacos-7-ene	GW	96313-98-3	$C_{25}H_{50}$
(Z)-Pentacos-9-ene	GW	n.a.	$C_{25}H_{50}$
Alcohols			
3-methylbutan-1-ol	GW	123-51-3	$C_5H_{12}O$
2-ethylhexan-1-ol	DJ[1]	104-76-7	$C_8H_{18}O$
Nonan-1-ol	DJ[1,2]	143-08-8	$C_9H_{20}O$
Decan-1-ol	DJ[1,2], GC[2]	112-30-1	$C_{10}H_{22}O$
Undecan-1-ol	DJ[1,2], GC[2]	112-42-5	$C_{11}H_{24}O$
Dodecan-1-ol	DJ[1,2], GC[2]	112-53-8	$C_{12}H_{26}O$
Tridecan-1-ol	BF, DJ[1,2], GC[2],ZF	112-70-9	$C_{13}H_{28}O$
Tetradecan-1-ol	BF, DJ[1,2], GC[2],R, YBB, ZF	112-72-1	$C_{14}H_{30}O$
13-methyltetradecan-1-ol	GW	58524-92-8	$C_{15}H_{32}O$
Pentadecan-1-ol	BF, DJ[1,2], GC[2],R, YBB, ZF	629-76-5	$C_{15}H_{32}O$
14-methylpentadecan-1-ol	GW	36311-34-9	$C_{16}H_{34}O$
Hexadecan-1-ol	BF, DJ[1,2], GC[2],R, YBB, ZF	36653-82-4	$C_{16}H_{34}O$
Hexadecan-1-ol (*isomers*)	BP[2]	n.a.	$C_{16}H_{34}O$
Heptadecan-1-ol	B, BF, BP[1], DJ[1,2], GC[2], ZF	1454-85-9	$C_{17}H_{36}O$
Octadecan-1-ol	B, BF, DJ[1], GC[2], R, YBB, ZF	112-92-5	$C_{18}H_{38}O$
Octadecan-1-ol (*isomers*)	BP[2]	n.a.	$C_{18}H_{38}O$
Nonadecan-1-ol	B, GC[2]	1454-84-8	$C_{19}H_{40}O$
Icosan-1-ol	B, BP[1], GC[2]	629-96-9	$C_{20}H_{42}O$
Henicosan-1-ol	B, BP[1]	51227-32-8	$C_{21}H_{44}O$
Docosan-1-ol	GC[2]	661-19-8	$C_{22}H_{46}O$
Hexocosan-ol (*isomers*)	BP[2]	n.a.	$C_{26}H_{54}O$
Hexadecen-1-ol	BF, ZF	n.a.	$C_{16}H_{32}O$
Octadecen-1-ol	BF	n.a.	$C_{18}H_{36}O$
Aldehydes			
3-methylbutanal	GW	590-86-3	$C_5H_{10}O$
Octanal	DJ[1]	124-13-0	$C_8H_{16}O$
Nonanal	DJ[1]	124-19-6	$C_9H_{18}O$
Decanal	DJ[1]	112-31-2	$C_{10}H_{20}O$
Undecanal	DJ[1]	112-44-7	$C_{11}H_{22}O$
Hexadecanal	BF, DJ[1], GW	629-80-1	$C_{16}H_{32}O$
Ketones			
Undecan-2-one	DJ[1,2]	112-12-9	$C_{11}H_{22}O$
Dodecan-2-one	DJ[1,2]	6175-49-1	$C_{12}H_{24}O$
6,10-dimethylundeca-5, 9-dien-2-one	DJ[1]	689-67-8	$C_{13}H_{22}O$
Tridecan-2-one	DJ[1], GC[2]	593-08-8	$C_{13}H_{26}O$
Tetradecan-2-one	DJ[1,2]	2345-27-9	$C_{14}H_{28}O$
Pentadecan-2-one	DJ[1,2], GC[2]	2345-28-0	$C_{15}H_{30}O$
Hexadecan-2-one	DJ[1,2], R, YBB	18787-63-8	$C_{16}H_{32}O$
Heptadecan-2-one	DJ[1,2], R, YBB	2922-51-2	$C_{17}H_{34}O$

Table 2 Continued

Chemical compound (IUPAC name)	Bird species	CAS number	Molecular formula
Aliphatic acid			
Acetic acid	GC[1,2]	64-19-7	$C_2H_4O_2$
Propanoic acid	GC[1], GW	79-09-4	$C_3H_6O_2$
2-methylpropanoic acid	GC[1]	79-31-2	$C_4H_8O_2$
Butanoic acid	EH, GC[1,2]	107-92-6	$C_4H_8O_2$
2-methylbutanoic acid	EH	116-53-0	$C_5H_{10}O_2$
3-methylbutanoic acid	GC[1,2]	503.74.2	$C_5H_{10}O_2$
Pentanoic acid	EH, GC[1,2]	109-52-4	$C_5H_{10}O_2$
2-methylpentanoic acid	GC[1]	97-61-0	$C_6H_{12}O_2$
4-methylpentanoic acid	EH, GW	646-07-1	$C_6H_{12}O_2$
Hexanoic acid	GC[1,2]	142-62-1	$C_6H_{12}O_2$
Heptanoic acid	GC[2]	111-14-8	$C_7H_{14}O_2$
Octanoic acid	BF, GC[2], ZF	124-07-2	$C_8H_{16}O_2$
Nonanoic acid	DJ[1,2], GC[2]	112-05-0	$C_9H_{18}O_2$
Decanoic acid	DJ[1,2]	334-48-5	$C_{10}H_{20}O_2$
Dodecanoic acid	DJ[1,2], GC[2]	143-07-7	$C_{12}H_{24}O_2$
3-methyltridecanoic acid	DJ[1]	n.a.	$C_{14}H_{28}O_2$
Tetradecanoic acid	DJ[1,2], GC[2]	544-63-8	$C_{14}H_{28}O_2$
3-methyltetradecanoic acid	DJ[1]	n.a.	$C_{15}H_{30}O_2$
3-methylpentadecanoic acid	DJ[1]	n.a.	$C_{16}H_{32}O_2$
Hexadecanoic acid	B, DJ[1,2], GC[2]	57-10-3	$C_{16}H_{32}O_2$
Octadecanoic acid	GC[2]	57-11-4	$C_{18}H_{36}O_2$
9-octadecenoic acid	GC[2]	112-80-1	$C_{18}H_{34}O_2$
Icosanoic acid	GC[2]	506-30-9	$C_{20}H_{40}O_2$
Docosanoic acid	GC[2]	112-85-6	$C_{22}H_{44}O_2$
Tetracosanoic acid	GC[2]	557-59-5	$C_{24}H_{48}O_2$
Hexacosanoic acid	GC[2]	506-46-7	$C_{26}H_{52}O_2$
Aromatic or cyclic			
1-methyl-4-propan-2-ylbenzene	DJ[1]	99-87-6	$C_{10}H_{14}$
Phenol	EH, GW	108-95-2	C_6H_6O
Benzaldehyde	EH, GC[2], GW	100-52-7	C_7H_6O
2-phenylacetaldehyde	EH	122-78-1	C_8H_8O
2-phenylethanol	GW	60-12-8	$C_8H_{10}O$
5-alpha-cholestan-3-beta-ol	BP[2]	80-97-7	$C_{27}H_{48}O$
3-phenylpropanoic acid	EH	501-52-0	$C_9H_{10}O_2$
2-Phenylethyl acetate	GW	103-45-7	$C_{10}H_{12}O_2$
1H-Indole	EH, GW	120-72-9	C_8H_7N
4-chloro-1H- indole	EH	25235-85-2	C_8H_6ClN
Amine			
Trimethylamine	GW	75-50-3	C_3H_9N
Sulfides			
Methyldisulfanylmethane	GW	624-92-0	$C_2H_6S_2$
Methylsulfanyl -disulfanylmethane	GW	85931-54-0	$C_2H_6S_3$
Other			
Henicosyl formate	BP[1]	77899-03-7	$C_{22}H_{44}O_2$

B, Budgerigar (*Melopsittacus undulates*) from Zhang et al. (2010); BF, Bengalese finches (*Lonchura striata domestica*) from Zhang et al. (2009); BP[1], Blue petrel from Mardon et al. (2010); BP[2], Blue petrel from Mardon et al. (2011b); DJ[1], dark-eyed junco (*Junco hyemalis*) from Soini et al. (2007); DJ[2], dark-eyed junco from Whittaker et al. (2010); EH: European hoopoe (*Upupa epops*) from Martin-Vivaldi et al. (2010); GC[1], gray catbird (*Dumetella carolinensis*) from Whelan et al. (2010); GC[2], gray catbird (*D. carolinensis*) from Shaw et al. (2011); GW, Green woodhoopoe (*Phoeniculus purpureus*) from Burger et al. (2004); R, rook (*Corvus frugilegus*) from Zhang et al (2009); YBB, yellow-browed bunting (*Emberiza chrysophrys*) from Zhang et al (2009); ZF, Zebra finches (*Taeniopygia guttata*) from Zhang et al. (2009); n.a., nonavailable.

are found (see GW in Table 2) including short-chain fatty acids, aldehydes, trimethylamine, indole, and dimethyl disulfide, all of which are suggested as responsible for the pungent smell of the secretion. The occurrence of volatile molecules together with relatively long-chain alkanes and alkenes (up to C_{25}) and heavy wax esters suggests that the uropygial gland may serve more than a waterproofing function, such as also reducing the predation risk (du Plessis et al. unpublished cited in Burger et al. 2004).

