

Preen oil and bird fitness: a critical review of the evidence

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ABSTRACT

The uropygial gland is a holocrine complex exclusive to birds that produces an oleaginous secretion (preen oil) whose function is still debated. Herein, I examine critically the evidence for the many hypotheses of potential functions of this gland. The main conclusion is that our understanding of this gland is still in its infancy. Even for functions that are considered valid by most researchers, real evidence is scarce. Although it seems clear that preen oil contributes to plumage maintenance, we do not know whether this is due to a role in reducing mechanical abrasion or in reducing feather degradation by keratinophilic organisms. Evidence for a function against pathogenic bacteria is mixed, as preen oil has been demonstrated to act against bacteria *in vitro*, but not *in vivo*. Nor is it clear whether preen oil can combat pathogenic bacteria on eggshells to improve hatching success. Studies on the effect of preen oil against dermatophytes are very scarce and there is no evidence of a function against chewing lice. It seems clear, however, that preen oil improves waterproofing, but it is unclear whether this acts by creating a hydrophobic layer or simply by improving plumage structure. Several hypotheses proposed for the function of preen oil have been poorly studied, such as reduction of drag in flight. Similarly, we do not know whether preen oil functions as repellent against predators or parasites, makes birds unpalatable, or functions to camouflage birds with ambient odours. On the other hand, a growing body of work shows the important implications of volatiles in preen oil with regard to social communication in birds. Moreover, preen oil clearly alters plumage colouration. Finally, studies examining the impact of preen oil on fitness are lacking, and the costs or limitations of preen-oil production also remain poorly known. The uropygial gland appears to have several non-mutually exclusive functions in birds, and thus is likely to be subject to several selective pressures. Therefore, future studies should consider how the inevitable trade-offs among different functions drive the evolution of uropygial gland secretions.

Key words: antiparasitic function, antipredator strategies, communication, hatching success, preen oil, sexual selection.

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I. INTRODUCTION

The uropygial (also called preen, oil, or coccygeal) gland is a holocrine gland, exclusive to birds, located in the integument above the posterior free caudal vertebrae (i.e. in the rump; Clark, 2004). It is present during embryonic development in all bird species studied, but may be absent in adults of several species of Struthioniformes, Piciformes, and Psittaciformes, as well as in some varieties of rock pigeons (*Columba livia*) (Johnston, 1988). The gland is embedded in a matrix of connective tissue that constitutes the uropygial capsule. It is usually bilobed, with lobes divided by the interlobular septum, although it is very variable among species in morphology, size, and structural proportions (Johnston, 1988). Each lobe contains glandular racemes of follicles where the uropygial secretion is produced. The secretion moves through secretory tubules to the primary sinus in the lobe, where it is stored. When stimulated by the bill of the bird, the secretion is expelled through a collector tube, the primary duct, which ends in a variable number (2–8) of pores, opening to the exterior through a nipple-like structure (the papilla). The papilla is often covered by a tuft of specialized feathers, the uropygial circlet feathers (Clark, 2004).

Birds spend much time preening (Walther & Clayton, 2005), an energetically costly activity that includes, among other behaviours, spreading of uropygial secretions onto the plumage. During preening, birds rub their bills over the uropygial gland, stimulating the secretion to emerge, and then spread it over their plumage and other teguments with the bill. The uropygial gland produces an oleaginous secretion (hereafter, preen oil) whose chemical composition is highly variable at the intraspecific (e.g. Whittaker *et al.*, 2010) and interspecific levels (Jacob & Ziswiler, 1982; Sweeney, Lovette & Harvey, 2004; Haribal *et al.*, 2005). It is composed of a complex mixture of substances formed mainly by lipids, such as monoester and diester waxes of fatty acids esterified with different types of alcohols (sometimes with methyl branching and diol groups), as well as free alcohols, terpenes, and fatty acids (Campagna *et al.*, 2012; Soini *et al.*, 2013). Fatty acids are usually synthesized in the gland (Salibian & Montalti, 2009) under hormonal control (e.g. Whittaker *et al.*, 2011b). According to the size of the carbon chain, compounds within the preen oil may be classified as volatile (short-chain) or non-volatile (long-chain). In addition, preen oil may contain other substances such as carotenoids (e.g. Amat *et al.*, 2011).

The uropygial gland has been hypothesized to have many possible non-mutually exclusive functions [reviews in Elder (1954); Jacob & Ziswiler (1982) and Salibian & Montalti (2009)]. It is likely that the uropygial gland is involved in several biological processes, potentially with important fitness consequences. In recent years, our knowledge has advanced considerably concerning the functions of preen oil. However, results for many of the potential functions have been mixed, while some hypothesized functions have received little attention. Consequently, debate regarding the functions of the uropygial gland and its oil continues. This review summarizes the evidence concerning most potential functions hypothesized for the uropygial gland, and indicates the main gaps in our knowledge about its adaptive function. Finally, I review evidence of the fitness consequences of the uropygial gland.

II. HYPOTHESIZED FUNCTIONS OF THE UROPYGIAL GLAND AND ITS SECRETIONS

(1) Plumage maintenance

Feathers have important functions in thermoregulation, flight, physical protection, and visual communication in birds (Clark, 2004). Nonetheless, feathers are dead structures that are prone to damage due to factors such as mechanical abrasion, ultraviolet (UV) irradiation, and ectoparasites feeding on keratin. Consequently, one function attributed to preen oil is plumage maintenance. Given that preen oil is composed mainly of waxes, it is thought that preening improves the flexibility of plumage, making feathers less prone to mechanical abrasion.

Supporting this assertion, house sparrows (*Passer domesticus*) with relatively large uropygial glands, implying greater levels of preen-oil production (Pap *et al.*, 2010), show reduced feather wear (Moreno-Rueda, 2011; Fülöp *et al.*, 2016). Moreover, given that melanin improves resistance against mechanical abrasion (Bonser, 1995), Roulin (2007) suggested that the uropygial gland should be larger in birds with whiter plumage to compensate for reduced feather resistance. Supporting this idea, barn owls (*Tyto alba*) with fewer black spots have larger uropygial glands than owls with darker plumage (Roulin, 2007). Elder (1954) reviewed several experiments involving the ablation of the uropygial gland and subsequent examination of plumage condition. The results were mixed, with only some studies supporting a function of preen oil against feather degradation (Elder, 1954).

