Pollen analysis as a tool to advance avian research and inform conservation strategies

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Abstract

Ornithologists use a range of methods to advance understanding of birds and inform optimal conservation strategies. These include field methods (e.g. censusing; ringing), laboratory analysis (e.g. molecular taxonomy; microbiology), and computational approaches (e.g. population modelling; habitat suitability mapping). Indirect metrics can also be important, for example, ptilochronology as a proxy for food availability and dominance hierarchies, stable isotopes as a proxy for diet, and first egg dates as a proxy for phenological responses to climate change. Recently, the potential to use palynology – the study of pollen and spores – within ecology has become increasingly recognised, but there has been no appraisal of the utility of palynology within ornithological contexts. In this scoping review, we synthesise research undertaken over 70 years across all seven continents covering the many diverse ways in which studying pollen associated with birds can advance ornithological understanding and inform optimal conservation strategies. We critique the use of palynology both directly and as a proxy to study avian habitat use, migration ecology, diet and feeding strategies, and population dynamics, offering constructive suggestions for future research at the end of each thematic section. We also explore the potential for analysing pollen on birds (or within avian deposits such as guano) to answer wider questions, especially in relation to pollination and environmental reconstruction, thereby offering cross-disciplinary collaborative research ideas. We conclude that the potential for uniting ornithology and palynology within research and conservation context is as extensive as it is exciting and urge avian biologists to think broadly about new opportunities.

Key Words:

Diet and feeding, habitat use, migration ecology, ornithological methods, palynology

Introduction

In his seminal opinion piece "Think Small", Burtt (1999) encouraged ornithologists to "adjust their investigative scale downwards" to consider bird-microbe interactions and the use of chemical analysis within avian systems. In particular, he pointed out that, at the time, there was little work on avian microbiology (and what research did exist was published in non-ornithological journals) and that research using chemical analysis, for example of feathers, was in its infancy. In the quarter century since Burtt's call to action, avian microbiology research has increased substantially (e.g. Lucas and Heeb, 2005; Wither et al., 2005; Kent and Burtt, 2016; Goodenough et al., 2017a), while chemical analysis, especially Stable Isotope Analysis of bird feathers, is increasingly used to reveal information on diet (e.g. Becker et al., (2007)), habitat (e.g. Hobson et al., 2001; Evans et al., 2012), and links between migration and breeding success (e.g. (Goodenough, 2017b)). However, there is another way in which ornithologists could benefit from "thinking small" - increasing the incorporation of palynology into avian research.

Palynology is the study of pollen grains from seed-producing plants (angiosperms and gymnosperms), as well as spores produced by bryophytes, pteridophytes, fungi and algae. These tiny reproductive cells, measuring on average 30 microns, are protected from degradation by a tough sporopollenin outer layer known as the exine. The exine not only protects the reproductive elements of the pollen, but it is also structured and sculptured in ways that allow grains to be identified (usually to family or genus, occasionally to species) via visual observation under a high-power microscope. Pollen and spores that do not reach a recipient plant for reproduction can become incorporated into sediments, trapped within fur or feathers, or form part of biological products such as honey.

Traditionally, palynology has been used principally to study past vegetation and climate change (Tzedakis, 1994; Miyoshi et al., 1999; Langgut et al., 2011; Birks and Berglund, 2018; Camuera et al., 2019; Marden et al., 2022), as well as to quantify more nuanced environmental trends such as monsoonal patterns (Wan et al., 2022), summer temperature fluctuations (Huntley and Prentice, 1988), and variability in seasonal rainfall (Vincens et al., 2007). Palynology can also be applied to study other past events, such as faunal population dynamics (Davies et al., 2017), disease outbreaks (Peglar and Birks, 1993) and the history of human occupation (Gauthier et al., 2010; Magyari et al., 2012). In more contemporary contexts, palynology can aid understanding of the provenance or source of items, for example, analysis of pollen on bees and in honey can be useful to identify foraging areas (Jones and Bryant, 1992; Sniderman et al., 2018). Using pollen to provenance items is also used in forensic investigations, both in traditional criminal cases and in relation to wildlife crime, through linking the pollen assemblage retrieved from items to suspects or places relevant to the investigation (Mildenhall, 2006).

Recently, the potential to use palynology within contemporary ecological research or to support monitoring, management and conservation has been recognised (Rull, 2010; Buma et al., 2019; Goodenough and Webb, 2022; Siggery et al., 2023). For example, in a novel study in East Africa, Gillson (2015) used palynology to identify the role of elephants in habitat change, demonstrating that natural feedback loops ensured long-term stability in the absence of anthropogenic management. Other examples include: using pollen on moths to track long-range movement in the USA (Hendrix and Showers, 1992); quantifying spatiotemporal variation in the diet of Norwegian Reindeer (*Rangifer tarandus platyrhynchus*) (Bjune, 2000), and informing reintroduction of *Pritchardia aylmerrobinsonii* palms on the Hawaiian island of Kaua'i (Burney and Burney, 2007).

In this scoping review, we provide an overview of the ways in which palynology can be used to advance understanding of multiple aspects of avian biology - including habitat use, migration ecology, diet and foraging strategies, and population dynamics - drawing on past examples from across the globe and offering thoughts on potential and future applications. We consider instances where pollen can be used directly (e.g. analysis of pollen in faeces to understand diet) or where pollen is used as a proxy to make indirect inferences (e.g. analysis of pollen on feathers to provide information on the location of migratory routes and stopover sites). We also explore the potential for analysing pollen on birds (or within avian deposits such as guano) to answer questions outside ornithology – especially in relation to plant pollination and environmental reconstruction – thereby offering cross-disciplinary collaborative research ideas. We conclude that there is untapped potential for linking ornithology with palynology and highlight exciting opportunities for future study.

