Physiological and biochemical aspects of the avian uropygial gland

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(With 1 figure)

Abstract

This review discusses different aspects of the uropygial gland of birds. The gland exhibits a striking morphological diversity in size, shape and presence/absence of tufts of feathers. It was shown that acidic mucins, neutral lipids, glycolipids and phospholipids are normal components of secretion. Several morphological and physiological aspects of the gland were studied on Rock Pigeon *Columba livia* Gmelin, 1879. The amount of the uropygial gland secretion, its lipid content and fatty acids profile were determined. The extracted lipid mixture contained of C14 to C20 fatty acids, mostly unsaturated; the saturated fatty acids were mainly 14:0, 16:0 and 18:0. No correlation was found between the size of the gland and the aquatic/terrestrial nature of the species. Ablation of the gland did not affect survival, body weight, feeding rate and serum cholesterol, total lipids or calcium levels after 32-120 days. The possible role of the gland in the protection against lipophilic compounds was discussed. The function of the gland is still a subject of controversy. It is accepted that its secretion confers water-repellent properties on the feather coat and maintain the suppleness of the feathers. Other physiological roles of the gland secretion may be associated to pheromone production, control of plumage hygiene, thermal insulation and defence against predators. Concerning the endocrine regulation of the uropygial function, there is scarce information presenting evidence for steroid regulated mechanisms.

Keywords: Columba livia, preen gland, uropygial gland, uropygial physiology, chemistry of secretion.

Aspectos fisiológicos e bioquímicos da glândula uropigial das aves

Resumo

Esta revisão discute diferentes aspectos da glândula uropigial das aves. A glândula exibe uma chamativa diversidade morfológica de tamanho, forma e presença/ausência de um tufo de penas. A glândula mostrou mucinas ácidas, lipídios neutros, glicolipídios e fosfolipídios como componentes normais de sua secreção. Diversos aspectos morfológicos e fisiológicos da glândula foram estudados na pomba doméstica *Columba livia*. Foi determinada a quantidade de secreção da glândula uropigial, seu conteúdo lipídico e o perfil de ácidos sebosos. A mistura lipídica extraída contém ácidos graxos C14 a C20, principalmente não saturados; os ácidos graxos saturados foram principalmente 14:0, 16:0 e 18:0. Não se encontrou correlação entre o tamanho da glândula e a natureza aquática/terrestre das espécies. A ablação da glândula não afetou a sobrevivência, peso corporal, alimentação e os níveis séricos de colesterol, lipídios totais ou cálcio depois de 32-120 dias. Discute-se o possível papel da glândula na proteção contra compostos lipofílicos. A função da glândula é ainda tema de controvérsia. Aceita-se que sua secreção confere às penas propriedades repelentes à água e as mantém flexíveis. Outras funções fisiológicas da secreção glandular podem estar associadas com a produção de feromonas, controle da higiene da plumagem, isolamento térmico e defesa contra predadores. Com relação à regulação endócrina da glândula, tem-se escassa informação, apresentando evidência de mecanismos de regulação de esteróides.

Palavras-chave: Columba livia, glândula uropigial, fisiologia uropigial, química da secreção.

1. Introduction

1.1. Description of the gland

The skin of birds is adapted to their life style. It is thinner than in mammals of equal size. Avian skin lacks sweat and sebaceous glands, yet the epidermis itself is lipogenic, producing neutral fats and phospholipids (Lucas, 1980). The entire skin acts as a sebaceous secretory organ, with the preen gland and the ear glands as specialized parts (Menon et al., 1981; Stettenheim, 2000).

There has been research into the uropygial gland since the middle of the thirteenth century and ever since then, researchers have gathered information on its anatomy, histology, secretion chemistry, function, etc. There are several valuable reviews, e.g. Elder (1954), Lucas and Stettenheim (1972), Jacob and Ziswiler (1982), Menon and Menon (2000) and Johnston (1988), that provide insight and discuss different aspects of the gland. Our aim is to present and discuss briefly the most relevant aspects referred to the gland and integrate our own results with those of other authors.