Elder (1954) himself performed uropygial gland ablation experiments in different species of ducks, and concluded that plumage condition worsened with time in glandless individuals compared to controls. Interestingly, glandless ducks not only showed poorer plumage, but also beaks and legs in bad condition, yet no study investigated the reasons for this, despite damage in these body parts often leading to infections and impairment of feeding, perching, and walking. More recent evidence for a function of preen oil against plumage deterioration come from Moyer, Rock & Clayton (2003), who ablated the uropygial gland in a group of rock pigeons and found that plumage condition worsened with time more than in control individuals. Similarly, Giraudeau *et al.* (2010*b*) blocked access to preen oil in a group of mallards (*Anas platyrhynchos*) by placing a catheter over the uropygial gland, and found that plumage condition worsened in ducks with restricted access to preen oil for 3 months. Additionally, biophysical experiments suggest that preen oil reduces wearing in feathers of barn owls and pigeons (Ott, Müsse & Wagner, 2016). However, most of these studies did not differentiate between plumage deterioration due to mechanical abrasion and plumage degradation by ectoparasites (see Section II.2), with the exception of Ott *et al.* (2016) who performed experiments directly on feathers. Therefore, it seems clear that preen oil reduces plumage deterioration, but it is unclear whether it has a protective role specifically against mechanical abrasion or from feather-degrading ectoparasites.

Reneerkens & Korsten (2004) found that preen oil produced by red knots (*Calidris alpina*) absorbs light from the UV spectrum. Accordingly, they proposed that preen oil might serve as protection against bleaching. This hypothesis was tested by Surmacki (2008) in great tits (*Parus major*) who found no evidence that feather fading with time was prevented or reduced by preen waxes.

(2) Defence against ectoparasites

Parasites take resources from their hosts and negatively impact host fitness. Accordingly, parasites constitute an important ecological and selective force shaping host evolution, giving rise to a suite of host defence mechanisms (Schmid-Hempel, 2011). Preen oil has been repeatedly proposed as a mechanism by which birds protect themselves against parasites that provoke feather degrading (bacteria, fungi, and chewing lice), or those that cause hatching failure.

(a) Defence against feather-degrading bacteria

Several bacteria inhabiting plumage produce keratinase, an enzyme capable of digesting keratin (Gunderson, 2008), with a potentially negative effect on fitness for the bird (Saag *et al.*, 2011). Jacob & Ziswiler (1982) proposed that uropygial gland oil may have an effect against feather-degrading bacteria and preen oil is known to contain compounds that inhibit bacterial growth [Bandyopadhyay & Bhattacharyya (1996); Jacob, Eigener & Hoppe (1997); see reviews in Clayton *et al.* (2010) and Rajchard (2010)]. The first formal test

of this protection hypothesis was carried out by Shawkey, Pillai & Hill (2003), who found that preen oil of the house finch (*Haemorhous mexicanus*) inhibits the *in vitro* growth of several (but not all) feather-degrading bacteria found in its plumage, including *Bacillus licheniformis*, one of the most widespread feather-degrading bacteria in birds (Burt & Ichida, 1999). An antimicrobial capacity of preen oil on feather-degrading bacteria *in vitro* has also been supported for red knot (Reneerkens *et al.*, 2008), hoopoe (*Upupa epops*; Soler *et al.*, 2008; Ruiz-Rodríguez *et al.*, 2009, 2012, 2013; Martín-Vivaldi *et al.*, 2010), and spotless starling (*Sturnus unicolor*) (Ruiz-Rodríguez *et al.*, 2015).

Therefore, it seems clear that preen oil has the potential to be used as antimicrobial compound. Some correlational studies support the hypothesis of protection against feather-degrading bacteria. Uropygial gland size is negatively correlated with feather degradation caused by bacteria in spotless starlings (Ruiz-Rodríguez *et al.*, 2015) and with the number of feather holes, now thought to be caused by feather-degrading bacteria, in the house sparrow (Moreno-Rueda, 2010, 2014; Fülöp *et al.*, 2016). Also, the abundance of feather-degrading bacteria, but not other microorganisms, is negatively correlated with uropygial gland size in the barn swallow (*Hirundo rustica*) (Møller, Czirják & Heeb, 2009). Additionally, social species (Vincze *et al.*, 2013) and barn swallows nesting in large colonies (Møller *et al.*, 2009) show larger uropygial glands than do non-social species and swallows nesting in small colonies, respectively. These species or individuals living at higher densities are more prone to cross-transmission of parasites than are solitary species (Møller & Erritzøe, 1996), which provides indirect support for the hypothesis. Moreover, several comparative studies have reported that species inhabiting riparian or aquatic habitats have larger uropygial glands (Galván *et al.*, 2008; Møller, Erritzøe & Rózsa, 2010*b*; Vincze *et al.*, 2013). Given that moisture favours microorganism growth and activity (Burt & Ichida, 2004), a possible explanation for this pattern is that species inhabiting humid habitats need a higher rate of preen-oil production to combat feather-degrading bacteria. However, it should be noted that all these studies providing indirect or correlational support might have alternative explanations. For example, larger uropygial glands in aquatic species may be related to waterproofing (see Section II.3).

A few studies have shown experimentally that birds with heavier loads of feather-degrading bacteria have an enlarged uropygial gland, a situation that is interpreted as heavily infected birds increasing their investment in preen oil (Jacob *et al.*, 2014; Leclaire *et al.*, 2014*a*; also see Fülöp *et al.*, 2016). Moreover, preen-oil composition varies in response to experimentally increased bacterial load (Jacob *et al.*, 2014), although the consequences of this variation remain unclear. The key experiment would be to block access to preen oil in living birds and examine effects on feather-degrading bacteria inhabiting the plumage. Surprisingly, Czirják *et al.* (2013) and Giraudeau *et al.* (2013) found that house sparrows and mallards without access to

preen oil did not show changes in feather-degrading bacterial load in comparison to control individuals. However, Cziráj *et al.* (2013) did find an effect of preen-oil availability on other bacteria, suggesting that perhaps preen oil is not specifically secreted to combat feather-degrading bacteria, but rather to inhibit other potentially pathogenic bacteria inhabiting the plumage and/or skin, such as *Pseudomonas*, *Staphylococcus* and/or *Salmonella*. Therefore, although a great deal of evidence from correlational studies supports a protective role for preen oil against feather-degrading bacteria, the clearest attempts to investigate the hypothesis (Cziráj *et al.*, 2013; Giraudeau *et al.*, 2013) failed to give it support.