Methods

Literature was searched using Google Scholar and Scopus. Our only eligibility criterion was that research should have been presented in a peer-reviewed output or (exceptionally) an examined postgraduate thesis; to ensure the widest possible scope, no geographical or date range criteria were applied. Boolean searching with wildcards was used, with key search terms being “bird*” OR “avian” OR “ornithol*” AND “pollen” OR “palynolog*” to encompass any type of research involving birds and pollen. We also took advantage of citation chaining to locate additional papers not found through our initial searches by checking the reference lists and citations in each paper we found. All candidate papers were read to determine whether the study was within the scope of this review and allocated to thematic sections. Publication dates and study locations were harvested to produce graphics on temporal and spatial patterns. In this way, we followed the fundamental precepts of PRISMA (Page et al., 2021), but with increased flexibility and a wider scope. We considered this to be appropriate since our intention was produce a comprehensive scoping review written in thematic narrative style (to offer a critical and constructive analysis of existing literature, identify current gaps in understanding, and provide recommendations to practitioners and researchers), rather than to undertake any formal meta-analysis where absolute objectivity is required to ensure consistency and repeatability.

Initial Findings

There are many potential sources of pollen within ornithological research. Palynological investigation can involve sampling live birds, recently deceased birds, museum skins, avian deposits, or material associated with birds (Table 1). Within this broad range of possibilities, feathers are a particularly useful source of palynological material. Pollen grains, particularly those that have evolved for insect or animal dispersal, have an ornate exine that means they are readily retained by the barbules and hooks of contour feathers. Thus, although partial pollen loss will occur with preening (and complete loss with moulting), feathers can provide a “palynological time capsule” for ornithological research. Sampling feathers of live birds needs to be conducted carefully with appropriate regard to ethics to ensure there is no unintentional deleterious impact. Ideally, sampling should be undertaken as part of existing ringing activities without unduly prolonging handling time, either using a sterile saline swab or (under additional licence endorsement if necessary) by clipping a small piece of feather. Although some studies have used other methods to extract pollen from feathers, such as glycerine gel swabs (Calviño-Cancela and Neumann, 2015) or sticky tape (Fernández de Castro et al., 2017), these are not recommended in live settings due to the potential for sticky residue to be left on the feathers. Alternatively, rather than direct sampling of birds, palynological investigation can make use of avian deposits, which is a non-invasive approach that can yield high pollen counts. Moreover, in addition to the potential to isolate pollen from recent faeces, pollen can be preserved in fossilised faecal material (coprolites), which can offer a unique "window on the past" (van der Knaap, 1988; Rozema et al., 2006;).

Table 1: Sources of pollen for avian research

Sources of pollen for avian research	**Live birds**	**Recently deceased birds**	**Museum skins of birds**	**Avian deposits or other material**
Feathers	✓	✓	✓	
Foot crevices	✓	✓	✓	
Sticky encrustations on bills	✓	✓	✓	
Air sacs		✓		
Digestive tract / crop		✓		
Faeces / coprolites	✓			✓
Pellets	✓			✓
Sediment surrounding fossilised birds				✓
Crime scene artefacts from avian cases				✓

The research cited in this review spans a 75-year period between 1959 and 2023 (Figure 1) - although there is a clear temporal trend within this date range with more papers being produced per year in later years - and is collated from studies undertaken in 25 different countries across all seven continents (Figure 2).

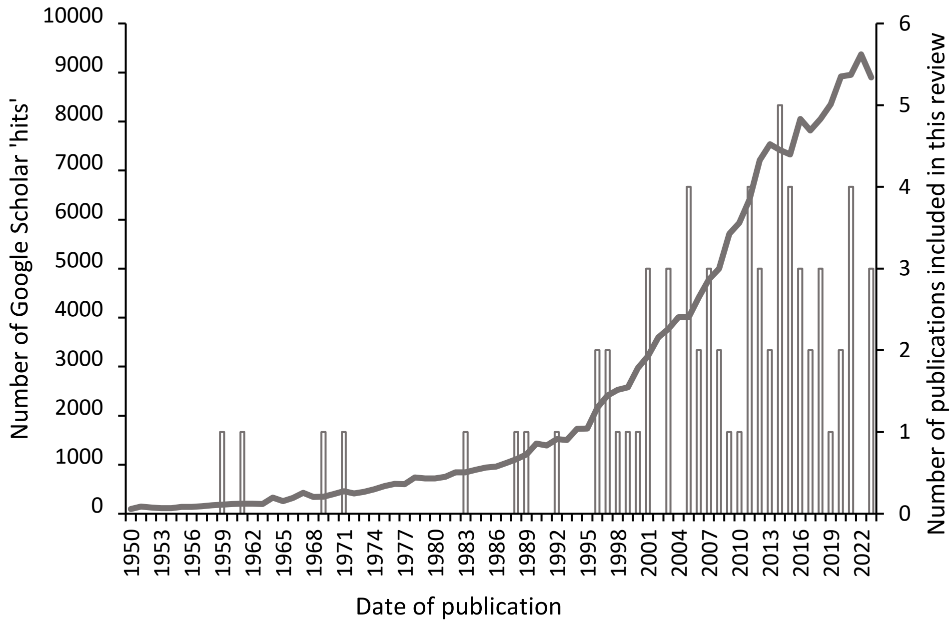

Figure 1. Temporal trend in publication of ornithological-palynological research from 1950 to 2023. The overall number of 'hits' (left y-axis) is based on a Boolean search via Google Scholar for any use of 'bird' AND 'pollen' OR 'palynology' in English language publications for each successive 12-month period (total number of hits = 189,731). The temporal spread of detailed publications that combine palynology and avian biology cited in this review (right y-axis) has been manually compiled.