The uropygial gland in birds is one of the integumentary glands that exist in birds. It is a bilobate sebaceous organ, variable both in shape and size (Lucas and Stettenheim, 1972; Sawad, 2006), located dorsally between the fourth caudal vertebrae and the pygostile. The gland is invariably present at embryonic stages, whereas it can be vestigial in adults of certain orders, families, genera and species. It is completely absent in Struthionidae, Rheidae, Casuaridae, Dromaidae and in a few species of Columbidae and Psittacidae (Johnston, 1988).

It is a holocrine gland enclosed in a connective tissue capsule made up of glandular acini that deposit their oil secretion into a common collector tube ending in a variable number of pores, most usually two. Each lobe has a central cavity that collects the secretion from tubules arranged radially around the cavity. The gland secretion is conveyed to the surface via ducts that, in most species, open at the top of a papilla (Jacob and Ziswiler, 1982).

Descriptions of the gland of different taxa and systematic classifications based on its morphology and the chemical nature of secretory lipids have been provided by several authors (Jacob and Zeman, 1972; Johnston, 1988; Sandilands et al., 2004a,b). There is a striking morphological diversity of the uropygial gland in regard to size, shape and the presence or absence of the tuft of feathers (Jacob and Ziswiler, 1982; Johnston, 1988; Montalti and Salibián, 2000). Figure 1 shows some morphological types of the gland in adults of different bird species representatives of the Neotropical and Antarctic Region.

The information available does not provide unequivocal proof of any possible relationship between the morphological features of the gland and their significance in environmental adaptation. It would be very interesting to determine the selection pressures that might explain the enormous variation in the morphology of this gland in the different avian species.

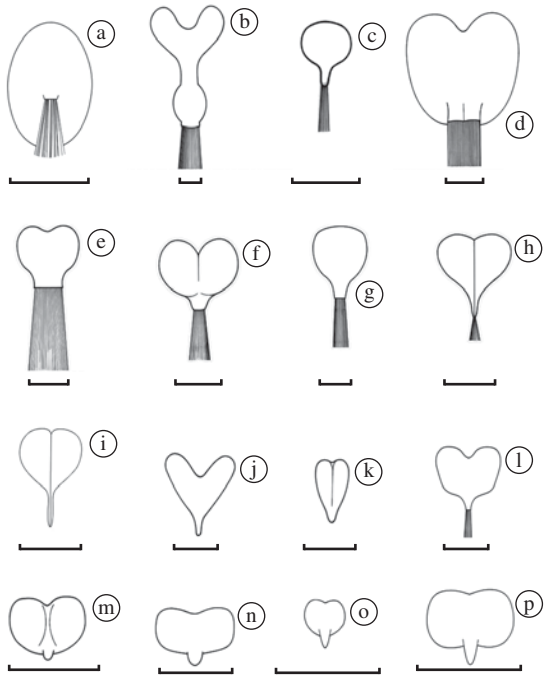

Figure 1. illustrations of the uropygial gland of some Neotropical and Antarctic birds, showing its morphological diversity. The linear scale equals 1 cm. a) *Nothura maculosa* (Temminck, 1815), b) *Pygoscelis adeliae* (Hombron and Jacquinot, 1841), c) *Oceanites oceanicus* (Kuhl, 1820), d) *Phalacrocorax olivaceus* (Humboldt, 1805), e) *Catharacta maccormicki* (Saunders, 1893), f) *Larus maculipennis* Lichtenstein, 1823, g) *Ara macao* (Linnaeus, 1758), h) *Tyto alba* (Scopoli, 1769), i) *Athene cunicularia* (Molina, 1782), j) *Guira guira* (Gmelin, 1788), k) *Columba livia* Gmelin, 1879, l) *Colaptes campestris* (Vieillot, 1818), m) *Furnarius rufus* (Gmelin, 1788), n) *Embernagra platensis* (Gmelin, 1789), o) *Carduelis magellanica* (Vieillot, 1805), and p) *Agelaioides badius* (Vieillot, 1819).