(b) *Defence against eggshell bacteria*

Bacteria on eggshells have an impact on fitness, given that they may cross the eggshell barriers and affect the embryo, sometimes causing its death (Cook *et al.*, 2003, 2005b). Cook *et al.* (2005a; see also Ruiz-de-Castañeda *et al.*, 2011) suggested that incubation reduces bacterial growth on the eggshell by keeping the surface dry, lowering the possibility of trans-shell infection [but see contrasting results in Wang & Beissinger (2011) and Giraudeau *et al.* (2014)]. Another less-explored possibility is that incubation negatively affects bacteria because birds transmit preen oil to eggs through the preening of the brood patch (Martínez-García *et al.*, 2015).

At the interspecific level, the eggshell-bacteria load correlates negatively with hatching success (Soler *et al.*, 2012). Møller *et al.* (2010b) reported that hatching success correlates positively with uropygial gland size, but Soler *et al.* (2012) found the reverse. Both results were from correlative studies, meaning that causation is difficult to establish, and thus these studies lack the power to falsify the hypothesis. Vincze *et al.* (2013), in another comparative study, found a positive correlation between uropygial gland size and egg surface area, but a negative correlation with incubation period, thus giving mixed support to the egg defence hypothesis. Females usually have larger uropygial glands than males during breeding in hoopoes (Martín-Vivaldi *et al.*, 2009) and house sparrows (Pap *et al.*, 2010), which might be considered indirect evidence in favour of this hypothesis, but Vincze *et al.* (2013) found no such pattern across species. Galván (2011) found no relationship between uropygial gland size and hatching success in the great tit.

To summarize, the relationship between uropygial secretion and hatching success is still unclear. In the hoopoe, application of protease to eggs catabolised the antimicrobial peptides in the preen oil, but this effect was not observed in starlings (Soler *et al.*, 2008). This treatment led to a higher growth of eggshell bacteria and an almost significant effect on hatching success. But later studies gave little or no support to this hypothesis. Giraudeau *et al.* (2014) blocked access to preen oil in incubating mallards, and found no effect on bacterial growth on eggs. Martín-Vivaldi *et al.* (2014) performed a similar experiment in hoopoes and found that the microbial community varied in eggshells as a

consequence of blocked access to preen oil, but they failed to find an effect of such changes on egg hatching success. Therefore, the evidence that preen oil has a function against eggshell bacteria is still insufficient.

(c) *Defence against fungi*

Preen oil can also contain fungicides (e.g. Pugh & Evans, 1970). For example, preen oil of Pelecaniformes contains dimethyloctan, which inhibits fungal growth *in vitro* (Jacob *et al.*, 1997). In the dark-eyed junco (*Junco hyemalis*), linear n-alcohols, which show antimicrobial and antifungal activity, are one of the main components of preen oil (Soini *et al.*, 2007). Bandyopadhyay & Bhattacharyya (1999) removed the uropygial gland in chickens (*Gallus gallus domesticus*), reporting that this glandectomization increased the growth of most fungi found on the skin. In a set of additional *in vitro* experiments, they found that different components of the preen oil inhibited the growth of several skin fungi. Therefore, preen oil appears to have anti-fungal properties, but this function has received limited attention.

(d) *Defence against arthropods*

Chewing lice (order Phthiraptera, formerly Mallophaga) are a paraphyletic group of ectoparasites that feed mainly on feather keratin (Price *et al.*, 2003), and thus deteriorate the plumage with negative consequences on bird fitness (Clayton *et al.*, 1999). Consequently, it has been proposed that preen oil might have insecticidal properties (Jacob & Ziswiler, 1982). Moreno-Rueda (2010) found a negative correlation in house sparrows between uropygial gland size and number of feather holes, which then were interpreted as caused by chewing lice (Møller, 1991; Vas *et al.*, 2008), an interpretation recently questioned (Vágási, 2014). In fact, a recent study suggests that feather holes are caused by feather-degrading bacteria (Fülöp *et al.*, 2016), and thus, the findings of Moreno-Rueda (2010) could be interpreted as supporting a protective function against feather-degrading bacteria (see Section II.2a). In a comparative study, Møller *et al.* (2010b) found that species with a larger uropygial gland seem to harbour a higher genus richness of Amblycera chewing lice (a marginally significant effect). The reasons for this result remain elusive, as correlative findings may have several underlying explanations. The hypothesis of a function of preen oil against chewing lice has been experimentally tested only by Moyer *et al.* (2003), who found that preen oil in the rock pigeon kills chewing lice *in vitro*. However, using ablation experiments they found no *in vivo* effect of preen oil on the chewing lice load. The rock pigeon may not be the best model organism for this investigation, given that pigeons do not always possess a uropygial gland (Johnston, 1988), and that their main defence against chewing lice is the mechanical use of the beak (Clayton *et al.*, 2005). Therefore, there is no conclusive evidence that preen oil serves as an insecticide against chewing lice.