Figure 2. Research cited in this review was undertaken in 25 different countries spanning six continents, plus Antarctica which is governed through the multilateral Antarctic Treaty.

Thematic Discussion

This discussion is divided into several thematic areas within avian biology: (1) habitat use; (2) migration; (3) diet and feeding strategies; (4) pollination as an ecosystem service; and (5) bird population dynamics. There are then two final sections to cover instances where it is possible to use avian-based pollen samples to advance research outside ornithology, firstly in relation to environmental reconstruction, and secondly in relation to establishing provenance of artefacts in criminal investigations.

Habitat Use

Pollen found on birds, particularly on feathers, can be a useful way of determining habitat use. Early work by Groenman-van Waateringe (1998) involved sampling single individuals of several species, including Little Owl (*Athena noctua*), Sparrowhawk (*Accipiter nisus*) and Hobby (*Falco subbuteo*) in the Netherlands. Pollen retrieval was limited but still constituted a useful proxy indicator of habitats used for hunting. For example, pollen from the Little Owl was dominated by grasses (Poeaceae), while the Sparrowhawk pollen assemblage was dominated by tree and shrub taxa. Development of this approach has led to some surprising results. Domínguez-Vázquez et al., (2021) assessed habitat usage of the Endangered Black-polled Yellowthroat (*Geothlypis speciosa*) around Lake Cuitzeo, Mexico. Palynological investigation suggested that birds were more terrestrial than had been expected for a seemingly obligate water-associated species, suggesting regular movement away from the lakeside. Pollen profiles also differed substantially between males and females, indicating intraspecific spatial resource partitioning. Surprising results were also found by Burhouse (2023) for Pied Flycatchers (*Ficedula hypoleuca*). This species is a woodland specialist and typically considered to forage for caterpillars in the canopy layer to feed their young (Goodenough, 2014), but pollen found on feathers of adults breeding in the UK was largely from field taxa, especially docks (*Rumex*) and grasses, with few instances of arboreal pollen. However, an important caveat for this research – and indeed any study where pollen is being used as a proxy for habitat use or behaviour – is that the relative timing of pollen production by different plant species could potentially confound how well a palynological profile on a bird reflects habitat use. This limitation, as well as other challenges and caveats, is explored in the penultimate section of this review paper.

It is also possible to quantify previous ranges or habitat use of extant species using fossilised material. Holm and Svenning (2014) considered shifts in distribution of multiple bird species across Europe over the last 180,000 years by combining paleontological and palynological evidence for Capercaillie (*Tetrao urogallus*). This obligate coniferous woodland specialist is now restricted to Scandinavia and upland areas of mainland Europe plus a small population in Scotland. However, 12,000 years ago Capercaillie were found in lowland areas of France, Belgium, Germany and Italy, despite pollen evidence that these areas had little woodland at this time (Huntley, 1988). There are two possible explanations: (1) habitat needs have changed over time; or (2) the species has a more general niche than commonly believed as current habitat *use* has become circularly confounded with habitat *needs.* Although the second possibility is speculative, this type of self-fulfilling prophecy when inferring habitat use has occurred for other taxa. For example, the Hazel Dormouse (*Muscardinus avellanarius*) was viewed as being dependent upon mature woodland (Bright, et al., 1996) but recent surveys using direct trapping has shown that it is actually found in scrub and hedgerows (Ehlers, 2012; Phillips et al., 2022). Such insights can have important implications for conservation, especially in relation to informing appropriate habitat management.

Analysis of fossil evidence can also allow the habitat that would have been used by extinct birds to be profiled. For example, fossilised avian footprints and feather impressions were found by Mansilla et al., (2012, 2014) on King George Island, Antarctica. These were created by ancient Eocene birds including *Gruipeda*, *Uhangrichnus* and *Avipeda* around 55 million years ago. A separate paper that considered pollen and spore evidence of the same geological formation (Poole et al., 2005) allowed the vegetation of that location during the Eocene to be reconstructed, thus providing information on the habitat use of these ancient avian species.

Potential and future opportunities: Although very few studies have used pollen to establish species-habitat interactions, palynology has considerable potential for such research. It is comparatively low-cost (although lab process time needs to be considered) and largely non-invasive, especially in relation to fieldwork-intensive methods such as radio tracking and colour ringing (Domínguez-Vázquez et al., 2021). It can be especially useful for researching cryptic, nocturnal or disturbance-sensitive species that can be challenging to study using more traditional survey methods, as well as for the study of microhabitat use such as specialisation in different woodland strata or use of different field margin types in agricultural landscapes. Palynological profiling of pollen on feathers of museum specimens can also reveal past habitat use by birds now extirpated or extinct, thereby providing information that would otherwise be unavailable (Oniki-Willis et al., 2020; Johansson et al., 2021).

Migration Ecology

Avian migration ecology is notoriously hard to study. In some cases, ringing recoveries are so low in parts of a species' migratory range that very little information can be elucidated. For example, there are more than a million ringing records of Willow Warbler (*Phylloscopus trochilus*) in the UK, but only 16 ringed birds have been recovered on wintering grounds in Central West Africa (Wernham et al., 2002; Robinson et al., 2023). Although modern tracking technologies can increase the quantity and quality of movement data, many species are too small to be fitted with a GPS transmitter (Bridge et al., 2013). Moreover, while geolocators (miniature data loggers that record and store light information to allow approximate latitude and longitude to be calculated) are sufficiently lightweight to be attached to any bird, they can only be used for species where most individuals reliably return to the same location each year so that devices (and data) can be recovered (McKinnon et al., 2013; Geen et al., 2019).