2. Gland Histology

The histology of the gland has been examined in a reduced number of species. It appears that the histological organization corresponds to a sebaceous gland (Wagner and Brood, 1975). The tubular epithelium is made up of four well-defined layers: a) a germinative layer where cell division occurs and consisting of one or two strata of flat or cuboidal cells with a basophilic cytoplasm and dark nucleus, b) an intermediate layer consisting of 1-5 strata of polygonal cells with a basophilic cytoplasm, c) a secretory layer formed by 1-10 layers of voluminous polygonal cells with secretory granules and, d) a degenerative layer characterized by cells with pycnotic nuclei and keratohyaline granules in the cytoplasm. Cell fragments, corneous plates and secretion from the sebum may also be found (Montalti et al., 2001).

The walls of the gland are similar in the studied species, with the exception of the Columbiformes. The epithelial cells of the lobe in Rock Pigeon *Columba livia* are surrounded by connective tissue septa and do not form tubules ending in a central cavity. There is a small germinative layer on the periphery of the cell bundles where the intermediate cells and voluminous secretion cells are arranged in a mosaic-like pattern. Degenerating cells are rarely seen.

The microscopic structure of the gland of *Columba livia* was studied in our laboratory using histochemical and lectin-histochemical methods. Acidic mucins, neutral lipids, glycolipids and phospholipids were normal components of the tubular secretion. The use of lectins showed the distribution of glycoconjugates during normal secretion in a mixture of lipid and carbohydrate compounds, the composition of which varied according to the stage of cellular differentiation and secretion formation (Table 1).

The germinative layer has a very strong binding intensity with some particular lectins, specifically with β-D-acetylglucosamine, N-acetylneuraminic acid and β-D-galactose. The degenerative layer displayed very intense binding specifically with α-D-mannose and α-D-glucose. Intermediate and secretory cell layers showed no significant affinity for any of the assayed lectins. Secretion products showed high affinity for some specific lectins found in the germinative and degenerative layers (Montalti et al., 2001).

Sandilands et al. (2004b) recently demonstrated that the histological characteristics and dimensions of the gland and the quantity of lipids found on feathers of *Gallus gallus* Linnaeus, 1758 were significantly affected by bird age, in particular during the first few weeks of development (up to 30 weeks).

3. Gland Physiology

The elucidation of the physiological and biochemical role of the gland has been the subject of numerous studies. However, results have been controversial (Johnston, 1988).

Many authors hold that the function of this gland is closely connected with the hydrophobic properties of secretion, which would have an essential role in protecting the body surface of the birds from the environment, particularly in plumage waterproofing (Jacob, 1992). Early studies showed that the secretion served as a water repellent, which prevented the birds from getting wet. However, we have shown that there is no clear-cut correlation between the size of the gland and the aquatic/terrestrial nature of the species (Montalti and Salibián, 2000).

Other authors have postulated that the change in wax viscosity may be related to the formation of the more brilliant plumage required for courtship (Piersma et al., 1999). Later Reneerkens and Korsten (2004) did not find support for their idea.

A possibility that cannot be disregarded is that the degree of contact with water might rather be associated with adaptive changes in the composition of the secretion, involving the lipid biosynthetic pathways of the gland. It is worth mentioning that more than four decades ago Bollinger and Varga (1961) showed the high content of fatty acids in the plumage of the emu *Dromaeus novaehollandiae* Latham, 1790 despite the fact that it does not have the gland, suggesting that water birds that have had their gland removed may remain dry because of the water-repellent capacity of the feather lipids.

The results of other studies suggest that the gland in females may be involved in the production and secretion of lipids with female pheromone activity (Kolattukudy and Rogers, 1987). The anti-rickets effect of secretion from the gland based on its vitamin D content was studied several decades ago (Hou, 1928; 1929; 1930). However, it was later shown that the presence of the gland was not essential for calcium metabolism altered by rickets, and that the sensitivity threshold for manifesting this disease varied among the different avian species (Rawles, 1960).

Bandyopadhyay and Bhattacharyya (1996; 1999) and Shawkey et al. (2003) offered evidence of the role of

Table 1. Lectin binding pattern in the uropygial gland of Rock Pigeon *Columba livia* (data from Montalti et al., 2001).