(3) Waterproofing

Given that preen oil is composed mainly of waxes, one of the first potential functions hypothesized was waterproofing (review in Elder, 1954). Comparative studies show that birds inhabiting aquatic habitats have larger uropygial glands [Johnston (1988); Galván *et al.* (2008); Møller *et al.* (2010b); Vincze *et al.* (2013); but see Montalti & Salibián (2000) and Soler *et al.* (2012) for two exceptions]. In addition, uropygial gland ablation experiments in ducks showed that plumage becomes more moist in glandectomized birds compared with controls (Elder, 1954). In a more recent study, Giraudeau *et al.* (2010b) blocked access to the uropygial gland in mallards and found greater water retention by the feathers. Moreover, water retention increased with time and as plumage condition worsened. Bakken *et al.* (2006, p. 568) argued that there is a 'lack of clear evidence that preen oil contributes to water repellency (except as it may maintain the feather structure of adults)'. However, they found that mallard ducklings covered by preen oil (or another oil) became less wet and lost heat more slowly than did controls (Table 1 in Bakken *et al.*, 2006). Therefore, this potential function would seem well supported by experimental and comparative studies. However, it is still unclear if preen oil improves waterproofing directly by providing plumage with a covering layer of lipids, or functions simply by maintaining feather structure, given that waterproofing worsened as plumage wear increased (see Bakken *et al.*, 2006).

(4) Drag reduction

Thomas *et al.* (2010) proposed that preen oil might reduce drag during flight, facilitating air flow. As they discuss, the use of waxes to reduce drag is very common in swimming organisms (Fish & Lauder, 2006). Moreover, Thomas *et al.* (2010) argued that this hypothesis is supported by the fact that preen-oil composition varies during migration and that some flightless birds such as species of Struthioniformes have no uropygial gland. Although this is an intriguing hypothesis, it has not yet been explicitly tested. The fact that preen oil composition varies during migration in some species may reflect different selective pressures that birds face over their life cycle (see Section II.6). One prediction of this hypothesis is that migratory birds should secrete more preen oil, and thus have larger uropygial glands. The only available data (Vincze *et al.*, 2013), however, show the reverse pattern: uropygial gland size is smaller in migrant species. A useful test of this hypothesis would be to examine the drag of birds with and without preen oil in a wind tunnel (Thomas *et al.*, 2010).

(5) Pollutant excretion

Many pollutants become concentrated in the adipose tissues of birds. Given that preen secretions are basically oily, they are a good vehicle for the removal of toxic substances from the body (reviewed in Salibián & Montalti, 2009). Several studies have reported that pollutants (including hydrocarbons

from petroleum, organochlorine pesticides, polychlorinated biphenyls, etc.) are secreted within preen oil (e.g. Johnston, 1976; Lawler, Loong & Laseter, 1978; Frank *et al.*, 1983; Yamashita *et al.*, 2007; Eulaers *et al.*, 2011; Jaspers *et al.*, 2013). However, the ecotoxicological role of the uropygial gland has received little experimental attention. Gutiérrez *et al.* (1998) exposed rock pigeons to the insecticide lindane (an organochlorine lipophilic xenobiotic) and found that this organochlorine accumulated in the uropygial gland, providing support for a role of the uropygial gland in expelling xenobiotic substances. Additional experiments are needed to understand if the uropygial gland functions to remove different types of natural toxins, or whether artificial pollutants are concentrated in the gland simply as a consequence of preen oil being composed of waxes.

(6) Interspecific communication

Birds must face predators and parasites, which, by reducing their fitness, constitute important ecological and evolutionary forces (Caro, 2005; Schmid-Hempel, 2011). Predators and parasites may detect their prey/hosts by olfaction (Zuk & Kolluru, 1998). Preen oil frequently includes volatile compounds that could be used by predators and parasites to detect birds. For this reason, birds are likely to develop adaptations to avoid detection. In this sense, preen oil may be under selection to be deterrent, cryptic, or allow camouflage.

It has long been known that uropygial secretions serve as a predator deterrent in hoopoes (family Upupidae; see Elder, 1954), which expel a malodorous uropygial secretion against potential predators during an encounter (see Burger *et al.*, 2004). Table II in Dumbacher & Pruett-Jones (1996) lists other species whose malodorous smell derives from uropygial secretions. However, to date there is only anecdotal evidence for this possible predator-deterrence function of preen oil (e.g. Ligon & Ligon, 1978) and experiments are needed.

Uropygial secretions, spread over the entire plumage, could also serve to make birds unpalatable. Interestingly, Møller, Erritzøe & Nielsen (2010a) found that goshawks (*Accipiter gentilis*) avoid preying on bird species with large uropygial glands. The authors interpreted this to indicate that species with larger uropygial glands have fewer feather-degrading bacteria, and thus plumage in better condition and with improved flight capacity. An alternative explanation is that species with larger uropygial glands are less palatable, and were avoided by goshawks for that reason.

The crypsis hypothesis of predator avoidance is better studied. Reneerkens, Piersma & Sinninghe Damsté (2002) [see also Kolattukudy, Bohnet & Rogers (1987) and Piersma, Dekker & Sinninghe Damsté (1999)] found that sandpipers (family Scolopacidae) change the composition of preen oil during incubation. Sandpipers usually produce monoester waxes, but during incubation they produce more diester waxes, which are less volatile. Reneerkens *et al.* (2002) proposed that diester waxes increase crypsis in the nest, reducing the detection of nests by olfactory-guided predators such as mammals. Reneerkens, Piersma & Sinninghe Damsté (2005) showed that dogs were less likely to detect objects

covered by diester than by monoester preen oils. In addition, diester preen oil was secreted mainly by the incubating sex in sandpipers with uniparental incubation, and by both sexes in species with biparental incubation (Reneerkens *et al.*, 2007a). Similarly, mallards in eclipse plumage (moulting their flight feathers, and thus at higher risk of predation) secrete lower quantities of short-chain fatty acids and increased levels of longer-chain fatty acids with less volatility (Kolattukudy, Bohnet & Rogers, 1985).

A related hypothesis that preen oil functions in camouflage, was proposed by Soini *et al.* (2007). These authors found that the main component of the preen oil of the dark-eyed junco during breeding is linear n-alcohols. This type of volatile is typically found in leaves (Vioque & Kolattukudy, 1997), thus Soini *et al.* (2007) suggested that preen oil could blend with environmental odours, making nests or birds less detectable by predators. There have been no experimental tests of this hypothesis.