Against this background context, pollen found on feathers of migratory birds, or within sticky encrustations on the bill, can be a useful tool in the identification of stopover sites or wintering grounds, especially for small species that are challenging to otherwise study. This palynological possibility was initially mooted by Ash (1959) and Ash et al. (1961) who observed pollen on birds arriving in Europe after spring migration, and empirically tested by Laursen et al., (1997) who studied migratory birds captured in Denmark. Pollen was extracted from nectar-rich sticky encrustations near the base of the bill. For five of the species studied – Willow Warbler, Chiffchaff (*Phylloscopus collybita*), Blackcap (*Sylvia atricapilla*), Lesser Whitethroat (*Curruca curruca*) and Garden Warbler (*Sylvia borin*) – the pollen profile was dominated by Eucalyptus (*Eucalyptus* spp.) and Citrus (*Citrus* spp.) There were hints of some differences in pollen profiles between bird species, but low sample sizes (14 samples) precluded meaningful analysis. Wood et al. (2014) developed this approach for the same warbler species (minus Lesser Whitethroat) as birds made landfall in the UK. Based on analysis of 113 samples, 19 plant taxa were identified. The two short-distance Mediterranean migrants (Blackcap and Chiffchaff) carried more Eucalyptus pollen and less Citrus pollen than sub-Saharan migrants (Garden and Willow Warbler). There was also a significant genus contrast, with *Phylloscopus* warblers carrying more Eucalyptus but less *Prunus* spp. than *Sylvia* warblers. Although no pollen was detected from plant taxa sufficiently range-restricted to infer exact migratory routes, this research provided evidence of species-specific differences in stopover habitats.

Using a different approach, (Cecere et al., 2010) visually assessed pollen in the field on the bill and head/chest feathers of 14,844 migrating warblers during migration as they refuelled at stopover sites on Western or Central Afro-Palearctic flyways in Spain, Italy and Greece. This study did not identify taxa as no samples were taken but incidence of birds carrying pollen was high (up to 59%) and many individuals carried fresh pollen - likely to be recently acquired from that stopover site - as well as dried pollen likely to have been picked up at a previous stopover site or on wintering grounds. This was succeeded by more detailed research at one stopover site, the Italian island of Ventotene (Cecere et al., 2011), for Subalpine Warbler (*Sylvia cantillans*) and Common Whitethroat (*Sylvia communis*) as well as Blackcap and Garden Warbler. In total, 38 different plant taxa were found, of which seven were absent from the island. Similar work, primarily on Blackcap and Lesser Whitethroat, on stopover sites on Eastern Afro-Palearctic flyways in Turkey (Karlioğlu Kiliç et al., 2023) found very different pollen assemblages, with Chinaberry tree (*Melia*) and Steeplebush (*Spiraea*) being dominant or co-dominant alongside *Prunus*, with Eucalyptus and Citrus being absent. This suggests that differences in flyways can be detected through pollen carried by the same migratory bird species, albeit at a relatively coarse spatial scale.

In the above-mentioned studies, pollen is used as a form of indirect evidence; a proxy for a habitat and/or location a bird has visited previously. However, these studies are directly supported by empirical work at stopover sites in Italy and Israel, where primary observation of birds feeding on plants has been linked to avian palynological profiles. For example, pollen from the shrub *Anagyris foetida* in Israel was transferred onto three species of wintering birds that would ultimately migrate to northwest Europe, including Spanish Sparrow (*Passer hispaniolensis*), and four passage migrants including Ruppell's Warbler (*Sylvia rueppelli*) and Orphean Warbler (*Sylvia crassirostris*) (Haran et al., 2018). Similar work in Italy documented use of Wild Cabbage (*Brassica fruticulosa*) and Giant Fennel (*Ferula communis*) by Subalpine Warbler (*Sylvia cantillans*) (Schwilch et al., 2001).

Finally, a couple of avian palynological studies have considered aspects of migration not linked to geography. Evans (1969) studied life-history traits of Mealy Redpoll (*Acanthis flammea*), an irruptive migrant that breeds in the UK but departs for south Europe in harsh winters. He found that the amount of Birch (*Betula*) pollen in the spring, quantified from traps that collected pollen rain within woodlands, was a predictor of the magnitude of irruptive migration in autumn (low spring pollen levels > low autumn seed availability > increased irruptive migration). Finally, pollen recovered from air sacs in the lungs of Common Coot (*Fulica atra)* postmortem was used to separate migratory birds from sedentary birds in a partial migratory population (Tamisier pers. comm. cited in Laursen et al. (1997)).

Potential and future opportunities: Pollen on migrating birds can be a useful proxy indicator of wintering/breeding grounds, migratory routes or flyways, and stopover sites, as well as establishing the likelihood of irruptive migration and the migratory status of specific individuals in a partial migrant population. However, such work is not without challenge. A key issue is the loss of pollen on birds over time, which can limit the window in which to exploit the “palynological time capsule”. This is evidenced by the lack of taxa from wintering grounds being found in studies of long-distance migrant birds on their breeding grounds (Laursen et al., 1997; Wood et al., 2014; Burhouse, 2023). An additional challenge for any studies that try to determine specific locations of migratory routes or stopover sites (as distinct from general region or habitat) is that microscopic analysis of pollen usually leads to identification at the level of Genus or Family. This means that the spatial area that identified using pollen information is usually extensive, especially for taxa such as oaks that have extensive ranges at Genus level. One way to refine this would be using DNA identification of pollen grains to species level, which, in many cases, would might provide a more precise location. This approach would be especially powerful if metabarcoding was performed on all pollen (Bell, et al., 2016), with locations being refined to areas where all species co-occur. This has yet to be applied to birds, but there are several published studied using pollen metabarcoding to establish migration routes for Lepidoptera including two species of noctuid moth in Asia (Chang et al., 2018; Jia et al., 2021) and Painted Lady (*Vanessa cardui*) butterflies from Africa caught in the Mediterranean (Suchan et al., 2019). Such advances could allow identification of new stopover sites that are vital for species survival and ensure that such locations are appropriately protected to aid conservation efforts.