Lectin	Cellular layer				
	Germinative	Intermediate	Secretory	Degenerative	Secretory product
PNA	++	–	–	–	–
WGA	+++	–	–	–	+++
RCA–1	+++	–	–	–	–
UEA–1	–	–	–	–	–
SBA	–	–	–	–	–
DBA	–	–	–	–	–
Con A	–	–	–	+++	+++

PNA: *Arachis hypogaea*, WGA: *Triticum vulgaris*, RCA-1: *Ricinus communis*, UEA-1: *Ulex europaeus*, SBA: *Glycine maximus*, DBA: *Dolichus biflorus*, ConA: *Concanavalin ensiformis*. Intensity of binding: (–) negative, (+) weak, (++) strong, (+++) very strong.

the gland secretion in plumage hygiene controlling skin fungi and bacteria and ectoparasites (Moyer et al., 2003). These antibiotic effects are modified when the gland is extirpated, causing significant alterations in the number and shape of the bacteria inhabiting the skin and feathers; these effects could have ecological and adaptive significance.

More recently, Haribal et al. (2005) have presented evidence suggesting that the evolution in the intraspecific qualitative and quantitative variations in preen gland secretion may be attributed to selective pressures caused by ectosymbionts that usually live on feathers and probably co-evolved with birds. Galván and Sanz (2006) have provided evidence of the possible relationship between the number of feather mites and the uropygial gland size in a breeding population of great tits *Parus major*. Since those arachnids feed on oil that birds spread from their gland, the abovementioned authors hypothesized and showed that the number of mites correlated positively with the size of the uropygial gland of their hosts, suggesting that the size of the gland may explain the variance in feather mite load among conspecifics.

Feathers provide birds with the essential insulation required for controlling body temperature, aerodynamic power required for flight, and colors that may be useful in communication and camouflage. Modified feathers are important in swimming, sound production, hearing, protection, hygiene, water repellence, water transport, tactile feeling, etc. (Gill, 1994; Stettenheim, 2000). It has been suggested that some of these properties may be associated with uropygial waxy secretion that birds apply on the feathers. However, not all lipids of the plumage originate in the uropygial gland; a proportion comes from the sebaceous secretions of the epidermis.

In considering the physiological role of the uropygial gland, it appears that the gland is not necessarily present in all groups of birds. This fact, observed in a number of species, together with the lack of a clear-cut ecological correspondence suggests that, when present, the function of the gland may be diverse but not essential. In this regard, it is interesting that the extirpation of the gland did not have any serious consequence for the survival of goslings, hens and passerine birds (Jacob, 0 1976; Chen et al., 2003). The surgical removal of the uropygial gland in *Columba livia* did not affect the behavior, survival, and body weight gain and feeding rates, over a two-month period (Montalti et al., 1998; 2000; Moyer et al., 2003).

We measured several biochemical parameters in relation to gland physiology (Montalti et al., 2006) comparing control specimens with gland-removed specimens. No differences were found in serum levels of cholesterol, total lipids, and calcium after 32-120 days. Thus, no alteration in two basic biochemical parameters associated with the metabolism of lipids and in a critical parameter related to mineral homeostasis, was noted four months after ablation of the gland. These results suggest that the uropygial gland may not relate, at least physiologically, to the homeostasis of lipids or to the regulation of calcium metabolism.

Based on the high content of lipids of the gland secretion, we postulated its possible ecotoxicological role in regulating the accumulation and/or excretion of lipophilic compounds. This hypothesis was checked by measuring the accumulation of lindane, an organochlorine lipophilic xenobiotic, in the liver and glands of *C. livia* after injection of sublethal doses of the insecticide (Gutiérrez et al., 1998). The results indicated a) a significant amount of the insecticide accumulated in the gland, b) that the lipid content of the gland was not altered, c) that the fatty acid composition profile of the gland lipids did not change relative to controls and, d) that the liver lipid content increased 2 to 4 times relative to control birds. These results suggest that the toxicity of lipophilic products may be regulated by the uropygial gland, which would have the role of capturing and depositing these substances. In addition, the liver weight of the birds exposed to lindane increased significantly. The liver somatic index LSI went from 1.7 (controls) to 2.9 (lindane injected birds); the difference could be attributed to the impact of the insecticide as a consequence of the liver enlargement secondary to exposure to the insecticide due to compensatory proliferation processes (Williams and Iatropoulos, 2002).