As for predators, chemical cues may be a source of information for parasites. Some studies have reported that preen oil may attract parasites such as *Culex* mosquitoes (Russell & Hunter, 2005), black flies (Simuliidae; Fallis & Smith, 1964; Bennett, Fallis & Campbell, 1972), or haematophagous mites (*Dermanyssus gallinae*; Zeman, 1988) (review in Rajchard, 2007). Given the negative effects of parasitism, preen oil could be selected to become cryptic, provide camouflage, or even to act as a repellent against odour-oriented parasites. Recently, Magallanes *et al.* (2016) found that house sparrows with large uropygial glands are less likely to be infected with haemosporidians, and suggested that this was a consequence of a possible repellent effect of preen oil on haemosporidian vectors (haematophagous diptera). By contrast, Allan, Bernier & Kline (2006) and Martínez de la Puente *et al.* (2011) found no attractive or repellent effect of preen oil on dipteran parasites.

(7) Intraspecific communication

Birds engage in intraspecific communication in several contexts such as parent–offspring relationships, mating, and competition. In such communication, birds use different channels to transmit information, with the visual channel the most used and studied. Given that preen oil is spread onto the plumage, and absorbs different wavelengths of light (Reneerkens & Korsten, 2004), it has been suggested that preen oil may influence plumage colouration (Piersma *et al.*, 1999). In addition, although birds are typically considered microsmatic (Roper, 1999), many experimental studies show that olfaction is an important means of communication in birds (reviews in Hagelin, 2007; Hagelin & Jones, 2007; Rajchard, 2007; Balthazart & Taziaux, 2009; Caro & Balthazart, 2010). Given that uropygial gland secretions include a number of volatile compounds that may be considered potential semiochemicals [reviewed in Campagna *et al.* (2012); see also Rajchard (2007) and Soini *et al.* (2013)], it has also been proposed that they may function in odour-mediated intraspecific communication.

(a) Colour-mediated intraspecific communication

Colouration of bird plumage is mainly the result of pigments embedded in feathers and the structural arrangement of the layers of keratin (review in Hill & McGraw, 2006). Pigment deposition as well as layer structure are determined during the moult. However, the colour of fully grown feathers may be altered cosmetically [reviews in Montgomerie (2006) and Delhey, Peters & Kempnaers (2007)], one of the main cosmetics in birds being uropygial gland secretions. Preen oil is coloured in several species (Table 1 in Delhey *et al.*, 2007). Therefore, by applying preen oil, birds may change the colour of their plumage, as for example in the greater flamingo (*Phoenicopterus roseus*) where the pink plumage is produced by carotenoids. Amat *et al.* (2011) found that the preen oil of this bird contains carotenoids that when applied to the feathers make feather colouration more intense. More colourful flamingos had a higher breeding success.

Pigmented preen oil might affect bird colouration in other ways. Reneerkens & Korsten (2004) found that preen oil produced by red knots during breeding absorbs more light. However, plumage reflectance was not altered by the addition of preen oil. Delhey *et al.* (2008) examined the optical properties of preen oil in 51 species. Application of preen oil generally reduced plumage brightness, but only to a degree not detectable by birds. Delhey *et al.* (2008) therefore concluded that preen oil does not alter colouration in birds. By contrast, Surmacki (2008; also see Surmacki & Nowakowski, 2007) found that preen waxes affected the colour of the feathers of great tits (decreasing brightness and changing hue). Pérez-Rodríguez, Mougeot & Bortolotti (2011) found that preen oil reduces plumage brightness, but increased UV hue and yellow chroma to a degree perceptible by the birds. These contrasting results may have several explanations, but the most clear confounding factor is that preen-oil composition varies with season (e.g. Haribal *et al.*, 2005). Therefore, it is possible that preen oil collected outside the mating season has no effect on colouration.

A number of studies on live birds provide additional evidence for a cosmetic function of preen-oil. Galván & Sanz (2006) found a positive correlation between plumage brightness in great tits and uropygial gland size, while Moreno-Rueda (2016) found a relationship between bib colour saturation and uropygial gland size in house sparrows. In nestling tawny owls (*Strix aluco*) preen oil was shown experimentally to reduce the brightness of the bill (Piault *et al.*, 2008); when preen-oil production was inhibited by the inoculation of an antigen [lipopolysaccharide (LPS) from the cell wall of *Escherichia coli*], bill brightness increased. López-Rull, Pagán & Macías García (2010) blocked the uropygial gland papilla in house finches and found that this caused their carotenoid-based colouration to become less red, thus decreasing plumage ornamentation. Application of preen waxes to museum skin specimens confirmed that preen waxes altered colouration in this species.

Preen oil might also affect colouration indirectly throughout its effect on feather-degrading bacteria (see Section II.2a). Feather-degrading bacteria degrade white

feathers more easily (Goldstein *et al.*, 2004; Gunderson *et al.*, 2008; Ruiz-de-Castañeda *et al.*, 2012; but see contrasting results in Grande, Negro & Torres, 2004). Therefore, the size of white spots or patches could be honest signals of anti-microbial capacity of the preen oil in males that females could use to identify high-quality mates. In accordance with this idea, Moreno-Rueda (2010) found a positive correlation between uropygial gland size and the size of the white wingbar in house sparrows. Similarly, Ruiz-Rodríguez *et al.* (2015) predicted that the ornamental elongated throat feathers in male spotless starlings should be more susceptible to degradation by bacteria, and thus this ornament specifically signals individual resistance to bacteria. Confirming this hypothesis, bacterial damage was greater in the throat feathers of males than in the throat feathers of females or non-ornamental feathers. Feather degradation may also affect other plumage patterns: it has been shown that plumage bacteria disproportionately affect blue, red, and iridescent colourations (Shawkey *et al.*, 2007; Gunderson, Forsyth & Swaddle, 2009; Shawkey, Pillai & Hill, 2009; Leclaire *et al.*, 2014a), but any mediating effect of preen oil remains to be demonstrated.

Finally, Soler *et al.* (2014a) demonstrated that hoopoes colour their eggs brown using preen oil. They suggested that such colouration acts as a signal of antimicrobial capacity of the female, analogous to the signalling properties of blue eggs in other species (see Moreno & Osorno, 2003).