Diet and Feeding Strategies

Palynology provides an innovative method for studying the feeding strategies and diet of birds, with pollen being isolated from feathers, sticky encrustations on the bill, or from faeces or pellets. In some cases, the aim of such research is simply to provide baseline understanding of the diet of an extant species, especially if that species is rare, cryptic, or otherwise hard to study. For example, Moe (2018) examined faeces of Wigeon (*Anas penelope*) at Lake Mannavatn, Norway, to better understand the relative dietary importance of aquatic and terrestrial plants after direct field observation proved challenging. This revealed surprising reliance on woody species, including Willow (*Salix*) and Heather (*Calluna vulgaris*). Meanwhile, Horrocks et al. (2008) analysed pollen from the faeces of the Kākāpō (*Strigops habroptilus*), a Critically Endangered flightless nocturnal parrot from New Zealand. They showed that the species has a wide dietary niche and is a versatile feeder, consuming woody species, grasses, ferns, mosses and liverworts. The authors concluded that their findings were positive from a conservation perspective, as diet is not likely to be a limiting factor in survival.

Pollen analysis can also be used to profile the diet of extinct species, where no other study methods are available, or examine change over time. For example, James and Burney, (1997) examined coprolites of an extinct duck, *Thambetochen chauliodous*, on the Hawaiian Island of Maui, revealing that the birds were folivores specialising on ferns, a diet that is uncommon in extant species. This concept of comparing modern and past avian diets was further developed in an innovative study by Wilmshurst (2003) on the South Island Takahē (*Porphyrio hochstetteri*) in New Zealand. This Lazarus species was considered extinct in 1898, only to be rediscovered in 1948. The study not only determined current diet, but also demonstrated that diet has radically altered diet over time, as plants that are consumed now were not present in the palaeoecological record. In rare cases, palynological evidence can even answer questions about evolutionary origins. By analysing coprolites of two lineages of Turkeys from an archaeological context in the USA (1000 B.C to 500 CE), Nott (2010) showed past diet was dominated by cultivated plants and that birds were likely to have been domesticated, and thus *Meleagris gallopavo domesticus* not *M. gallopavo*.

In addition to providing a baseline understanding of diet, palynology can be used to analyse spatiotemporal variation. Moe and Bjune (2009) identified pollen in faeces of Willow Grouse (*Lagopus lagopus*) in Norway to quantify seasonal shifts in diet, finding that Birch and Willow were important immediately after snow-melt, before birds switched to use herbs as spring progressed. In an entirely contrary strategy, Austral Parrakeets (*Enicognathus ferrugineus*) in Argentina depend so much on pollen as a protein source in spring that they track *Nothafagus* seasonal flowering by moving altitudinally, thus keeping their diet temporally consistent (Díaz and Kitzberger, 2006). Bińka (2005) considered spatiotemporal variation in diet, this time for Barn Swallow (*Hirundo rustica*) in Poland to profile both spatial and temporal variation. Faeces were pollen-rich with >100 taxa represented overall. There were pronounced differences between nesting sites, with seasonal patterns superimposed upon these, either because birds were consuming different invertebrates at different times or, more likely, because the diet of invertebrate prey was seasonally idiosyncratic. Finally, research by Fernández-Jalvo et al. (1999) on pollen within pellets produced by Spotted Eagle Owl (*Bubo africanus*) in South Africa demonstrated it was possible to profile the habitat in which different individuals were foraging, thereby suggesting palynological approaches could be effective in determining individual home ranges.

Palynology can also be used to compare dietary niche between sympatric species, which can link to other life-history traits. For example, Borgella et al. (2001) studied pollen on the feathers of 21 species of Hummingbird in Costa Rica. Different species had differing levels of food plant specificity, and thus different dietary niche widths, with some species being highly specialised and others being generalist. This links to conservation as species that rely on fewer plants will need larger forest fragments to sustain populations. Grant (1996) also drew links between palynologically-informed understanding of avian diet, life history traits, and conservation in a study of Small Cactus Finch (*Geospiza scandens*) and Medium Ground Finch (*G. fortis*) on the Galapagos island of Daphne Major. Both species usually breed after the first annual rains, but Small Cactus Finches breed before rains in some years. Field studies suggested this only happened when Galapagos Prickly Pear Cactus (*Opuntia galapageia*) flowered early, and it was hypothesised females were benefiting from protein- and nitrogen-rich pollen for egg formation. Although both these bird species (and many others) make use of flowering plants during the peak flowering season (Traveset et al., 2015), use of Prickly Pear Catus by Small Cactus Finch (and not by Medium Ground Finch) early in the flowering season was corroborated by faecal analysis, which showed that >90% of pollen was digested (i.e. nutrition had been obtained from grains rather than grains simply passing through the digestive tract. The importance of pollen as a source of protein and nitrogen has also been shown for the Lesser Double-collared Sunbird (*Cinnyris chalybeus*) in South Africa (van Tets and Nicolson, 2000) and Lorikeets (*Trichoglossus*) in Australia, where birds preferentially consume pollen that is easily digestible so the intake needed to obtain the same protein and amino acid concentration is smaller (Gartrell and Jones, 2001; McDonald, 2003). Understanding the importance of pollen as a source of nutrition has implications for husbandry in captivity because while offering replacement (non-pollen) sources of protein could be effective, if they lack the correct amino acid composition this could cause ill health.