It is interesting that other authors have postulated that the gland may have a role in protecting wild animals exposed to organochlorine insecticides (Charnetski and Stevens, 1974; Johnston, 1976; 1978) and to heavy metals which might be of great importance in species inhabiting highly polluted areas (Pilastro et al., 1993; Dauwe et al., 2002). In relation to this particular role of the gland, it is worth mentioning the results of a recent study (Janssens et al., 2001); significant increases were found in the content of 13 heavy metals in feathers of *Parus major* Linnaeus, 1758 captured in the vicinity of an industrial plant. More recently, Scheifler et al. (2005) reported the presence of mercury in feathers of the king penguin (*Aptenodytes patagonicus* Miller, 1778) living on remote sub-Antarctic islands.

It is possible that the heavy metals found in feathers may originate either from internal deposition or through the secretion of the uropygial gland during preening. Alternatively, it cannot be disregarded that part of the detected metals in feathers may have originated from external deposition and consequently reflect local environmental contamination levels in a particular habitat.

In connection with the chemical defense mechanisms, Dumbacher (1999) and Dumbacher et al. (1992; 2000), reported that the skin and plumage of three passerine species of the *Pitohui* genus may be considered poisonous due to the high content of a steroid neurotoxic alkaloid found until that time only in the skin of some neo-tropical amphibians. These authors attributed this alkaloid with the function of chemical defense against natural predators such as snakes, raptors, and possibly some arboreal marsupials. However, considering that the concentration

of this alkaloid is three orders of magnitude lower than that registered in amphibians of comparable size, Poulsen (1993) questioned this function and suggested, instead, that they might have a significant role in controlling and regulating avian ectoparasite arthropods.

Little information is available on the endocrine regulation of the uropygial function and the molecular and biochemical mechanisms involved in the synthesis of glands' lipids. Bhattacharyya and Chowdhury (1978) have shown that in prepuberally castrated adult male pigeons, testosterone administration promotes the synthesis of lipid secretory material of the gland as well as an acceleration of the secretion rate. These results suggested the existence of an androgen regulated mechanism of release of lipids in the gland.

In contrast, Kolattukudy and Rogers (1987), Bohnet et al. (1991) and Hiremath et al. (1992) have presented evidence that the changes required in the biosynthetic pathways involved in the production and secretion of female pheromones in male and female mallards (*Anas platyrhynchos* Linnaeus, 1758) can be induced by estradiol. It is interesting to note that estradiol induces the proliferation of peroxisomes the enzymes of which are involved in those biochemical changes. Likewise, the levels of estradiol reach their highest point during eclipse, the post-nuptial molt period. It is also known that thyroxine increases the proliferative effects of steroid hormones. In confirmation of this behavior, the simultaneous injection of estradiol and thyroxine accentuated the above mentioned effects when they were administered separately.

The studies carried out by Asnani and Ramachandran (1993) on male *Columba livia* have concluded that adrenal corticosteroids play a primary role in maintaining the structure and function of the gland. Their results pointed out the existence of an adrenal-gonadal relationship. They also suggested that thyroid hormones may probably be involved in maintenance of the metabolic functions of the gland.

4. Gland Size and Habitat

If the function of the gland could be closely connected to the hydrophobic properties of its secretion and were consequently, essential for plumage waterproofing, it could be hypothesized that the size or degree of development in this gland should be greater in aquatic birds than in terrestrial species. To check out this hypothesis, we measured gland mass relative to body mass in 1,164 adult individuals from 126 species and 49 families, concluding that there was no correlation between the degree of development in this gland and the animals' contact with water (Montalti and Salibián, 2000). The largest gland was found in *Cinclus mexicanus* Swainson, 1827 (0.7% of body mass) while the smallest was recorded in *Bubulcus ibis* (Linnaeus, 1758) (0.01%) (Johnston, 1988; Montalti and Salibián, 2000).