A similar study was carried out on the uropygial secretion from European hoopoe (*Upupa epops*) (Martin-Vivaldi et al. 2010). Ten volatile chemicals are found (9 are identified, see EH in Table1) in the dark secretion of nestlings that are absent in the chromatogram profile of white uropygial secretions of males and nonbreeding females. Some volatiles, such as benzaldehyde, phenol, 4-methyl pentanoic acid, and indole, are commonly shared by European hoopoes and woodhoopoes. Phenyl acetaldehyde and 4-chloro indole are exclusive to hoopoes. Trimethylamine, propanoic acid, 3-methylbutanal, 3-methylbutanol, dimethyl di and trisulfide, 2-phenyl ethanol, and 2-phenyl acetate seems to be exclusive to woodhoopoes. However, the methods used for extracting and analyzing these data are slightly different in the 2 studies (Table 5) and some molecules, such as trimethylamine might have been undetected due to the methodology. Symbiotic *Enterococcus* bacteria, found within the gland of Upupiformes, appears to be one of the factors

promoting the special properties of the secretion (darkness and smell) in this avian group (Law-Brown and Meyers 2003; Martin-Vivaldi et al. 2009). It is therefore possible that some of the unusual volatile molecules detected in the preen secretions as aromatic compounds (phenol, indole, benzaldehyde) are produced by the bacteria. Aromatic alcohols and indole in particular are indeed among the chemical compounds identified from the headspace above bacteria-containing solutions (Lindh et al. 2008). Most volatiles disappeared from dark secretions of antibiotic-treated birds, confirming the central role of bacteria in the presence of these compounds (Martin-Vivaldi et al. 2010).

The seasonal change observed in the volatiles from preen secretion of females European hoopoes is also observed in the dark-eyed junco (*Junco hyemalis*) (Soini et al. 2007). In this study, the volatile and semivolatile chemical composition of the preen gland secretions from male and female dark-eyed juncos was analyzed during the breeding and nonbreeding season using a Twister stir-bar sorptive extraction methodology (Table 5). The diet of the captive birds was maintained constant and the temperature simulated the conditions that the birds would experience in the wild. Moreover, the birds were held in long-day or short-day regimes to simulate breeding and nonbreeding conditions, respectively. Different classes of molecules are found such as alcohols, aldehydes, acids, methylketones and minor components as branched acids, saturated, and unsaturated hydrocarbons (DJ in Table 2). Linear alcohols (C_{10}–C_{18}) are the major components of the volatile fraction and both sexes show elevated levels of these alcohols during the breeding conditions compared with the nonbreeding state. The authors proposed that during the breeding season, wax ester synthesis may slow down, leading to more *n*-alcohols as fatty acid reduction products. The concentrations of some linear methylketones (tridecan-2-one, tetradecan-2-one, and pentadecan-2-one) also increase but only for breeding males. Linear carboxylic acids also exhibit seasonal variation because a statistically significant increase of linear hexadecanoic acid is observed during breeding for both sexes, whereas dodecanoic acid increased for females and tetradecanoic acid for males.

In contrast, a decline of short-chain carboxylic acids (propanoic, 2-methylpropanoic, and butanoic acids) is observed in the preen secretions of captive gray catbirds (*Dumetella carolinensis*) kept under increased photoperiod to simulate migratory activity (Whelan et al. 2010) (GC in Table 2). A reduced signal strength is also observed for propanoic and 2-methylpropanoic acid when the testosterone level, another seasonal variable, is elevated in males over that observed in free-ranging breeding birds. Sex has no observed effect on the relative abundance of identified carboxylic acids. However, a sex signal in the preen secretion of gray catbirds cannot be ruled out because the study focused only on highly volatile acids. Indeed, the use of static headspace SPME sampling and polar GC stationary phase as analytical tools (Table 5) led to the detection of only a small number of concentrated volatile compounds. Interestingly, a similar study was carried out on free-ranging birds, and meaningful differences were observed in the composition of the volatile compounds compared with the study of captive birds (Shaw et al. 2011). For example, the uropygial secretion of free-ranging birds includes greater abundance of some carboxylic acids (heptanoic, octanoic, and nonanoic), fewer branched carboxylic acids, and the appearance of benzaldehyde (Table 2). Semivolatile compounds were also examined, unlike the previous study on captive gray catbirds (Table 5). Similar chemical functional groups already observed in other passerines (Soini et al. 2007; Zhang et al. 2009) are detected, including carboxylic acids, alcohols, methyl ketones, and an ester. Moreover, the ages and season/locations of birds have an impact on the composition of the uropygial secretion. In juvenile birds, greater amounts of volatile C_4 through C_7 acids and semivolatiles C_{20} through C_{26} acids are produced with large variation among individuals. A possible explanation is that a less volatile more persistent uropygial secretion may be beneficial to young birds, given that they are still developing adult preening behaviors. Concerning the effect of season/locations on adult catbirds, it appears that secretions from birds sampled during winter at a Florida site display the heaviest carboxylic acids, whereas methyl ketones are more abundant in samples from the Ohio breeding grounds during summer. This observation could reflect dietary differences or population-level genetic variation.

The growing evidence that birds can use olfaction for chemical communication has encouraged the search of molecules that could be involved in modulating social behavior. The existence of an individual olfactory signature has been proposed, for example, in the uropygial secretions of dark-eyed juncos, based on large individual variations in linear and branched fatty acids content (Soini et al. 2007). Recent studies have been entirely dedicated to the search of an individual signature, like the search for sex- and species-specific chemosignals in the volatile fraction of the uropygial secretion (Zhang et al. 2009, 2010; Whittaker et al. 2010).

In the work of Zhang et al. (2009), the search of chemosignals was investigated in wax compounds of preen secretions of a few different species (Bengalese finches, zebra finches, yellow-browed buntings, and rooks), as described above for large esters (Table 1). Volatile chemosignals were also investigated (respectively, BF, ZF, YBB, and R in Table 2), with the focus on the most volatile molecules obtained after dichloromethane extraction (Table 5). In Bengalese finch, 16 compounds are identified: 8 fatty alcohols (6 saturated ranging from C_{13} to C_{18} and 2 unsaturated: hexadecenol and octadecanol), an aldehyde (hexadecanal), a fatty acid (octanoic acid), a monoester (heptanoic acid hexadecylester), and 5 diesters (only one is identified as hexenedioic acid diethyl ester). In terms of relative abundance (in percent using the total area of the 16 compounds),

hexadecanol and octadecanol are the most common compounds in both males and females. Hexadecanol relative abundance is higher in males than in females, whereas octadecanol is higher in females than in males. Thus, hexadecanol might be a male ''pheromone'' candidate, whereas octadecanol might be a female pheromone. Concerning interspecific comparison among the 4 Passeriform species, the composition of saturated straight-chain C_{13}–C_{18} alkanols appeared to be phylogenetically informative. The domestic Bengalese finch shares more alkanols with the phylogenetically closer zebra finch than with the 2 other species. In the uropygial gland secretion from rooks, the presence of 3 branched heptadecanols and 5 branched octadecanols that are not found in the secretions from the 3 more distant species could provide species information. However, the size of the samples was very limited ($n = 2$ in some cases), so the use of variation in chemical secretions as phylogenetic information appears premature and needs to be further investigated.

The search for sex determinants in the volatile fraction of uropygial secretions was also carried on in Budgerigars (*Melopsittacus undulatus*) (Zhang et al. 2010). After dichloromethane extraction, the most volatile peaks of the GC chromatogram are identified as hexadecanoic acid and linear alcohols from C_{17} to C_{21} (see B in Table 2). Other compounds not identified are detected at a higher retention time and are mainly composed of pentanoates with linear alkanols or alkenols chains (C_{16}–C_{20}). No compound unique to males is found, but the gland secretions from males displayed a significantly higher relative abundance of hexadecanoic acid and alkanols. It must be noted that females' secretions have more abundant pentanoates than males, resulting in a higher ratio of acid and alkanols. Three alkanols (C_{18}, C_{19}, and C_{20}) that constituted 73% of the male volatiles have a relative abundance (in percent using the total area of 23 selected compounds) 4 times greater than in females, though it should be noted that females' secretions have a higher content of these alkanols. However, the author's decisions concerning the processing of the chromatographic data is questionable. For example, by converting a 4-fold ration in the relative abundance of alkanols into a 4-fold ratio of absolute abundance in their bioassays, they mimicked a ''male'' odor 4 times more concentrated than the ''female'' odor despite the fact that the absolute quantities of the compounds used in the blend are similar in both sexes (for detailed comments, refer to Mardon et al. [2011a] see also; Zhang [2011]).