Potential and future opportunities: there is considerable potential to expand use of pollen to study avian diet, especially for work that informs conservation. This includes research that takes a comparative approach to assess differences in diet for sympatric species to understand niche partitioning and identify species that are vulnerable to habitat fragmentation by virtue of narrow dietary niches. There might also be opportunities to study wild individuals of species that are Critically Endangered to inform captive husbandry in the event that *ex-situ* conservation is needed. Linking diet to other aspects of life-history, especially breeding success, is also a potential research avenue, whereby the focus is on advancing understanding of causal mechanisms within functional ecology.

Pollination as an Ecosystem Service

Without pollinators many plants would not reproduce, and thus understanding of pollination processes is vital. Although wind or insect pollination are the most well-studied pollination strategies, vertebrates – including birds – can undertake this ecosystem service in return for nectar and/or pollen as a food source. Indeed, in the tropics, ornithophily can be the most prevalent pollination strategy (Valido et al., 2004; Wester and Claßen-Bockhoff, 2006; Cronk and Ojeda, 2008; Mayr and Wilde, 2014; Krauss et al., 2017). In temperate areas, ornithophily is much less common but is likely to be underestimated (Ortega-Olivencia et al., 2005; da Silva et al., 2014).

Studying the pollen on head feathers, within bill encrustations, or in faeces is not only useful in researching avian diet and feeding strategies – as discussed above – but it can also provide insights into the importance of pollination by birds from a plant or ecosystem perspective. Indeed, while field observations can confirm visitation rates of avian nectivores to plants, bird-based palynology is uniquely placed to confirm the success of pollen transfer to the bird as a vector. Analysis of pollen on birds has shown that species that are not obligate nectivores, and that are therefore non-specialist pollinators, are important in pollinating native species (Fernández de Castro et al., 2017). Moreover, birds are important pollinators of non-native plants, thereby demonstrating the importance of ornithophily in anthropogenically altered landscapes (Búrquez and Burquez, 1989; Rodríguez et al., 2015). Where landscapes are severely fragmented, pollination by highly mobile pollinators, such as birds, can be key to the survival of plants including the One-sided Bottlebrush (*Calothamnus quadrifidus)* in Western Australia (Byrne et al., 2007) and Japanese Camellia (*Camellia japonica*) in Japan (Abe et al., 2011; Abe et al., 2013).

Understanding avian pollinator relationships has important implications for applied conservation of birds and plants. Sekercioglu (2011) reports greater-than-average extinction rates for nectarivores, up to 46% in some instances, which could have important cascade effects for the plant community, especially in island or fragmented landscapes with limited functional redundancy. Moreover, research into pollination networks, by sampling pollen on birds, is important in avian conservation status assessments: where a bird species is the sole pollinator of one or more plants, increased protection might be appropriate (Wester and Claßen-Bockhoff, 2006; Calviño-Cancela and Neumann, 2015a; Calviño-Cancela and Neumann, 2015b; Nakanishi et al., 2020) because highly-specialised plants that have lost an exclusive mutualistic pollinator will struggle to reproduce (Aslan et al., 2014). A specific example is afforded by three endemic plant species on Hawaii in the *Clermontia* genus, which are characterised by curved, tubular flowers that co-evolved with curve-billed Hawaiian honeycreepers (Fringillidae), only half of which are now extant (Spiegel et al., 2006). In rare cases, such changes might move an ecosystem beyond a tipping point and towards ecological collapse.

It is not only contemporary pollinator relationships that can be profiled using palynology; past patterns can be quantified for extinct birds using museum specimens. Cox (1983) used scanning electron microscopy of multiple specimens to reveal a wide range of birds once pollinated the Hawaiian ‘ie’ie vine (*Freycinetia arborea*). With many of those species now extinct, Cox (1983) was the first to understand how pollination was being maintained when he noted a pollinator shift to the non-native Japanese White-eye (*Zosterops japonica*).

Potential and future opportunities: The study of ornithophily is inherently interlinked with research into avian diet and feeding strategies, due to the mutualistic nature of the relationship between bird pollinated plants and their pollinators. As such, any future research into either topic might result in important research insights in the other. For example, exploring changing pollination strategies by further analysing bird skins held by museums specimens could simultaneously explore the feeding habits of extant or extinct birds. Research into past ornithophily as an ecosystem service should not be restricted to museum specimens, but also consider using private collections. Work on live birds where information on life strategies can also be collected also offers opportunities where research insights could extend beyond pollination into food webs more generally. For instance, depredation of bird nests by omnivorous predators might be higher when other food sources fail in ways that could leave a palynological signature (for example, lower pollen loads or absence of pollen of important plant taxa on feathers or in nest material or other associated sediments). Such seasonal carry-over effects are challenging to study using traditional methods, especially when they involve multiple taxa.

Bird Population Dynamics

In the absence of direct data from bird censuses or ringing, there are very few proxies that enable modelling of past populations. Analysis of pollen retrieved from sediments associated with avian deposits has the potential to assist in understanding avian population dynamics, including long-term change over thousands of years. While pollen records themselves cannot usually reveal absolute population size, palynology can be a useful tool in establishing relative change in population (Gillson, 2015). For example, Murray et al. (2023) analysed sediments from lakes in North Dakota, USA, that have been used by breeding waterfowl for the last 13,000 years. They found that nitrogen in lake sediments was enriched by bird faeces, with levels being highest during wet summers when the local breeding population was especially high. This in turn led to increased levels of Amaranthaceae pollen in areas where the lakebed subsequently desiccated, as well as Ragweed (*Ambrosia*) pollen in areas that remained moist. The strong and significant positive correlation between these plant taxa and waterfowl in this example means that it would be possible to use the number of pollen grains of focal taxa in a radiocarbon dated sediment layer as an effective proxy for waterfowl abundance. Similarly, on the Galapagos island of Genovesa, Conroy et al. (2015) used the nitrogen stable isotope δN^{15} and resulting increases in Red Mangrove (*Rhizophora mangle*) pollen within sediment as a proxy for the number of breeding Red-footed Booby (*Sula sula*). This allowed change in seabird population dynamics to be modelled over a 400-year period.