Within this context of the discussion it is accepted that species that plunge into the water to capture their prey would require larger glands than species that pick their prey off the surface almost without touching the water (see Jacob and Ziswiler, 1982). If we assume that the volume of gland secretion constitutes a valid parameter for determining the degree of gland development, our results indicate that the physiological role of the gland does not depend upon gland mass. However, the relative gland weight appeared to have no clear relationship with the degree of adaptation to water environment of the species under consideration. For instance, in spite of being a fully aquatic species, the relative gland size of Sternidae was one of the largest among the species studied; similar findings were reported by Johnston (1979). If the mean gland weight is compared to the body weight of glands in aquatic vs. land birds (Table 2), both will show comparable values in spite of their different habitat; for instance, *Anas georgica* Gmelin, 1789 (0.250%) versus *Guira guira* (Gmelin, 1788) (0.296%); *Pygoscelis adeliae* (Hombron and Jacquinot, 1841) (0.159%) versus *Colaptes campestris* (Vieillot, 1818) (0.174%).

One alternative that should not be dismissed is the likelihood of waterproofing being affected by the feather structure, as shown by Elowson (1984).

Several authors have reported differences in the relative gland weights attributing them to factors like seasonal changes (Kennedy, 1971), habitat (Jacob and Ziswiler, 1982), body weight (Johnston, 1988), inter-individual variations, and gender (Johnston, 1988). In our studies statistically significant differences were found in the relative gland size between males and females in most species (see Table 2). However, no coherent explanation has as yet been found for these results.

5. The Chemical Composition of the Gland Secretion

The uropygial gland specializes in the synthesizing of lipids. The chemical composition of the gland secretion has been extensively studied. In adult birds, natural esters are made up of an extraordinarily diverse mixture of fatty acids and long-chain alcohols. The secretion is a complex and variable mixture of substances formed mainly by lipids, aliphatic monoester waxes, made of fatty acids (with various degrees of methyl branching), and long-chain monohydroxy wax-alcohols. However, some types of diester waxes containing hydroxyfatty acids and/or alkanediols exist in the secretions of the gland in some groups of birds (Jacob and Ziswiler, 1982; Downing, 1986; Jacob, 1992). In addition to branched fatty acids and alcohols, there were also molecules carrying up to four or five methyl groups on internal C atoms of the chain lipids. The secretion was also shown to contain linear saturated fatty acids esterified by linear saturated diols.

The gland showed a very high capacity for **de novo** fatty acid synthesis, the rate of which showed seasonal variation (Kolattukudy et al., 1985; Kolattukudy and Rogers, 1987; Urich, 1994; Stevens, 1996).

Some authors have demonstrated sex differences in the chemical composition of the secretion during the reproduction period (Jacob et al., 1979; Kolattukudy et al.,

Table 2. Uropygial gland weight (in g) relative to body mass (gland mass x 100/body mass) in several bird species discriminated by sex. Common names are included. Data is given as mean ± S.D., minimum and maximum values in parenthesis; number of samples, in brackets. Asterisks indicate statistically significant differences ($p < 0.01$) between males and females (Mann-Whitney U test) (part of the data was taken from Montalti and Salibián, 2000).