Potential sex-specific chemosignals were also identified in the preen oil of dark-eyed juncos (Whittaker et al. 2010) (DJ in Table 2). In the volatile profile of female secretions, higher proportions of undecan-1-ol, dodecanoic acid, tetradecanoic acid, and hexadecanoic acid are found, whereas in the male profile, higher proportions of the methyl ketones undecan-2-one through 2-pentadecan-2-one are detected. In particular, the relative proportion of tridecan-2-one and pentadecan-2-one is 2–4 times higher in males than females. The presence of dominant tridecan-2-one and pentadecan-2-one in male samples could be the result of enzymatic β-oxydation of carboxylic acid (tetradecanoic and hexadecanoic acid, respectively), though the presence of such a biosynthetic pathway in the uropygial gland is not known. The volatile composition of the preen secretion was also analyzed considering either individual repeatability or intraspecific variations. A high individual repeatability is observed, suggesting that volatile chemicals from the uropygial gland may be correlated with genotypes. The time period covered by this study, however, was only 2 weeks. The comparison between 2 different populations of dark-eyed juncos that recently diverged (one population from the San Diego campus, University of California, and one population from the Laguna Mountain Recreation Area in the Cleveland National Forest) was also performed. Interestingly, male and female juncos from the San Diego campus exhibited reduced genetic diversity at neutral microsatellite loci and also exhibited reduced variation in preen oil volatiles compared with the Laguna Mountain juncos.

The effect of sex can sometimes be detected only in juvenile birds and not in adults, as was in gray catbirds (Shaw et al. 2011). Moreover, this effect is observed only in part of the secretion chemical profiles because only the level of volatile carboxylic acids (C4 through C7) is significantly affected and no effect is observed for semivolatile compounds.

Molecules from the feathers

Another source of molecules from birds that could be involved in social communication is the feather. Chemical substances present on the feather surface may originate from uropygial oil that is used by birds for feather preening but also from the degradation of preen oil compounds and from other glands such as sebaceous glands. As expected, similarities between GC profiles of the uropygial gland secretion and feather from same individuals have been reported (Sandilands et al. 2004; Soini et al. 2007; Zhang et al. 2009; Mardon et al. 2011b). On the other hand, important qualitative differences were also highlighted between the 2 signals. For instance, Bolliger and Varga (1961)'s examination of feather lipids across 14 bird species led them to the conclusion that feather lipids are of dissimilar qualitative composition to the preen secretion. The authors hypothesized that feather lipids could be by-products of the keratinization process associated with feather development. Similarly, a chemical investigation of marabou feather lipids showed a significant difference with those of the uropygial secretions by the presence of sterols, sterols esters, di- and monoglycerides, and free fatty acids (Jacob and Pomeroy 1979). The most significant result on the question comes from wood pigeons, where only 6.7% of the whole-plumage lipids were considered to originate from the uropygial contents (Jacob and Grimmer 1975 in Jacob and Ziswiler 1982).

Different hypothesis have been proposed to explain the presence of the molecules only found on the feather surface and not in preen secretions as chemical conversions, bacterial enzymatic activities, epidermal lipids, or environmental sources. Moreover, the uropygial gland is not the sole source of molecules; for example emus, a species that lacks a preen gland, displays lipids on their plumage (Bolliger and Varga 1961).

As for the uropygial gland, 2 methods are often used to analyze chemical components from feathers: 1) SPME and 2) solvent extraction, although the choice of the solvent is variable (Table 5). Additionally, Soini et al. (2006) developed an original technique to collect volatile compounds from the wing surface using a rolling-stir bar in situ method without any further sample manipulation.

Different species of birds were used for exploring the presence of chemicals deposited onto feathers, with particular attention to birds displaying a marked odor such as crested auklets (*Aethia cristatella*) and petrels.

The crested auklet is a highly social and monogamous seabird that emits a pungent tangerine-like odor. This odor comes from specialized wick feathers that are translucent and hair-like feathers from the interscapular region (Douglas 2008). During courtship, females and males intertwine necks and display a repeated sniffing behavior that might indicate chemical communication (Jones and Hunter 1993). This behavior might also facilitate the distribution of odorant from wick feathers to other plumage (Douglas 2008). Solvent extraction was carried out on feathers from the neck region (Douglas et al. 2001b), that is the region of the body where the tangerine odor appears to be the more intense (Jones and Hunter 1993). The volatile compounds identified by mass spectrometry are mainly aldehydes, carboxylic acids, and long-chained alcohols (C_{16}, C_{18}, and C_{20}) (CA^1 in Table 3). The aldehydes (73.7% of the identified molecules) constitute the main part of the volatile extract with *n*-octanal and *n*-hexanal, in particular being the compounds responsible for the citrus scent (Douglas et al. 2001b). The main constituents (hexanal, octanal, decanal, (Z)-4-decenal, (Z)-4-dodecanal, (Z)-6-dodecenal) are detected in all feather samples (feathers from the mantle, nape, and crown), whereas putative oxidation products of aldehydes (hexanoic and octanoic acid) are not present in all samples. Notably, aldehyde concentrations are 2 orders of magnitude greater for wick feathers than for contour feathers (Douglas 2008). These results illustrate the need for all studies to indicate exactly where the samples are collected for chemical analysis. A similar study, using SPME from the headspace of plumage vials was carried out without any solvent extraction (Hagelin et al. 2003) (Table 5). Some molecules (octanal, Z-dec-4-enal, and hexanoic acid) are identical to the one previously described by Douglas et al. (2001b), whereas some new aldehydes (heptanal, undecanal, tridecanal, and Z-dec-2-enal) and one alcohol (octanol) are also detected (CA^2 in Table 3). This illustrates the difficulty of comparing data not only from different species but also from different studies working on similar samples with different methods.

In crested auklets, 3 influences on the production of volatiles were evaluated: effects of captivity, season (breeding season or winter), and sex (Hagelin et al. 2003). Scented feathers of wild and captive crested auklets were compared and no striking differences were observed, suggesting that diet and environment may have at best a moderate effect on the feather's volatiles. Because these wild birds disperse to unknown regions of the Arctic seas during winter, the seasonal comparison of volatile compounds was made using feathers from wild and captive animals for the breeding season but only from captive birds for the nonbreeding season. Significant seasonal variation in concentrations of 9 compounds (hexanoic and octanoic acid, octanol and 6 aldehydes including octanal) leads to the loss of the typical citrus scent during winter, coinciding with the absence of "sniffing" behavior outside the breeding season (observed in captive birds). In addition, these compounds are not detected on the feathers of parakeet auklets (*Cyclorrhynchus psittacula*), a species that lacks the tangerine scent, thus confirming that these molecules (or at least some of them) are responsible for the citrus scent. No significant difference in the concentration of the above-cited 9 compounds is observed between males and females.

The procellariiforms are another group of seabirds displaying a characteristic odor (viz., a musky scent). Moreover, they possess a particularly developed olfactory system compared with most birds (Bang and Cobb 1968), although the number of functional olfactory receptor genes is estimated to be relatively small (Steiger et al. 2008). The good olfactory capabilities of procellariiforms have been well documented, as birds from this family can use their sense of smell for foraging (Nevitt and Bonadonna 2005a), navigation (Nevitt and Bonadonna 2005b; Bonadonna et al. 2006), recognition of their burrow (Bonadonna et al. 2003, 2004), and also for social interactions via individual recognition (Bonadonna and Nevitt 2004; Bonadonna et al. 2009; Mardon and Bonadonna 2009; Mardon et al. 2010). Therefore, procelleriiforms appear to exhibit an individual chemical signature. This hypothesis was tested using feathers from Antarctic prions (*P. desolata*) (Bonadonna et al. 2007). After solvent extraction and GC/FID analysis, only compounds with a retention index below 1700 were examined to focus on molecules that might have a sufficient vapor pressure to be detected by individuals. Samples were collected for 3 consecutive years from ringed individuals (males and females). Thirty-five compounds are identified that belong to various chemical classes including mainly carboxylic acids, aldehydes, and alcohols (AP in Table 3). Compounds are separated in 2 groups for statistical comparison: "high occurrence compounds" and "low occurrence compounds." Chemical analysis indicates that the profile of an individual is more similar to itself from year to year that to other birds. Analysis of the variation in high occurrence compounds fails to identify