In other contexts, palynology can assist in confirming the presence or likely absence of large avian herbivores. Wood et al. (2011) and Wood and Wilmshurst (2013) used palynology to document spatial extirpation patterns, and the eventual extinction, of several large flightless bird species from New Zealand, including Heavy-footed Moa (*Pachyornis elephantopus*), Upland Moa *(Megalapteryx didinus*), South Island Giant Moa (*Dinornis robustus*) and Coastal Moa (*Euryapteryx curtus*), in the period immediately following human settlement. Loss of *Sporormiella* fungal spores after Moa extinction was indicative of a 400-year megaherbivore gap at ecosystem level, which resulted in cascade effects including an increase in Red Mangrove abundance.

In some cases, analysis of pollen and spores can even be used to identify ecosystem engineers. For example, large colonies of seabirds transfer and concentrate nutrients from widespread feeding grounds to coastal cliff and inland breeding locations. This enrichment can alter primary productivity and, in turn, transform vegetation species richness and community composition (Wagner and Melles, 2001; Liu, X. et al., 2005; Boutin et al., 2011; Duda et al., 2021). Duda et al. (2020) used palynological analysis to demonstrate that guano-enrichment by Leach's Storm-petrel (*Hydrobates leucorhous*) in Newfoundland, Canada, engineered the ecosystem by facilitating the growth of ferns, grasses, and mosses, all of which became more abundant in the pollen record. Although initially an allogenic-mediated process via guano enrichment, subsequent autogenic feedback mechanisms (plant decay and nutrient recycling) meant this was a permanent change, being resilient to subsequent decline in the size of the seabird colony.

Potential and future opportunities: While palynology has not yet been used to quantify absolute population size (all the above examples rely either on response of vegetation to a change in the nutrient status of sediment due to changes in bird population size, or use palynology to detect presence/absence of a species) there is potential, if the right records are available, to use pollen to estimate avian population size directly. Anderson et al. (2011) explored the impact of tropical bird extinctions on plant density, where loss of an avian pollinator led to a decline in plant reproduction. This suggests that records of bird-pollinated taxa in the pollen record could potentially be used to estimate bird populations in tropical areas over time, especially in situations where there is an exclusive bird-plant relationship. Given the difficulty and expense of obtaining suitable pollen samples, a quicker 'win' may be sought by mining established international palaeoecological databases for pollen data. The Neotoma database (Williams et al. 2018) provides a repository for the Latin American, African and Indo-Pacific pollen databases, as well as (non-tropical) datasets including the Canadian Pollen Database, Pollen Database for the Russian and Far East, and European Pollen Database (Fyfe et al. 2009), which would provide international opportunities for research regardless of researcher location and without the laborious task of retrieval and identification of pollen. Calibration to known bird records (such as those held by the Organisation for Tropical Studies or the Institute for Bird Populations) would be important to test this opportunity before assuming the existence and strength of relationships between bird pollinated plant taxa and bird populations.

Environmental Reconstruction

While most of this scoping review paper has focused on the use of palynology to better understand avian biology, it is also possible to benefit from avian-created opportunities to gain palynological insights for the reconstruction of past environments. Analysis of past climate and environmental changes is important since this is integral to predicting how ecosystems may respond to future (anthropogenically accelerated) climate change (Birks and Berglund, 2018 and references therein). This section thus focuses on opportunities for ornithologists to collaborate with palynologists in answering broad questions relating to environmental change.

Most environmental reconstructions use sub-fossilised pollen grains and spores trapped within lake or bog sediments. Because these have been deposited chronologically in sediments that can be radiocarbon dated, it is possible to reconstruct how the vegetation and, by extension, the environment has changed. Guano offers a uniquely different depositional environment in which pollen, ingested and excreted by birds, is preserved with a stratigraphy similar to that of lake or bog sediments. For example, in Svalbard, Norway, Rozema et al. (2006) analysed guano below cliffs used by breeding Brünnich's Guillemots (*Uria lomvia*), Northern Fulmars (*Fulmarus glacialis*) and Black-legged Kittiwakes (*Rissa tridactyla*). The resultant pollen profile was effective in quantifying long-term vegetation change. In another example from Svalbard, guano from Artic Skua (*Stercorarius parasiticus*) became incorporated into peaty hillocks that have built up over 4,500 years as birds used these areas for territorial defence. As there are relatively few high-quality sites available for palynological analysis of sediment within the archipelago, profiling these guano-fed peaty hillocks presented a unique opportunity to understand climate change based on shifting patterns of vegetative species with different moisture tolerance values (van der Knaap, 1988).