Species	Males	Females	Males + Females
Nothura maculosa *	0.152 ± 0.049	0.133 ± 0.038	0.144 ± 0.045
(Temminck, 1815)	(0.082-0.226)	(0.054-0.186)	(0.054-0.226)
Spotted Nothura	[16]	[11]	[27]
Pygoscelis adeliae	0.170 ± 0.047	0.171 ± 0.071	0.174 ± 0.055
(Hombron and Jacquinot, 1841)	(0.103-0.292)	(0.105-0.318)	(0.103-0.318)
Adelie penguin	[15]	[11]	[26]
Oceanites oceanicus	0.459 ± 0.088	0.453 ± 0.049	0.456 ± 0.071
(Kuhl, 1820)	(0.353-0.627)	(0.346-0.514)	(0.346-0.627)
Wilson storm petrel	[9]	[8]	[17]
Plegadis chihi *	0.214 ± 0.049	0.188 ± 0.030	0.206 ± 0.045
(Vieillot, 1817)	(0.143-0.346)	(0.147-0.240)	(0.143-0.346)
White-faced Ibis	[21]	[9]	[30]
Anas georgica *	0.228 ± 0.076	0.277 ± 0.065	0.250 ± 0.071
Gmelin, 1789	(0.111-0.316)	(0.217-0.368)	(0.111-0.368)
Yellow-billed Pintail	[5]	[4]	[9]
Milvago chimango *	0.145 ± 0.043	0.137 ± 0.027	0.142 ± 0.035
(Vieillot, 1816)	(0.064-0.192)	(0.105-0.180)	(0.064-0.192)
Chimango Caracara	[9]	[8]	[17]
Calidris fuscicollis *	0.242 ± 0.018	0.256 ± 0.048	0.251 ± 0.037
(Vieillot, 1819)	(0.214-0.275)	(0.176-0.368)	(0.176-0.368)
White-rumped Sandpiper	[10]	[12]	[22]
Larus maculipennis *	0.231 ± 0.037	0.241 ± 0.047	0.237 ± 0.042
Lichtenstein, 1823	(0.176-0.319)	(0.146-0.308)	(0.146-0.319)
Brown-hooded Gull	[20]	[21]	[41]
Columba livia *	0.026 ± 0.011	0.036 ± 0.016	0.030 ± 0.014
Gmelin, 1879	(0.009-0.049)	(0.014-0.080)	(0.009-0.080)
Rock Pigeon	[28]	[23]	[51]
Zenaida auriculata	0.026 ± 0.011	0.026 ± 0.009	0.026 ± 0.010
(Des Murs, 1847)	(0.012-0.054)	(0.011-0.039)	(0.011-0.054)
Eared Dove	[19]	[10]	[29]
Guira guira *	0.290 ± 0.129	0.312 ± 0.083	0.296 ± 0.111
(Gmelin, 1788)	(0.05-0.590)	(0.183-0.448)	(0.05-0.590)
Guira Cukoo	[21]	[15]	[36]
Colaptes campestris	0.180 ± 0.038	0.176 ± 0.036	0.177 ± 0.036
(Vieillot, 1818)	(0.120-0.232)	(0.126-0.262)	(0.121-0.262)
Field Flicker	[11]	[14]	[25]
Tyrannus savana *	0.085 ± 0.025	0.156 ± 0.060	0.116 ± 0.056
Vieillot, 1808	(0.053-0.128)	(0.089-0.270)	(0.053-0.270)
Fork-tailed Flycatcher	[14]	[11]	[25]
Mimus saturninus *	0.183 ± 0.05	0.230 ± 0.090	0.210 ± 0.077
(Lichtenstein, 1823)	(0.129-0.259)	(0.149-0.415)	(0.129-0.415)
Chalk-browed Mockingbird	[6]	[8]	[14]
Embernagra platensis *	0.271 ± 0.065	0.310 ± 0.104	0.287 ± 0.083
(Gmelin, 1789)	(0.136-0.398)	(0.126-0.473)	(0.126-0.473)
Great Pampa-Finch	[32]	[16]	[48]

1987, Reneerkens et al., 2002). In this respect, we were unable to find differences in rock pigeon, probably due to the fact that we performed our measurements out of the breeding season.

Another function of the glands' secretion could be the protection against adverse environmental factors (e.g. temperature variations). That may be the case of secretions that are liquid at room temperature, forming a

permanent dry film when exposed to air and would therefore act as protective factors preserving the structure of feathers.

The chemical composition of the gland's secretory lipids may vary according to the developmental (Kolattukudy and Sawaya, 1974) or breeding stage. Kolattukudy et al. (1991) noted chemical differences in *Anas platyrhynchos* between the time immediately after hatching and later when the down feathers are replaced by adult feathers. The initial long-chain wax esters were replaced by short-chain esters (Kolattukudy et al., 1987). Piersma et al. (1999) and Reneerkens et al. (2005) showed that the usual mixtures of monoester preen waxes of *Calidris canutus* (Linnaeus 1758) at the beginning of incubation are replaced by mixtures of less volatile diester waxes, probably more difficult to smear onto the plumage; they set forth the hypothesis that diester waxes reduce bird smell and thereby reduce predation risk. This fact would represent an important selective advantage for the birds (Reneerkens et al., 2006).