To summarize, several different hypotheses have been proposed in which preen oil is used by birds to alter their colouration. It seems clear that some species, such as flamingos, use preen oil to colour their plumage. Even where preen oil has no obvious colour, it may be used to modify plumage colouration. Further experiments in which the uropygial gland is blocked are necessary to determine whether preen oil inhibits the action of feather-degrading bacteria, and thus limits their effect on plumage colouration, and to investigate any effects of this on the attractiveness of the birds to mates.

(b) *Odour-mediated intraspecific communication*

Balthazart & Schoffeniels (1979) demonstrated that odour and olfaction play an important role in regulating sexual behaviour in mallards. In mallards, preen-oil composition differs between the sexes during breeding, but not outside the breeding season (Jacob, Balthazart & Schoffeniels, 1979), suggesting that diester waxes produced seasonally by females could act as a sexual pheromone. Other studies have found sex-related changes in preen-oil composition during the mating season (e.g. Haribal *et al.*, 2005; Zhang, Sun & Zuo, 2009; Mardon *et al.*, 2010; Whittaker *et al.*, 2010; Leclaire *et al.*, 2011; Tuttle *et al.*, 2014). However, seasonal changes in preen-oil composition may have other underlying causes (for example, crypsis; Reneerkens *et al.*, 2005). Moreover, although the uropygial gland secretes a highly variable number of volatiles (Soini *et al.*, 2013), bird odour is not exclusively produced by this gland as birds secrete volatiles potentially used in chemical communication through other

glands and even the skin (Hagelin, 2007). Nonetheless, odour derived from preen oil is found on plumage (Mardon, Saunders & Bonadonna, 2011). Whittaker *et al.* (2015) suggested that birds might leave odour footprints by bill-wiping, a behaviour in which they scrape their bill on the substrate.

Support for the hypothesis that the uropygial gland produces pheromones comes from Galván & Møller (2013), who found a positive correlation between olfactory bulb size and the size of the feather tuft present on the uropygial gland of several bird species, suggesting that the tuft could function to accumulate preen oil and slowly release its odour. Experiments removing the tuft could test this idea. Experimental studies offer stronger evidence of a role of the uropygial gland in sexual communication. Hirao, Aoyama & Sugita (2009) showed that control male chickens preferred female chickens with the uropygial gland *versus* glandectomized hens, but anosmic males showed no preference for hens with intact uropygial glands. Zhang *et al.* (2010) showed that female budgerigars (*Melopsittacus undulatus*) recognized males by odour in Y-maze experiments. They established that male preen oil differed from female oil mainly in higher concentrations of a number of alkanes and showed that females were attracted by the alkanes present in male preen oil. Similarly, spotless starlings and dark-eyed juncos show sexual differences in the composition of uropygial gland secretions, and these birds may discriminate the sex of conspecifics by odour – both males and females prefer male scent (Whittaker *et al.*, 2010, 2011a; Amo *et al.*, 2012).

If the uropygial gland is involved in sexual communication then (i) males are expected to differ in preen-oil composition, (ii) these differences should be correlated with male 'quality', and (iii) females should prefer the odour of males of higher 'quality' (see also Johansson & Jones, 2007). Whittaker *et al.* (2011a) found that smaller dark-eyed junco males secreted a less 'male-like' preen oil (with a composition more similar to that of females). However, females appeared to prefer the odour of smaller males. In a subsequent study, Whittaker *et al.* (2013) showed that male dark-eyed juncos with more 'male-like' preen-oil composition sired more offspring and suffered less cuckoldry. Moreover, males with a more 'male-like' volatile profile fledged more nestlings (own or extra-pair). These findings provide key evidence that preen-oil scent is under sexual selection.

Birds might signal by their odour their alleles for the major histocompatibility complex (MHC). Birds mate according to the composition of MHC alleles (e.g. Griggio *et al.*, 2011), which could be recognized by olfaction (Zelano & Edwards, 2002). A good candidate emitter is the uropygial secretion. Leclaire *et al.* (2014b) found a positive correlation for similarity between MHC alleles and chemical composition of the preen oil in the black-legged kittiwake (*Rissa tridactyla*). In addition, Leclaire *et al.* (2012) found that the components of uropygial gland secretion were correlated with genetic heterozygosity. Therefore, the basis for signalling of genetic 'quality' clearly exists and future studies should test whether it is used in mate choice.

Most studies analysing the volatile components of uropygial gland secretions have found that the amount and composition of preen oil varies with sex (e.g. Whittaker *et al.*, 2010; Amo *et al.*, 2012), age (Amo *et al.*, 2012), hormone levels (e.g. Whelan *et al.*, 2010), and among individuals (Mardon *et al.*, 2010; Whittaker *et al.*, 2010; Leclaire *et al.*, 2011), suggesting that it may convey potentially useful information during intraspecific interactions such as in individual recognition. That is, it seems clear that each bird could have an individual smell, but this does not imply that birds can use this as a signal. The available studies give mixed results. Grubb (1974) found that Leach's petrels (*Oceanodroma leucorhoa*) preferred the odour of their own nest in a Y-maze experiment, but not the odour of their own preen oil. Female dark-eyed juncos have been shown to reduce incubation time in response to foreign preen-oil odour (Whittaker *et al.*, 2009), suggesting that they can distinguish their own preen oil. Spotless starlings do not recognize their own offspring on the basis on the preen-oil odour (Amo *et al.*, 2014).

Several studies have analysed whether birds use odour for species recognition. Chickens exposed to an artificial hen preen oil odour were less stressed than control chickens (Madec *et al.*, 2008). Dark-eyed juncos discriminate the preen-oil odour of conspecifics *versus* heterospecifics (Whittaker *et al.*, 2011a). Zhang, Du & Zhang (2013) showed that uropygial scent allows species recognition in two sympatric waxwings (*Bombycilla* spp.). Soler *et al.* (2014b) tested whether odour affected egg-ejection behaviour in the magpie (*Pica pica*), a species parasitized by the great spotted cuckoo (*Clamator glandarius*). Although these researchers found that strong unnatural odours affected rejection behaviour, their trials with uropygial gland scent gave unclear results.