In most cases, pollen is only preserved in damp conditions that provide the all-important anaerobic necessary for successful long-term preservation. It is for this reason that most palynological environmental reconstruction work occurs in wetlands, marshes, or areas with boggy features such as ditches or depressions. On occasion, therefore, ornithological deposits can provide rare opportunities for palynologists in locations that are otherwise challenging to survey, even when those deposits do not take on sediment-like properties. Indeed, bird faeces have been used as a source of pollen for environmental reconstructions of arid and semi-arid environments in Tarkastad, South Africa (Scott and Cooremans, 1992) and Negev Desert, Israel (Ramsay et al., 2016). It should be noted, however, that such work is not without challenge due to structural changes to pollen grains as they pass through the avian gut (and, in the case of avian insectivores, also through the invertebrate gut), which can affect appearance (Bińka, 2003). Given that digested pollen in faeces may have been subject to some structural changes that can cause identification difficulties, palynologists might choose to exploit another type of avian deposit: the pellets produced by owls, raptors and corvids. These can be useful in environmental reconstruction, although care should be taken to understand any underlying predator-prey cycles (Fernández-Jalvo et al., 1996).

Potential and future opportunities: Use of avian deposits to help reconstruct past environments is undeniably niche because it is restricted to instances where there are pollen-rich avian deposits in the absence of more traditional palynological opportunities. However, where there are pollen-rich ornithological deposits, the potential for research is exciting for ornithologists (to understand the pre-historical knowledge of ranges and habitats of birds) and for palynologists (to allow environmental reconstruction using novel deposits)..

Forensic Ornithology

Palynology can be useful in assisting in criminal investigations, including those involving birds via forensic ornithology. This is especially useful when wildlife crime involves species that are rare and/or legally protected. For example, pollen was pertinent to a case where a man was detained in the UK in the possession of two juvenile Eleonora's Falcon (*Falco eleonorae*) that were believed to have been imported illegally from a nest site in Mallorca. A search of the suspect's house revealed climbing kit including a used climbing rope, which was subject to palynological and sedimentological investigation. Both pollen and sediment indicated a profile that matched areas in Eleonora's Falcon habitat in Mallorca, and this evidence contributed to a successful conviction (Morgan et al., 2006). Similarly, Yadav and Dixit (2016) report a case where a suspect had outdoor clothing seized following an accusation of destroying a raptor nest. Comparison of pollen on these items and in relation to the nesting site were important evidence in the suspect's conviction.

Potential and future opportunities: While reported examples of ornithological crimes solved by palynology are relatively rare, the approach is an important part of the toolkit of crime scene investigators, which could be used in instances of illegal harvesting of birds, illegal transport (especially via the pet trade for parrots) and illegal release of previously captive birds into the wild.

<u>Challenges, limitations and caveats</u>

This review has explored some of the many ways in which pollen associated with birds (or bird deposits) can be used to answer research questions, but it is also important to highlight that there are also important challenges, limitations and caveats associated with this approach. Particularly important are taphonomic factors relating to pollen availability, adhesion and retention, and degradation that affect how well the pollen assemblage derived from birds reflects the actual vegetation of the area of interest, and thus how reliable bird-associated pollen is as a proxy for location, habitat or diet. These are explored below:

- **Differential pollen availability**: most plants produce pollen annually in a relatively narrow seasonal window (Glick et al., 2021). The availability of pollen for transference onto a bird is thus fundamentally determined not only by the presence of each plant species, but also by the timing of bird presence in relation to pollen production. Further decoupling could occur because different plant species vary in their pollen productivity, with some insect-pollinated flowering plants producing thousands of grains compared to the prolific production of wind pollinated trees, for example, which may produce millions of grains (Moore et al., 1991). Moreover, although pollen signature might link an individual bird to a particular habitat type, it doesn't necessarily indicate behaviour in that habitat. The combination of these factors means that the pollen profile on/in a bird could potentially be partial and/or misleading.

- **Differential pollen adhesion and retention**: pollen grains that have evolved for insect or animal dispersal have an ornate outer structure that means that they adhere readily to birds, whereas pollen grains of plants that are wind- or water-pollinated often lack this external ornamentation and have much lower adherence potential. Thus, in addition to issues relating to pollen the timing of pollen availability, it is important to consider differential pollen adhesion and retention within palynological interpretation.

- **Differential pollen degradation**: the degradation of pollen grains can hinder the process of identification or cause the complete loss of grains. For example, pollen from Yew (*Taxus*) and Willow (*Salix*) degrade rapidly (Havinga, 1984), such that even if pollen from these species was initially available and adhered to birds, the time lag between adherence and palynological processing might be problematic. The issues are magnified when lag times are extensive (e.g. in the analysis of pollen on museum specimens). Degradation can also occur in the avian gut, such that pollen within faeces might be an incomplete record of the pollen ingested.

In addition to considering the above taphonomic factors, it is also important to remember that the pollen associated with birds can be the result of indirect processes, and thus be representative of a regional pollen signal rather than a local pollen signal. For example, pollen in bird faeces can come from direct ingestion of pollen or via ingestion of invertebrate prey that had previously fed on plants (possibly in a different spatial area).

Conclusion

This review has synthesised research undertaken over 70 years, and all seven continents, to highlight the many diverse ways in which studying pollen associated with birds can advance ornithological research and inform optimal conservation strategies. Although there are undoubted challenges to be overcome when involving palynology in ornithological research, there are also exciting opportunities. The potential advances that would be afforded by identifying pollen on birds to species level using DNA metabarcoding are especially exciting, as this would greatly refine the taxonomic resolution of pollen data in relation to use of microscopy. In this way, use of pollen as a proxy for habitat use or to identify migratory routes, or to profile diet, would become much more detailed and thus more useful in both research and applied contexts.

Overall, we conclude that possibilities for using palynology with avian research and conservation, or for ornithologists to become involved with wider ecological and environmental research because of pollen associated with birds, are as extensive as they are exciting. We hope that this review, and especially the potential and future opportunities highlighted for each of the thematic areas, will encourage more ornithologists to include pollen when they follow Burtt's (1999) advice to "Think Small".

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