Table 3 Molecules from feather samples collected on different birds

Chemical compound (IUPAC name)	Bird	CAS number	Molecular formula
Alkanes			
Octane	AP	111-65-9	C_8H_{18}
Decane	AP, DC[2]	124-18-5	$C_{10}H_{22}$
Undecane	DC[1]	1120-21-4	$C_{11}H_{24}$
Dodecane	DC[1]	112-40-3	$C_{12}H_{26}$
2,2,4,6,6-pentamethylheptane	AP	31807-55-3	$C_{12}H_{26}$
Tridecane	DC[1]	629-50-5	$C_{13}H_{28}$
2-methyldodecane	AP	1560-97-0	$C_{13}H_{28}$
Tetradecane	BP, DC[1]	629-59-4	$C_{14}H_{30}$
Pentadecane	AP, BP, DC[2]	629-62-9	$C_{15}H_{32}$
2-methyltetradecane	AP	1560-95-8	$C_{15}H_{32}$
Hexadecane	BP, DC[2]	544-76-3	$C_{16}H_{34}$
Heptadecane	AP, BP	629-78-7	$C_{17}H_{36}$
Octadecane	BP	593-45-3	$C_{18}H_{38}$
Octadecane (*isomers*)	BP	n.a.	$C_{18}H_{38}$
Nonadecane	BP	629-92-5	$C_{19}H_{40}$
2-methyloctadecane	BP	1560-88-9	$C_{19}H_{40}$
2,6,10-trimethylhexadecane	BP	55000-52-7	$C_{19}H_{40}$
2-methylicosane	BP	1560-84-5	$C_{21}H_{44}$
Henicosane (*isomers*)	BP	n.a.	$C_{21}H_{44}$
5-methylhenicosane	BP	25117-37-7	$C_{22}H_{46}$
Docosane (*isomers*)	BP	n.a.	$C_{22}H_{46}$
Tricosane (*isomers*)	BP	n.a.	$C_{23}H_{48}$
2,21-dimethyldocosane	BP	n.a.	$C_{24}H_{50}$
Tetracosane (*isomers*)	BP	646-31-1	$C_{24}H_{50}$
Alkenes			
7-Methyl-3-methylidene octa-1,6-diene	DC[1]	123-35-3	$C_{10}H_{16}$
Heptadec-1-ene	AP	26266-05-7	$C_{17}H_{34}$
Octadec-1-ene	DC[1]	112-88-9	$C_{18}H_{36}$
Octadec-9-ene	DC[1]	5557-31-3	$C_{18}H_{36}$
Icos-3-ene	DC[1]	n.a.	$C_{20}H_{40}$
Alcohols			
Hexan-1-ol	DC[2]	111-27-3	$C_6H_{14}O$
Hexan-2-ol	DC[2]	626-93-7	$C_6H_{14}O$
Hexan-3-ol	AP, DC[2]	623-37-0	$C_6H_{14}O$
Heptan-1-ol	AP	111-70-6	$C_7H_{16}O$
Octan-1-ol	AP, CA[2]	111-87-5	$C_8H_{18}O$
Nonan-1-ol	AP, DJ	143-08-8	$C_9H_{20}O$
Decan-1-ol	DJ	112-30-1	$C_{10}H_{22}O$
Undecan-1-ol	DJ	112-42-5	$C_{11}H_{24}O$
Dodecan-1-ol	AP, DJ	112-53-8	$C_{12}H_{26}O$
Tridecan-1-ol	BP, DJ	112-70-9	$C_{13}H_{28}O$
3-methyltridecan-1-ol	AP	n.a.	$C_{14}H_{30}O$
Tetradecan-1-ol	BF	112-72-1	$C_{14}H_{30}O$
Pentadecan-1-ol	BF	629-76-5	$C_{15}H_{32}O$
Hexadecan-1-ol	BF	36653-82-4	$C_{16}H_{34}O$
Hexadecanol (*isomers*)	BP	n.a.	$C_{16}H_{34}O$
Heptadecanol	BF	1454-85-9	$C_{17}H_{36}O$
Octadecanol (*isomers*)	BP	n.a.	$C_{18}H_{38}O$
Octadecan-1-ol	AP	112-92-5	$C_{18}H_{38}O$
Nonadecanol (*isomers*)	BP	n.a.	$C_{19}H_{40}O$
Nonadecan-2-ol	BP	26533-36-8	$C_{19}H_{40}O$
Henicosanol (*isomers*)	BP	n.a.	$C_{21}H_{44}O$
23-methyltetracosan-1-ol	BP	n.a.	$C_{25}H_{52}O$
Hexacosanol (*isomers*)	BP	n.a.	$C_{26}H_{54}O$
Hex-3-en-1-ol	DC[2]	544-12-7	$C_6H_{12}O$
(E)-dodec-2-en-1-ol	AP	69064-37-5	$C_{12}H_{24}O$
Octadec-9-en-1-ol	BP	593-47-5	$C_{18}H_{36}O$
Aldehydes			
Hexanal	AP, CA[1], DC[1,2]	66-25-1	$C_6H_{12}O$
Heptanal	CA[2], DC[2]	111-71-7	$C_7H_{14}O$
Octanal	CA[1,2], DC[2]	124-13-0	$C_8H_{16}O$
Nonanal	AP, DC[1,2], DJ	124-19-6	$C_9H_{18}O$
Decanal	AP, CA[1], DC[2], DJ	112-31-2	$C_{10}H_{20}O$
Undecanal	CA[2]	112-44-7	$C_{11}H_{22}O$
Dodecanal	AP	112-54-9	$C_{12}H_{24}O$
Tridecanal	AP, CA[2]	10486-19-8	$C_{13}H_{26}O$
Tetradecanal	AP	124-25-4	$C_{14}H_{28}O$
Pentadecanal	AP, BP	2765-11-9	$C_{15}H_{30}O$
Hexadecanal	BF, BP	629-80-1	$C_{16}H_{32}O$
(E)-hex-2-enal	AP	505-57-7	$C_6H_{10}O$
Hept-2-enal	DC[2]	2463-63-0	$C_7H_{12}O$
(E)-oct-2-enal	AP	2363-89-5	$C_8H_{14}O$
(Z)-dec-2-enal	CA[2]	3913-71-1	$C_{10}H_{18}O$

Table 3 Continued

Chemical compound (IUPAC name)	Bird	CAS number	Molecular formula
(Z)-dec-4-enal	CA[1,2]	30390-50-2	$C_{10}H_{18}O$
(Z)-undec-9-enal	AP	143-14-6	$C_{11}H_{20}O$
Tetradec-4-enal	AP	n.a.	$C_{14}H_{26}O$
Ketones			
Hexan-2-one	DC[2]	591-78-6	$C_6H_{12}O$
Hexan-3-one	DC[2]	589-38-8	$C_6H_{12}O$
Hexane-2,4-dione	DC[2]	3002-24-2	$C_6H_{10}O_2$
Hexane-2,5-dione	DC[1,2]	110-13-4	$C_6H_{10}O_2$
Aliphatic acid			
Acetic acid	DC[2]	64-19-7	$C_2H_4O_2$
Propanoic acid	DC[2]	79-09-4	$C_3H_6O_2$
Hexanoic acid	CA[1,2], DC[2]	142-62-1	$C_6H_{12}O_2$
Heptanoic acid	DC[2]	111-14-8	$C_7H_{14}O_2$
Octanoic acid	BF, CA[1,2], DC[1,2]	124-07-2	$C_8H_{16}O_2$
2-ethylhexanoic acid	DC[1]	149-57-5	$C_8H_{16}O_2$
4-methyloctanoic acid	AP	54947-74-9	$C_9H_{18}O_2$
Nonanoic acid	AP, BP, DC[2]	112-05-0	$C_9H_{18}O_2$
3-methylnonanoic acid	AP	35205-79-9	$C_{10}H_{20}O_2$
4-methylnonanoic acid	AP	45019-28-1	$C_{10}H_{20}O_2$
Decanoic acid (*isomers*)	BP	n.a.	$C_{10}H_{20}O_2$
Decanoic acid	AP, BP	334-48-5	$C_{10}H_{20}O_2$
4-methyldecanoic acid	AP	24323-24-8	$C_{11}H_{22}O_2$
Dodecanoic acid	BP, DJ, DC[1]	143-07-7	$C_{12}H_{24}O_2$
2-methylundecanoic acid	BP	24323-25-9	$C_{12}H_{24}O_2$
3-methylundecanoic acid	AP	65781-38-6	$C_{12}H_{24}O_2$
Tetradecanoic acid	BP, DC[1]	544-63-8	$C_{14}H_{28}O_2$
Pentadecanoic acid	DC[1]	1002-84-2	$C_{15}H_{30}O_2$
Hexadecanoic acid	BP, DC[1]	57-10-3	$C_{16}H_{32}O_2$
Heptadecanoic acid	DC[1]	506-12-7	$C_{17}H_{34}O_2$
3-(3,5-di-tert-butyl-4-hydroxyphenyl)propanoic acid	DC[1]	20170-32-5	$C_{17}H_{26}O_3$
(Z,Z)-octadeca-9,12-dienoic acid	DC[1]	60-33-3	$C_{18}H_{32}O_2$
Octadecanoic acid	BP, DC[1]	57-11-4	$C_{18}H_{36}O_2$
Nonadecanoic acid	DC[1]	646-30-0	$C_{19}H_{38}O_2$
Icosenoic acid	DC[1]	n.a.	$C_{20}H_{38}O_2$
Icosanoic acid	DC[1]	506-30-9	$C_{20}H_{40}O_2$