(8) Symbiotic mediation

Several authors have proposed diverse ways by which preen oil may affect bird fitness by an indirect effect on symbiotic and mutualistic organisms living on birds. This hypothesis may be considered a refinement of the hypotheses discussed above, in which symbiotic organisms have a special role. For example, feather mites (Acari, suborder Astigmata) are small arthropods that live inside bird plumage feeding on microbes, fungi, and particles trapped in the uropygial secretions (Proctor, 2003). Most feather mites seem to be commensal or mutualistic (Blanco *et al.*, 2001; Galván *et al.*, 2012). Galván & Sanz (2006) proposed that preen oil serves to maintain plumage in prime condition by favouring feather mites, thereby triggering a mite-mediated effect. They found a positive correlation between uropygial gland size, feather-mite load, and more colourful plumage in great tits. In a comparative study, Galván *et al.* (2008) found that bird species with larger uropygial glands also harboured higher loads of feather mites.

Soler *et al.* (2012) found that bird species with a higher feather-mite load had a lower eggshell-bacteria load (given that mites feed on bacteria). They predicted that birds with larger uropygial glands should harbour more feather mites and should show higher hatching success, but did not test

these predictions. By contrast, Galván & Sanz (2006) reported that great tits with heavier mite loads showed lower hatching success.

Both of these studies were correlational and therefore their conclusions may have alternative interpretations. For example, it could be speculated that birds with greater bacterial loads would have a larger uropygial gland (see Jacob *et al.*, 2014), and given that feather mites feed on bacteria, feather-mite loads would also be greater, leading to a correlation without causality. Pap *et al.* (2010) examined seasonal covariation between uropygial gland size and feather-mite load in house sparrows, finding that both traits follow reverse rather than positive covariation (see their fig. 1). Additionally, they found no effect of uropygial glandectomy on mite abundance. The available evidence thus does not support a mite-mediated effect.

Soler *et al.* (2010) proposed that preen oil might differentially promote growth of symbiotic bacteria that exclude pathogenic bacteria (i.e. those that damage plumage or eggs). However, at least in house finches, red knots, spotless starlings, and house sparrows the known anti-microbial properties of preen oil are direct (Shawkey *et al.*, 2003; Reneerkens *et al.*, 2008; Ruiz-Rodríguez *et al.*, 2015; Magallanes *et al.*, 2016), and there is no evidence of indirect effects mediated by symbiotic bacteria. The symbiotic-mediation hypothesis, nonetheless, deserves formal investigation, especially given that some studies have reported positive effects of preen oil on some bacteria and fungi (Pugh & Evans, 1970; Bandyopadhyay & Bhattacharyya, 1996).

In the hoopoe, the antimicrobial capacity of preen oil is due to the presence of symbiotic bacteria inhabiting the uropygial gland (mainly *Enterococcus faecalis*; Martín-Platero *et al.*, 2006; Martín-Vivaldi *et al.*, 2009; Ruiz-Rodríguez *et al.*, 2012, 2013; also see Law-Brown & Meyers, 2003). This was demonstrated with experiments in which injection of antibiotics into the uropygial gland reduced the production of preen oil (Martín-Vivaldi *et al.*, 2009) and changed its composition, with the resulting preen oil proving ineffective against bacteria (Martín-Vivaldi *et al.*, 2010). However, in other species such as the spotless starling, the preen oil shows antimicrobial properties against feather-degrading bacteria (Ruiz-Rodríguez *et al.*, 2015) despite the absence of symbiotic bacteria in its uropygial gland (Soler *et al.*, 2008).

Finally, it should be highlighted that not all chemicals found on feathers are secreted by the uropygial gland. The toxins present in the feathers of pitohuis (*Pitohui* spp.) or the tangerine-like odour of the crested auklet (*Aethia cristatella*) are not secreted by the uropygial gland (Dumbacher *et al.*, 1992; Hagelin, 2007). Both of these chemicals are known to have anti-ectoparasite properties (Dumbacher, 1999; Douglas, Malenke & Clayton, 2005). Jacob & Ziswiler (1982) suggested that some chemicals secreted by the uropygial gland might become active (as pheromones, defensive chemicals, etc.) only after their metabolic processing by bacteria inhabiting the plumage and skin.

III. PREEN OIL AND FITNESS: A REVIEW OF THE EVIDENCE

(1) Do we have evidence that preen oil affects bird fitness?

There is an implicit assumption common to all studies on the function of preen oil: uropygial gland secretions affect bird fitness. Therefore, intraspecific variation in secretion composition or quantity (frequently estimated as uropygial gland size) is presumed to correlate with bird fitness. Most studies discussed herein tested the mechanisms by which preen oil could impact fitness without considering whether preen oil actually affects bird fitness. This should be addressed before searching for the underlying mechanisms. For example, preen oil seems to improve plumage condition (although the exact mechanism remains to be clarified), but it is unknown whether intraspecific variation in uropygial functioning is related to fitness through plumage condition. Indeed, the final target of selection for improving plumage with preen oil could be one of several possibilities: enhanced insulation for thermoregulation, flight capacity for foraging, or flight ability for escaping from predators.

Salibian & Montalti (2009) addressed the fitness consequences of the uropygial gland in the rock pigeon, finding that glandectomization had no effect on survival over a period of several months. However, rock pigeons do not always possess a uropygial gland, and thus may not be the best model system for such studies. Elder (1954) also provided no clear information regarding the survival consequences of uropygial gland ablation in ducks. Møller *et al.* (2010a) reported higher risk of predation in species with small uropygial glands, but it is unknown whether a similar pattern exists at intraspecific level (i.e. the level at which natural selection acts).

The only experimental study to address this key question is Giraudeau *et al.* (2010a). Blocking access to preen oil in reproducing mallards resulted in mass loss, increased plasma lysozyme levels (related to infection), reduced egg size, and higher yolk carotenoid content. Reduced egg size is negative for chick survival (Krist, 2011), but increased carotenoid content is positive (Saino *et al.*, 2011), thus it is unclear whether breeding success was higher, unaffected, or lower in gland-blocked mallards. Clearly further studies are needed to determine the importance of the uropygial gland on bird fitness. It is important to understand whether preen oil affects breeding success (preferably measured as offspring recruitment) and/or survival prospects. It is surprising that there are few correlational studies analysing the relationship between reproductive success or survival with uropygial gland size, although Whittaker *et al.* (2013) showed that preen-oil composition is related to breeding success in dark-eyed juncos.