The fatty acid composition of the lipids in both the uropygial gland in the rock pigeon and its secretion were determined in our laboratory. Measurements were carried out to establish the amount of secretion, the total lipid content and the fatty acids composition of the secretion. The fatty acid composition of the lipids extracted from the gland secretion consisted of C14 to C20 chains, most of which unsaturated, with a prevalence of oleic acid and a low content of linoleic and arachidonic acids. The saturated long chain fatty acids were mainly 14:0, 16:0 and 18:0 (Montalti et al., 2005).

The percentage of saturated fatty acids in the secretion was lower than that of the unsaturated in both sexes; the saturated: unsaturated ratio was 0.58. However, when the profile of these fatty acids was determined in the whole gland, the ratio was 1.17 (Table 3; Gutiérrez et al., 1998). This finding must be interpreted as a consequence of the different chemical composition of the conjunctive capsule, which was analyzed together with the glandular secretion. In analyzing the whole gland, the measurements include some compounds that are not part of the secretion (e.g. conjunctive tissue) and therefore not involved in the function of the gland secretion (Gutiérrez et al., 1998).

Another important factor that affect the fatty acids profile of the gland was the age of birds, which, in turn, may be related to sexual maturity and therefore to their hormonal state at the particular moment when the measurements were carried out (Sandilands et al., 2004a). Most of our experiments were carried out on adult animals, thus the results presented here would not be affected by the age of the birds under study.

To avoid "contamination" of the assayed material from the surrounding tissues that are rich in triglycerides (Jacob, 1975), the secretion of each gland was analyzed. In this way it was possible to determine precisely the lipid content and its fatty acid composition, which, in turn, is what the birds use in preening their feathers (Moyer et al., 2003).

The chemical composition of the gland secretion has been suggested as a valuable taxonomic tool (Jacob and Grimmer, 1975; Jacob and Ziswiler, 1982; Hoerschelmann and Jacob, 1996). Our results suggest that the gland developmental trend was independent of the bird lineage. Thus, the gland is present in phylogenetically distant birds (e.g. Tinamidae-Hirundinidae) or absent in phylogenetically close taxa (some Psittacidae-Columbidae). Sweeney et al. (2004) showed that the feather wax composition is unlikely to be highly informative for reconstructing phylogenetic relationships. Levy and Strain (1982) have also noted that the use of the secretion's chemical composition with chemotaxonomic purposes could be inappropriate considering this a parameter with a large amount of circannual variations associated to bird reproduction cycles, and conditioned by environmental, hormonal and physiological factors.

The information available in connection with the function of this gland, which is known to be present only in birds is, for the time being, only partial. However, this provides the means to establish that the uropygial gland is a very variable organ in regard to morphology, chemical composition of its secretion, and the variety of functions it is involved in. These observations, as a whole, suggest this gland is a functionally plastic organ, involved in the

Table 3. Fatty acid composition of total lipids from the whole Rock Pigeon Columba livia uropygial gland and its secretion. Data is expressed as a percentage; mean ± S.D. Mean body weight of the birds, 443 g (data from Gutiérrez et al. 1998; Montalti et al., 2005).

Fatty acid	Gland Secretion N = 12	Whole gland N = 6
Saturated	33.97 ± 0.82	52.57 ± 3.30
Monounsaturated	46.22 ± 1.09	23.81 ± 0.32
Polyunsaturated	12.27 ± 0.22	14.82 ± 1.12
Total unsaturated	58.48 ± 0.01	38.63 ± 5.44
Saturated/unsaturated	0.58 ± 0.01	1.17 ± 0.18
Unsaturation index	84.04 ± 1.57	41.15 ± 2.28

modulation of several ecophysiological mechanisms of environmental adaptation in birds.

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