Table 3 Continued

Chemical compound (IUPAC name)	Bird	CAS number	Molecular formula
Aromatic or cyclic			
1,4-dimethylbenzene	DC[2]	106-42-3	C_8H_{10}
Propylbenzene	DC[2]	103-65-1	C_9H_{12}
1-ethyl-4-methylbenzene	DC[2]	622-96-8	C_9H_{12}
1,2,3-trimethylbenzene	DC[2]	95-36-3	C_9H_{12}
1,2,4-trimethylbenzene	DC[2]	95-63-6	C_9H_{12}
1,3,5-trimethylbenzene	DC[2]	108-67-8	C_9H_{12}
1-methyl-3-propylbenzene	DC[2]	1074-43-7	$C_{10}H_{14}$
1-methyl-4-propylbenzene	DC[2]	1074-55-1	$C_{10}H_{14}$
Trimethyl-2,6,6-bicyclo(3.1.1)hept-3-ene	DC[1]	80-56-8	$C_{10}H_{16}$
Nonylcyclopropane	DC[1]	74663-85-7	$C_{12}H_{24}$
1-methylcyclopentan-1-ol	DC[2]	1462-03-9	$C_6H_{12}O$
Benzaldehyde	DC[1,2]	100-52-7	C_7H_6O
2-pentylfurane	DC[2]	3777-69-3	$C_9H_{14}O$
5-alpha-cholestan-3-beta-ol	BP	80-97-7	$C_{27}H_{48}O$
Esters			
Methyl hexanoate	DC[2]	106-70-7	$C_7H_{14}O_2$
Diethyl hexenedioate	BF	n.a.	$C_{10}H_{16}O_4$
Methyl nonanoate	AP	1731-84-6	$C_{10}H_{20}O_2$
Ethyl-3-methylundecanoate	AP	n.a.	$C_{14}H_{27}O_2$
Dimethyl tetradecanoate (*isomers*)	BP	n.a.	$C_{17}H_{38}O_2$
2,3-bis(acetyloxy)propyl isohexadecanoate	BP	n.a.	$C_{23}H_{42}O_6$
Tridecyl decanoate (*isomers*)	BF	n.a.	$C_{23}H_{46}O_2$
Tetradecyl decanoate (*isomers*)	BP	n.a.	$C_{24}H_{48}O_2$
Pentadecyl nonanoate (*isomers*)	BP	n.a.	$C_{24}H_{48}O_2$
Hexadecyl octanoate (*isomers*)	BP	29710-31-4	$C_{24}H_{48}O_2$
Tridecyl dodecanoate (*isomers*)	BP	n.a.	$C_{25}H_{50}O_2$
Pentadecyl decanoate (*isomers*)	BP	n.a.	$C_{25}H_{50}O_2$
Hexadecyl nonanoate (*isomers*)	BP	n.a.	$C_{25}H_{50}O_2$
Tetradecyl dodecanoate (*isomers*)	BP	n.a.	$C_{26}H_{52}O_2$
Pentadecyl undecanoate (*isomers*)	BP	n.a.	$C_{26}H_{52}O_2$

Table 3 Continued

Chemical compound (IUPAC name)	Bird	CAS number	Molecular formula
Hexadecyl decanoate (*isomers*)	BP	n.a.	$C_{26}H_{52}O_2$
Hexadecyl undecanoate (*isomers*)	BP	n.a.	$C_{27}H_{54}O_2$
Heptadecyl decanoate (*isomers*)	BP	n.a.	$C_{27}H_{54}O_2$
Octadecyl nonanoate (*isomers*)	BP	n.a.	$C_{27}H_{54}O_2$
Hexadecyl dodecanoate (*isomers*)	BP	n.a.	$C_{28}H_{56}O_2$
Heptadecyl undecanoate (*isomers*)	BP	n.a.	$C_{28}H_{56}O_2$
Octadecyl decanoate (*isomers*)	BP	n.a.	$C_{28}H_{56}O_2$
Octadecyl undecanoate (*isomers*)	BP	n.a.	$C_{29}H_{58}O_2$
Amine/amide			
Octadecanamide	BP	124-26-5	$C_{18}H_{37}NO$
Nonadecanamide	BP	n.a.	$C_{19}H_{39}NO$
Sulfides			
Ethyldisulfanyl ethane	DC^2	110-81-6	$C_4H_{10}S_2$

AP: Antarctic prions (*Pachyptila desolata*) from Bonadonna et al. (2007); BF: Bengalese finches (*Lonchura striata*) from Zhang et al. (2009); BP: Blue petrel from Mardon et al. (2011b); CA^1, crested auklet (*Aethia cristatella*) from Douglas et al. (2001); CA^2, crested aucklet (*A. cristatella*) from Hagelin et al. (2003); DC^1, domestic chicken (*Gallus gallus domesticus*) from Williams et al. (2003); DC^2, domestic chicken (*G. gallus domesticus*) from Bernier et al. (2008); DJ, dark-eyed junco (*Junco hyemalis*) from Soini et al. (2007); n.a., nonavailable.

significant "signature compounds," whereas some of the low occurrence compounds display significant differences in concentration between individuals. Therefore, these molecules (octane, isododecane, isotridecane, isopentadecane, 3-methylundecanoic acid, tetradecanal, E(2)-octenal, and E(2)-dodecenol) are likely candidates for an individual olfactory signature that is repeatable over years. A quite similar study was carried out in another procellariiform of the Kerguelen Archipelago, the blue petrel (*H. caerulea*) (Mardon et al. 2011b). Analysis of chemical compounds found in feather samples and also in uropygial secretions was carried out on the same ringed individuals. Across 2 years of study, 98% of the secretion contents are also detected on feathers and represent 85% of feather compounds. However, some chemical differences are also found, including both qualitative and quantitative variations. The appearance of new relatively short-chained analytes is observed on the feather surface, principally free fatty acids (C_9–C_{18}), aldehydes (C_{15}–C_{18}), and alkanes (C_{15}–C_{24}) (BP in Table 3). Moreover, an increased amount of several short-chain alkanes (C_{15}–C_{21}) and alcohols (C_{16}–C_{18}) is detected in feather samples compared with uropygial secretions. Several benzene-based compounds are present only on the plumage suggesting environmental pollution from external deposition. Previously reports of organic pollutants on bird feathers also detected the pollutants in preen oils and internal tissues (Yamashita et al. 2007; Jaspers et al. 2008). A distance-based multivariate analysis of the data indicates that the sex-specific and individual-specific chemical signature revealed in the uropygial secretions is still present in a remarkably consistent form on the feathers of blue petrels (Mardon et al. 2011b).

A comparison between preen secretions and feather molecules was also reported in domestic chickens, focusing on one class of compound: the fatty acids extracted from wax esters after splitting the ester bond (Sandilands et al. 2004). Seven fatty acids of 18 display distinct differences in composition between the 2 sources. The total percentage of decanoic, hexadecanoic and octadecenoic acid in feathers is twice as high as in preen secretion, while the opposite is observed for nonadecanoic, icosanoic, and henicosanoic acids. For tetracosanoic acid, a very low percentage is observed in the feather extracts but this compound is not detected in uropygial secretions. One possible explanation for these differences is that epidermal secretions could produce enough lipids to affect the composition of feather lipids (Menon GK and Menon J 2000). Contrary to expectations, only few recent data are available as regards the volatile components of domestic chicken's feathers (DC in Table 3). The search of avian-specific cues for mosquito attraction has lead to a chemical analysis of these volatiles (Williams et al. 2003; Allan et al. 2006; Bernier et al. 2008). Three different solvents were used for extraction: hexane (Williams et al. 2003; Bernier et al. 2008), methanol (Williams et al. 2003), and diethyl ether (Bernier et al. 2008). An SPME sampling method was also tested using PDMS/DVB fiber to capture the most volatile components (Williams et al. 2003). Hexane and diethyl ether extracts give similar components with the exception of some ketones (2-hexanone and 3-hexanone) and alcohols (2-hexanol and 3-hexanol) that are only present in hexane extracts (Bernier et al. 2008). The main compounds found on feather surface using solvent extraction are aldehydes (nonanal mainly), acids (C_6 to C_9), ketones, and some small alkanes and alkenes. Nonanal, hexanal and beta myrcene (7-Methyl-3-methylene-1,6-octadiene), alpha pinene (trimethyl-2,6,6-bicyclo(3.1.1)hept-2-ene), and benzaldehyde are the main compounds found using SPME volatile sampling (Williams et al. 2003). The presence of monoterpenes (myrcene and pinene) usually found in plants is surprising and could result from incorrect identification or external contamination, as the birds were housed in a cage with sawdust bedding.