(2) The costs of preen-oil production

The assumption that the production of preen oil is costly lies at the centre of the idea that variation in preen oil impacts

fitness. However, information on these costs is scarce. Since preen oil is likely the product of natural selection, and different species and populations will differ in their selective pressures, the chemical composition of preen oil as well as the mechanisms underlying its costliness are likely to vary among species and individuals. All species will face production costs, physiological costs, and time and energy-budget costs for the application on preen oil to plumage and eggs. However, the underlying causes of intraspecific variation in uropygial gland size or preen-oil composition have received very little attention, perhaps due to the difficulty of measuring uropygial gland size or preen oil volume.

Given that preen oil is composed of waxes, which are energy-rich, it seems plausible that its production is energetically costly. However, there is little available evidence. Uropygial gland size is positively correlated with body condition in house sparrows (Moreno-Rueda, 2010; Magallanes *et al.*, 2016). Reneerkens, Piersma & Sinninghe Damsté (2007b) submitted red knots to different food-availability treatments. Food restriction subtly affected the capacity to produce diester waxes, which were presumably more costly to produce. Moreover, given that testosterone has an important role in regulating the activity of the uropygial gland (e.g. Whelan *et al.*, 2010; Whittaker *et al.*, 2011b), and is immunosuppressive, an immunological cost to preen-oil production is likely (Delhey *et al.*, 2007). Piau *et al.* (2008) and Moreno-Rueda (2015) showed that inoculation of the antigen LPS reduced the size (or growth) of the uropygial gland in tawny owls and house sparrows, respectively. Similarly, infection with coccidians reduces uropygial gland size in house sparrows (Pap *et al.*, 2013). Increased feather-degrading bacterial load in rock pigeons led to greater effort in preening, which resulted in reduced immune capacity (Leclaire *et al.*, 2015). Therefore, it seems that there is a trade-off between mounting an immune response and producing preen oil.

Finally, uropygial gland secretions may be involved in various ways in courtship, by acting as pheromones or in the signalling function of colouration patches (see Section II.7). Such signals could evolve as Zahavian signals, carrying a handicap that guarantees their honesty (Searcy & Nowicki, 2005). Here, the cost of preen-oil production could guarantee the honesty of the signal (Delhey *et al.*, 2007). Some uropygial secretions contain carotenoids, and there may be costs involved in obtaining carotenoids and in the uptake, transport, metabolism and allocation of these pigments.

(3) Trade-offs among different functions of preen oil

This review discusses many hypotheses on the role of uropygial gland secretions. Most of the proposed hypotheses remain to be validated, and some have been barely considered (e.g. the drag-reduction hypothesis). The hypotheses discussed are not mutually exclusive; it is possible that different functions of preen oil apply simultaneously in the same bird, meaning that there will be trade-offs between these different functions. For example, antimicrobial compounds may differ from pheromonal chemicals or colourants. Mating males

may therefore face a trade-off between self-maintenance and reproduction. Seasonal variation in preen-oil composition or uropygial gland size may thus reflect how the optimal resolution of such trade-offs varies over the year. These potential trade-offs between different functions of preen oil remain completely unexplored, and deserve investigation. Only then will we fully understand the evolution of this organ.

IV. CONCLUSIONS

(1) Preen oil probably contributes to plumage maintenance, but we do not know whether this is due to a reduction in mechanical abrasion or feather degradation by keratinophilic organisms. Many studies have analysed the effect of preen oil on feather-degrading bacteria, but evidence for a function against pathogenic bacteria is mixed, as preen oil has been demonstrated to be effective against bacteria *in vitro*, but not *in vivo*. Studies on action against dermatophytes are scarce and only descriptive. There is no evidence of a function against chewing lice, nor that preen oil improves plumage through a positive effect on feather mites.

(2) It is not clear whether preen oil helps to combat pathogenic bacteria on eggshells, thus improving hatching success, as the available evidence is inconclusive.

(3) It seems clear that preen oil improves waterproofing, although more biophysical studies are necessary to establish whether preen oil contributes to water repellency or simply improves waterproofing by maintaining feather structure.

(4) Preen oil may have a function in flight (the drag-reduction hypothesis), but this awaits detailed investigation.

(5) There is evidence that the uropygial gland may allow the secretion of pollutants, but it is unclear whether this is adaptive or simply a consequence of preen oil being composed of waxes.

(6) A predator-repellent effect of preen oil in some species has been gathered only from anecdotal reports. The possibility that preen oil makes birds unpalatable has not been analysed, although one study reported a relationship between predation and uropygial gland size. It seems well supported that preen-oil composition varies over the breeding cycle to allow crypsis in some incubating birds (Scolopacidae and perhaps in Anatidae). The hypothesis of a function in camouflage, however, awaits investigation.

(7) More studies are necessary to analyse a possible impact of ectoparasites as a selective force in the evolution of uropygial secretions.

(8) A growing body of work now shows that preen oil can change plumage colouration. Preen oil might potentially affect colouration through its effect on feather-degrading bacteria. That bacteria can impact plumage colouration is clear, but the idea that preen oil acts in this way to alter plumage colour remains a hypothesis.

(9) Several studies show important implications of volatiles of preen oil in the social communication of birds. However, much work remains to be done, particularly to demonstrate

that variation in preen-oil composition correlates with variation in mating success. Our understanding of the role of the different chemical compounds of preen oil in intraspecific communication is still poor. Its role in individual or species recognition remains controversial. There is no evidence that preen-oil functions in egg or nestling recognition.

(10) The impact of preen oil on fitness remains unknown. This information is fundamental to understanding its evolution.

(11) The costs or limitations to preen-oil production remain poorly known, despite their importance in understanding the evolution of uropygial gland secretions, especially in their hypothesised role in communication.

(12) Future studies should consider how trade-offs among different functions might drive the evolution of uropygial gland secretions.

(13) Our understanding of the uropygial gland is still in its infancy. Even for functions that are considered valid by most researchers, real evidence remains scarce.

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