Among the different techniques used to study the volatile compounds found on feathers, an original sorptive stir-bar sampling method has been developed that allows collection in situ of different compounds (Soini et al. 2006). This sampling method appears very promising because it is not

Table 4 Molecules from other sources than uropygial gland secretion or feather

Chemical compounds (IUPAC name)	Bird	CAS number	Molecular formula
Alkanes			
Decane	DC[3,4]	124-18-5	$C_{10}H_{22}$
Pentadecane	DC[3,4]	629-62-9	$C_{15}H_{32}$
Hexadecane	DC[3,4]	544-76-3	$C_{16}H_{34}$
Alcohols			
Methan-1-ol	DC[2]	67-56-1	CH_4O
Ethanol	BWD	64-17-5	C_2H_6O
Propan-1-ol	BWD, DC[2]	71-23-8	C_3H_8O
Butan-1-ol	BWD, DC[2]	71-36-3	$C_4H_{10}O$
Butan-2-ol	BWD	78-92-2	$C_4H_{10}O$
Hexan-2-ol	DC[3,4]	626-93-7	$C_6H_{14}O$
Hexan-3-ol	DC[3,4]	623-37-0	$C_6H_{14}O$
2-ethylhexan-1-ol	BWD	104-76-7	$C_8H_{18}O$
Octan-1-ol	DC[1]	111-87-5	$C_8H_{18}O$
Octan-3-ol	DC[2]	589-98-0	$C_8H_{18}O$
Pent-1-en-3-ol	DC[2]	616-25-1	$C_5H_{10}O$
Hex-3-en-1-ol	DC[3,4]	544-12-7	$C_6H_{12}O$
Oct-1-en-3-ol	DC[2]	3391-86-4	$C_8H_{16}O$
Aldehydes			
Propanal	DC[2]	123-38-6	C_3H_6O
Hexanal	BWD, DC[2,3,4]	66-25-1	$C_6H_{12}O$
Heptanal	DC[3,4]	111-71-7	$C_7H_{14}O$
Octanal	CA	124-13-0	$C_8H_{16}O$
Nonanal	DC[1,3,4]	124-19-6	$C_9H_{18}O$
Decanal	CA, DC[3,4]	112-31-2	$C_{10}H_{20}O$
Undecanal	DC[1]	112-44-7	$C_{11}H_{22}O$
Dodecanal	DC[1]	112-54-9	$C_{12}H_{24}O$
Tetradecanal	DC[1]	124-25-4	$C_{14}H_{28}O$
Pentadecanal	DC[1]	2765-11-9	$C_{15}H_{30}O$
Hexadecanal	DC[1]	629-80-1	$C_{16}H_{32}O$
Heptadecanal	DC[1]	629-90-3	$C_{17}H_{34}O$
Octadecanal	DC[1]	638-66-4	$C_{18}H_{36}O$
But-2-enal	DC[2]	4170-30-3	C_4H_6O
(E)-oct-2-enal	DC[2]	2363-89-5	$C_8H_{14}O$
(E)-dec-2-enal	DC[1]	3913-81-3	$C_{10}H_{18}O$
(Z)-dec-4-enal	CA	30390-50-2	$C_{10}H_{18}O$

Table 4 Continued

Chemical compounds (IUPAC name)	Bird	CAS number	Molecular formula
ketones			
Propan-2-one	BWD	67-64-1	C_3H_6O
Butan-2-one	BWD	78-93-3	C_4H_8O
3-hydroxybutan-2-one	DC[2]	513-86-0	$C_4H_8O_2$
3-methylbutan-2-one	DC[2]	563-80-4	$C_5H_{10}O$
Pentan-2-one	BWD	107-87-9	$C_5H_{10}O$
Pentan-3-one	BWD, DC[2]	96-22-0	$C_5H_{10}O$
Hexan-2-one	DC[2,3,4]	591-78-6	$C_6H_{12}O$
Hexan-3-one	DC[3,4]	589-38-8	$C_6H_{12}O$
4-methylhexan-3-one	BWD	17042-16-9	$C_7H_{14}O$
Heptan-2-one	DC[2]	110-43-0	$C_7H_{14}O$
Tridecan-2-one	DC[1]	593-08-8	$C_{13}H_{26}O$
Butane-2,3-dione	DC[2]	431-03-8	$C_4H_6O_2$
Pentane-2,3-dione	DC[2]	600-14-6	$C_5H_8O_2$
Hexane-2,4-dione	DC[3,4]	3002-24-2	$C_6H_{10}O_2$
Hexane-2,5-dione	DC[3,4]	110-13-4	$C_6H_{10}O_2$
Pent-1-en-3-one	DC[2]	1629-58-9	C_5H_8O
Hex-3-en-2-one	DC[2]	763-93-9	$C_6H_{10}O$
Aliphatic acid			
Acetic acid	DC[3,4]	64-19-7	$C_2H_4O_2$
Propanoic acid	DC[2]	79-09-4	$C_3H_6O_2$
Hexanoic acid	DC[2]	142-62-1	$C_6H_{12}O_2$
Aromatic or cyclic			
Benzaldehyde	DC[3,4]	100-52-7	C_7H_6O
Butyrolactone	DC[2]	96-48-0	$C_4H_6O_2$
Phenol	BWD, DC[2]	108-95-2	C_6H_6O
1-methylcyclopentan-1-ol	DC[3,4]	1462-03-9	$C_6H_{12}O$
4-ethylphenol	DC[1], DC[2]	123-07-9	$C_8H_{10}O$
Azacyclopropane	BWD	151-56-4	C_2H_5N
1H-Pyrrole	DC[2]	109-97-7	C_4H_5N
3,4-dihydro-2H-pyrrole	BWD	5724-81-2	C_4H_7N
2,5-dimethylpiperazine	DC[2]	106-55-8	$C_6H_{14}N_2$
1H-Indole	DC[1]	120-72-9	C_8H_7N
2,3,5,6-tetramethylpyrazine	BWD	1124-11-4	$C_8H_{12}N_2$
2-ethyl-3,5,6-trimethylpyrazine	BWD	17398-16-2	$C_9H_{14}N_2$
2,5-diisopropylpyrazine	BWD	29294-83-5	$C_{10}H_{16}N_2$

Table 4 Continued

Chemical compounds (IUPAC name)	Bird	CAS number	Molecular formula
Esters			
Methyl acetate	BWD	79-20-9	$C_5H_6O_2$
Methyl butanoate	DC[2]	623-42-7	$C_3H_{10}O_2$
Ethyl ethanoate	DC[2]	141-78-6	$C_4H_8O_2$
Propyl ethanoate	DC[2]	109-60-4	$C_5H_{10}O_2$
Methyl pentanoate	DC[2]	624-24-8	$C_6H_{12}O_2$
Methyl propanoate	DC[2]	554-12-1	$C_4H_8O_2$
Ethyl propanoate	DC[2]	105-37-3	$C_5H_{10}O_2$
Amine/amide			
Azane (ammonia)	BWD	7664-41-7	NH_3
Methanamine	BWD	74-89-5	CH_5N
N-methylmethanamine	BWD	124-40-3	C_2H_7N
N,N-dimethylmethanamine	BWD	75-50-3	C_3H_9N

BWD, faeces from black-bellied whistling ducks (*Dendrocygna autumnalis*) from Robacker et al. (2000); CA, body odor of crested aucklet (*Aethia cristatella*) from Douglas et al. (2001); DC[1], acidified faeces of domestic chicken (*Gallus gallus domesticus*) from Cooperband et al. (2008); DC[2], faeces of domestic chicken (*G. gallus domesticus*) from Garner et al. (2008); DC[3], feet of domestic chicken (*G. gallus domesticus*) from Bernier et al. (2008); DC[4], skin of domestic chicken (*G. gallus domesticus*) from Bernier et al. (2008).

intrusive and only volatile compounds are collected. No further sample manipulation is required as the molecules are thermodesorbed directly from the stir-bar. A cryotrapping technology (TDSA-CIS-4 system from Gerstel, Germany) allows a direct analysis of the thermodesorbed components without passing through a second trap that could induce the binding/loss of some highly volatile components. This method was applied to feathers from dark-eyed juncos (DJ in Table 3) (Soini et al. 2007). Although several compounds (alkanols and aldehydes) were obviously from the preen gland, numerous molecules not detected in the uropygial secretions were also present on the plumage but no chemical identification was proposed by the authors.

Another comparison between components found in preen secretions and those detected on feather surfaces was achieved for Bengalese finches (Zhang et al. 2009). The molecules were extracted with dichloromethane and analyzed using a polar column (Table 5). The chromatographic profiles of the 2 different samples display a high similarity in the volatile fraction as well as for wax esters. As for the uropygial secretions of this species, differences between males and females are observed for some components present on feathers, in particular for hexadecanol and octadecanol (BF in Table 3). This observation reinforces the hypothesis that some information present in uropygial secretions is transferred onto feathers and contributes to chemical communication.

Molecules from other sources

Other sources of avian odors have been explored as the "body odor" (probably a mixture of compounds found in feathers, preen oil, skin glands, etc.), feces, and skin secretions.

A headspace analysis of volatiles trapped on an SPME fiber and collected directly from the crested auklet's neck revealed the presence of nearly pure *n*-octanal and small amounts of *n*-decanal and Z-4-decenal (Douglas et al. 2001b). A different and original method for collecting the volatiles was also tested by the same authors in another study (Douglas 2006) (Table 5). Instead of trapping the volatiles from the neck with an SPME fiber, the bird was placed in a glass reaction kettle and volatile emissions from the whole body were collected in a purified airstream onto polymer traps. Chemical emission of octanal displayed different rates among individuals with a 7-fold difference between the highest and lowest chemical emission, whereas no significant differences were detected between sexes (Douglas 2006). Higher rates of octanal are apparently associated with lower prevalence of tick parasitism. Octanal emissions also appeared correlated with size of the crest ornament in male crested auklets, suggesting a social and behavioral basis for differences in odorant production (Douglas et al. 2008). The difference in octanal emission probably represents a difference in the ability to produce odor and, therefore, chemical potency and associated repellence of parasites may be a basis for mutual selection in crested auklets (Douglas et al. 2001a, 2001b, 2004). Seasonal changes occur in odorant secretions; for example, the concentration of hexanal, octanal, and decanal in winter is 5- to 6-fold less than during breeding (unpublished results cited in Douglas 2008). Covariance of P4 hormone with octanal emissions in males suggests a possible association between steroid hormones and odorant production. Seasonal elevation of circulating hormones could trigger activation of a biochemical pathway that leads to odor production, and/or sex steroids and odor production could be regulated independently in response to the same cues (Douglas et al. 2008).

The feces, skin, and feet of birds also represent sources of odorant molecules. A few studies have been made of chemical molecules from these sources, mainly to characterize the components with an attractant effect on mosquitoes (Bernier et al. 2008; Cooperband et al. 2008). Interest is mainly due to the fact that ornitophagous mosquitoes can be vectors of viruses like West Nile virus or Western equine encephalitis. Volatiles from chicken feces were identified in order to find what kind of compounds from the hosts is attractive to mosquitoes (Cooperband et al. 2008). With the use of coupled gas chromatography-electroantennogram, a number of compounds from both acidified and unaltered chicken feces were shown to elicit antennal responses from female mosquitoes. Compounds that elicited responses include mostly aldehyde as (E)-2-decenal, nonanal, undecanal, dodecanal,

Table 5 Methods used in the studies presented in previous tables

Order/bird	Complementary informations on birds	Types of molecules analyzed	Method of extraction	GC column	Method of analysis with GC/MS	References
Black-bellied whistling duck (*Dendrocygna autumnalis*)	Faeces collected from a natural habitat near Weslaco, Texas.	Volatiles from Fa	SPME extraction on PDMS or Carboxen/PDMS fibers for 15–30 min for GC-MS analyses or 60 min for GC-FID or GC-FTD analyses.NaCl or NaOH was added before for some analyses.	Apolar: DB-1 (J & W Scientific)	Desorption at 200 °C. 50 °C (1 min), ramp at 10 °C min^{-1} to 200 °C or 250 °C. For GC-FID or GC-FTD: 100 °C (30 min), ramp at 20 °C min^{-1} to 200 °C	Robacker et al. (2000)
Crested auklet (*Aethia cristatella*)	Wild (n = 3), Kiska, Aleutian Islands, Alaska. Frozen birds.	-Volatiles from body -Volatiles from F	SPME extraction on PDMS/DVB fibers for 4.5 h near the specimen's neck. F samples: Methylene chloride or methanol extraction for 2 min.	Apolar: RTX-5 (Restek)	Desorption at 260 °C, 5 min for SPME fibers. All samples: 60 °C (3 min), ramp at 10 °C min^{-1} to 250 °C (hold)	Douglas et al. (2001)
Crested auklet (*A. cristatella*)	Wild (n = 6) in breeding condition and captive birds (n = 4) in nonbreeding condition. Wild birds are from Buldir Island, Aleutian Islands, Alaska. Captive birds are from the Aquarium of the Pacific, Long Beach, California.	Volatiles from F	SPME extraction on PDMS fibers.	Apolar: DB-1 (J & W Scientific)	Desorption at 250 °C, 10 min. 40 °C (4 min), ramp at 6 °C min^{-1} to 200 °C then ramp at 2 °C min^{-1} to 235 °C	Hagelin et al. (2003)
Domestic chicken (*Gallus gallus domesticus*)	English game bantam hen (n = 3)	Volatiles and semivolatiles from F	a) Hexane and methanol extraction (24 h) followed by methylation with boron-trifluoride-methanol complex. b) SPME extraction on PDMS/DVB fiber, 2 min at 40 °C.	a and b) Apolar: SGE-BPX5 silicone (SGE)	Desorption 200 °C, 3 min for SPME fibers. a and b: 50 °C (1 min), ramp at 8 °C min^{-1} to 250 °C	Williams et al. (2003)
Green woodhoopoe (*Phoeniculus purpureus*)	Wild birds.	Volatiles and semivolatiles from UGS	a) Dichloromethane extractionb) SPME extraction on PDMS fiber Headspace sampling times from 7 h at 22 °C to 72 h at 40 °C.	Apolar: PS-089 or OV-1701 (Ohio Valley) equivalent to DB-5[1]	Desorption at 220 °C for SPME fibers. a and b: Cold-trap at ca. 30 °C, ramp from 40 to 280 °C at 4 °C min^{-1}	Burger et al. (2004)
Crested auklet (*A. cristatella*)	Wild (n = 56), Big Koniuji Islands, Alaska.	Volatiles from body	Birds were placed into a glass reaction kettle under a purified airstream. Volatile emissions were collected for 50 min on SuperQ or Tenax trap.	Apolar: 5% phenylsiloxane (Alltech)	60 °C, ramp at 4 °C min^{-1} to 120 °C, hold 4 min then ramp at 8 °C min^{-1} to 250 °C (hold 2 min).	Douglas (2006)

Table 5 Continued

Order/bird	Complementary informations on birds	Types of molecules analyzed	Method of extraction	GC column	Method of analysis with GC/MS	References
Dark-eyed junco (*Junco hyemalis*)	Wild birds bred in captivity, "artificial" breeding and nonbreeding seasons (10 males and 10 females)	-Volatiles and semivolatiles from UGS	UGS samples: dissolved in water with ammonium sulfate followed by stir bar sorption (Twister) for 60 min.	Apolar: DB-5MS (Agilent)	Desorption at 250 °C, 3 min for stir bar.	Soini et al. (2007)
		-Volatiles from F	F samples: in situ rolling stir bar (Twister) sorption[a]	Apolar: HP-5MS [2] (Agilent)	All samples: 50 °C (2 min), ramp at 3 °C min^{-1} to 200 °C (12 min.)	
Antarctic prion (*Pachyptila desolata*)	Wild birds (7 females and 6 males) in breeding condition. Ile verte, Kerguelen Archipelago	Volatiles and semivolatiles from F	Dichloromethane extraction (24 h).	Apolar: CP Sil-5B Low Bleed MS (Varian)	50 °C (2 min), ramp at 3 °C min^{-1} to 100 °C, then at 2.7 °C min^{-1} to 140 °C, then at 2.4 °C min^{-1} to 170 °C and finally at 10 °C min^{-1} to 290 °C.	Bonadonna et al. (2007)
Domestic chicken (*G. gallus domesticus*)	White Leghorn hens	Volatiles from F	a) Hexane extraction.	a) Polar: DB Waxetr (Agilent)	a) 35 °C (6 min), ramp at 10 °C min^{-1} to 260 °C (hold 5 min)	Bernier et al. (2008)
			b) Diethyl ether extraction	b) Polar: DB-FFAP (Agilent)	b) 35 °C (5 min), ramp at 6°C min^{-1} to 245 °C (hold 10 min)	
Domestic chicken (*G. gallus domesticus*)		Volatiles from Fe	a) SPME on PDMS fiber (4 h) using acidified feces.	a) Apolar: DB-5 (J & W Scientific)	a and b: 40 °C (1 min), ramp at 10 °C min^{-1} to 250 °C (hold 30 min)	Cooperband et al. (2008)
			b) Headspace volatiles from acidified feces in water collected on activated charcoal solution (4 d). Extraction with dichloromethane.	b) Apolar: HP-5MS (Agilent)		
Domestic chicken (*G. gallus domesticus*)	31, 20, and 20 faeces samples from 3 different farms (Southwest England). The chickens were the same breed and fed with the same diet.	Volatiles from Fa, feet and skin	SPME on Carboxen/PDMS fiber (20 min after heating at 60 °C for 1 h).	Apolar SPB-1 sulfur (Supelco) conjoined with polar ZB-FFAP (Phenomenex)	Desorption at 280 °C. 35 °C (5 min), ramp at 7 °C min^{-1} to 250 °C (hold 12 min)	Garner et al. (2008)
Bengalese finch (*Lonchura striata domestica*); Zebra finch (*Taeniopygia guttata*); Yellow-browed bunting (*Emberiza chrysophrys*); Rook (*Corvus frugilegus*)	All birds were in the breeding condition. Except the domesticated Bengalese finches (9 males and 8 females), the other birds were wild birds bred in captivity: Zebra finches (3 males); Yellow-browed buntings (2 males) and Rooks (2 animals, sex unknown).	Volatiles and semivolatiles from UGS and F	Dichloromethane extraction.	Polar: DBWAX (Agilent)	100 °C, ramp at 5 °C min^{-1} to 250 °C (hold 10 min)	Zhang et al. (2009)

Table 5 Continued

Order/bird	Complementary informations on birds	Types of molecules analyzed	Method of extraction	GC column	Method of analysis with GC/MS	References
European hoopoe (*Upupa epops*)	Wild birds, breeding season (11 nestlings, 7 adults including 3 nonbreeding females and 4 males), Hoya de Guadix, Spain.	Volatiles from UGS	Dichloromethane extraction.	Apolar: Silica DB-5 (J&W scientific)	40 °C (1 min), ramp at 7 °C min^{-1} to 250 °C (hold 5 min)	Martin-Vivaldi et al. (2010)
Bengalese finch (*L. striata domestica*)	Domesticated Bengalese finches (8 males and 8 females) at 6–14 months of age from 3 large colonies.	Volatiles and semivolatiles from UGS and F	Dichloromethane extraction.	Apolar: HP5-MS (Agilent)	70 °C, ramp at 5 °C min^{-1} to 280 °C	Zhang et al. (2010)
Blue petrel (*Halobaena caerulea*), Antarctic prion (*P. desolata*)	Wild birds, breeding season, Ile verte, Kerguelen Islands. Twenty Blue petrels (16 males and 4 females) and 16 Antarctic prions (10 males and 6 females)	Semivolatiles and nonvolatiles from UGS	Dichloromethane/ n-hexane 1: 3 (v/v) extraction.	Apolar: Rtx-5MS (Restek)	40 °C (3 min.), ramp at 8 °C min^{-1} to 150 °C then 6 °C min^{-1} to 200 °C and then 2 °C min^{-1} to 250 °C (hold 15 min).	Mardon et al. (2010)
Gray catbird (*Dumetella carolinensis*)	Wild birds from 3 sites in north central Ohio captured and housed in individual cages in the University of Southern Mississippi. Birds were fed ad libitum with a semisynthetic diet.	Volatiles from UGS	Samples placed in sealed vials at 44 °C and SPME (90 min) on Carboxen-PDMS fiber.	Polar: AT-WAX (Alltech)	Desorption at 250 °C, 3 min. 50 °C (1 min), ramp at 15 °C min^{-1} to 200 °C	Whelan et al. (2010)
Dark-eyed junco (*J. hyemalis*)	Wild birds bred in captivity, artificial breeding and nonbreeding seasons: 6 males and 8 females from Laguna mountain, Cleveland National forest, USA; 6 males and 6 females from University of California, San Diego, USA.	Volatiles from UGS	Samples dissolved in water with ammonium sulfate followed by stir bar sorption (Twister) for 60 min.	Apolar: DB-5MS (Agilent)	Desorption at 20 °C (0.5 min) then 60 °C min^{-1} to 250 °C (3 min). 50 °C (2 min), ramp at 3°C min^{-1} to 200°C (hold 12 min).	Whittaker et al. (2010)
Blue petrel (*Halobaena caerulea*)	Wild birds, breeding season, Ile verte, Kerguelen Islands. Thirty-six secretion samples and 36 feather samples were analyzed (8 females and 28 males).	-Volatiles and semi volatiles from UGS -Volatiles and semivolatiles from F	UGS samples: Extraction with dichloromethane/ hexane (1: 3, v/v). F samples: Extraction with dichloromethane/ hexane (1: 3, v/v) for 2.5 h on ice. Filtration on glass wool and concentration 10 times.	Apolar: Rtx-5MS (Restek)	All samples: 40 °C (3 min.), ramp at 8 °C min^{-1} to 150 °C then 6 °C min^{-1} to 200 °C and then 2 °C min^{-1} to 250 °C (hold 15 min).	Mardon et al (2011b)

Table 5 Continued

Order/bird	Complementary informations on birds	Types of molecules analyzed	Method of extraction	GC column	Method of analysis with GC/MS	References
Gray catbird (*D. carolinensis*)	Wild birds captured in summer (n = 64) at Killbuck Marsh Wildlife area, Ohio, USA and in winter (n = 18) at Archbold Biological Station, Florida, USA.	-Volatiles and semivolatiles from UGS	a) Volatiles compounds: samples placed in sealed vials at 44 °C and SPME (60 min) on Carboxen-PDMS fiber.	a) Polar: AT-WAX (Alltech)	a) Desorption at 225 °C, 10 s. 50 °C (1 min), ramp at 15°C min^{-1} to 200 °C (hold 2 min)	Shaw et al. (2011)
			b) Semivolatiles compounds: samples dissolved in dichloromethane and heated at 44 °C, 30 min.	b) Apolar: DB-5MS (Agilent)	b) 50 °C (1 min), ramp at 4 °C min^{-1} to 90 °C then 30 °C min^{-1} to 280 °C (hold 15 min) and then 1 °C min^{-1} 320 °C (hold 5 min)	

DVB, divinylbenzene; F, feathers; FID, flame ionization detection; Fa, faeces; FTD, flame thermionic detection; GC, gas chromatography; PDMS, polydimethylsiloxane; UGS, uropygial gland secretion.
[a]Analyzed by GC with element specific atomic emission detection.

tetradecanal, pentadecanal, hexadecanal, heptadecanal, and octadecanol. Some of these molecules have also been described in human skin odor (Curran et al. 2007).

A similar study was carried out using extracts from chicken feathers, skin, and feet (Bernier et al. 2008) (DC^2 in Table 3; DC^3 and DC^4 in Table 4). Hexane extracts from those 3 different samples display similar compounds, mainly in the most volatile part of the GC chromatograms but with some differences in relative compound abundance. Additional less volatile compounds are also detected in skin extract. Hexane and diethyl ether extraction carried out on feathers display differences, mainly in ketones and alcohols. Hexane extracts elicit attraction of female mosquitoes *Culex quinquefasciatus*, whereas nonpolar ether extracts are inefficient (Allan et al. 2006). The hexane extracts display hexan-2-ol, hexan-3-ol, hexan-2-one, and hexan-3-one that were not present in the ether extract. Aldehydes are detected in both extracts with nonanal being the most abundant. Some of the identified aldehydes, for example, heptanal, octanal, and decanal, were not previously identified in chicken feathers. Two di-ones (hexan-2,4-dione and hexan-2,5-dione) are also detected. Interestingly, similarities in abundances are observed between ketones and alcohols, ketones and diones, and the aldehydes and acids. This suggests that similar microbial degradation pathways occur.

Insect attraction to bird feces was also conducted with another biological model, the Mexican fruit fly (Robacker et al. 2000). Feces from ring-necked doves (*Streptopelia capicola*), feces from unknown birds collected from leaf surfaces and feces from black-bellied whistling ducks (*Dendrocygna autumnalis*) were tested for attractiveness. Because feces from ducks were the most attractive, their volatiles molecules were collected by SPME and analyzed by GC-MS (Table 5). Interestingly, the addition of NaCl or NaOH in the extracts allows the identification of trace components, such as methylpyrazine and methylamine derivatives (BWD in Table 4). The major peaks identified by GC-MS using carboxen-PDMS fibers are ethanol, propan-1-ol, butan-1-ol, phenol, butan-2-one, pentan-3-one, and N,N-dimethylmethanamine (trimethylamine). The use of GC-FID combined with PDMS fibers led to some differences as the major peaks were ethanol, propan-1-ol, 2-ethylhexan-1-ol, phenol, azane (ammonia), 3,4-dihydro-2H-pyrrole, and pyrazine derivatives. These differences can be explained in part by the use of different SPME fibers in the 2 analyses. When sugar-fed and protein-starved, flies are attracted only to chemicals containing nitrogen. Sugar-starved, protein-starved flies are attracted to phenol, 2-ethylhexan-1-ol, N-methylmethanamine (dimethylamine), N,N-dimethylmethanamine, and 3,4-dihydro-2H-pyrrole. In both cases, 2,5-diisopropylpyrazine is a repellent.

Volatile compounds from bird feces were analyzed as putative markers of bacterial infection by *Campylobacter* (Garner et al. 2008). The use of volatile biomarkers detected by GC-MC should then avoid the time-consuming conventional culture-based methods. Different volatile compounds are identified from chicken feces (DC^2 in Table 4), some of them arising from the environment of the animal. Some farm-specific compounds could allow linking chicken to their rearing farm. Clear differences are also observed in the volatile profile between chickens with or without bacterial infection, although none of the compounds were associated with the presence or absence of *Campylobacter*. Six nonfarm-specific volatile compounds were needed to build a predictive model that could be used to classify fecal samples as positive or negative for *Campylobacter*.

Conclusions

The correct and detailed identification of bird semiochemicals is an essential precursor to testing the activity of these

compounds in field. Although a more detailed picture of the compound types is slowly emerging, more standardized methods of analysis are needed for facilitating comparisons among studies. Indeed, the choice of many different chromatographic columns, methods of extraction, and analysis etc. makes the interspecies and intraspecies comparison very difficult. The use of different chemical nomenclature is also problematic. This review is a first step in bringing together chemical information that is useful to all the ecologists working in the field of avian chemical communication. This could also be helpful in defining a ''guideline'' for further chemical analyses, not in order to restrict methodologies but rather to establish some common starting foundations.

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