The ecology and taxonomy of the louse flies (Diptera: Hippoboscidae) and their role as vectors of avian disease

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DECLARATION

I declare that this thesis is entirely my own work, and except where otherwise stated, describes my own research. Where applicable, I have acknowledged the contributions of all co-authors in the “Author Contributions” section of each manuscript included in this thesis.

This work has not been submitted for any degree, diploma, professional qualification or other certificate at this University or elsewhere.

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Dedication

To citizen scientists and amateur naturalists everywhere

OUTPUTS

Chapter 2.1 is IN SECOND REVIEW (Acta Parasitologica) as **Wawman DC,** Bailey A, Fiddaman SR, Jones BJ, Johnson N, Smith AL. Clarifying the taxonomy of the Finch Louse Fly *Ornithomya fringillina* (Curtis) (Diptera: Hippoboscidae) – an analysis of morphotypes. (first submitted 11 March 2025)

Chapter 2.2 is IN REVISION as **Wawman DC,** Bailey A, Fiddaman SR, Smith AL. A first cytochrome c oxidase subunit I (COX1) DNA sequence of the Nightjar Louse Fly *Pseudolynchia garzettae* (Rondani, 1979) (Diptera: Hippoboscidae). (rejected after submitted 24 February 2025)

Chapter 3.1 is published as **Wawman, Denise C**. 2024. *Ornithomya biloba*, *Pseudolynchia garzettae* and *Pseudolynchia canariensis* (Diptera: Hippoboscidae): three new United Kingdom colonists and potential disease vectors. Medical and Veterinary Entomology, 38(2), 160-171. https://doi.org/10.1111/mve.12703
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The dataset for Chapter 3.2 is available on the Dryad website as **Wawman, Denise.** 2025. Louse Flies (Diptera: Hippoboscidae): United Kingdom, Republic of Ireland and Isle of Man: Citizen Science data: Part 1, Mapping [Dataset]. Dryad. https://doi.org/10.5061/dryad.zs7h44jkh

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(Ornithomya avicularia, Ornithomya biloba, Stenepteryx hirundinis and *Melophagus ovinus*, collected as part of the project, are currently in the DNA sequencing pipeline)

Up to date list, including species other than Hippoboscids, available at https://wellcomeopenresearch.org/gateways/treeoflife/browse?all=Wawman

Poster:
Royal Entomological Society "Impact of Extreme of Extreme Events Meeting 25 April 2024 Mapping the UK's flat flies (Diptera: Hippoboscidae)

Presentation:
BAVP ECR Online Conference 2-3 May 2024 Mapping the UK's Flat Flies

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ABSTRACT

Vectors play a major role in the transmission of disease, and anthropogenic changes leading to shifts in parasite ranges, phenology and host associations can modify the risk of disease outbreaks. The Hippoboscidae are a family of Dipteran ectoparasites of birds (louse or flat flies) and mammals (keds) that are known to vector diseases. The last major United Kingdom (UK) studies of these flies took place in the 1950's and 1960's, and some aspects of their taxonomy remain confused. Avipoxvirus (APV) is mechanically vectored by a range of arthropods, and causes seasonal outbreaks of avian pox in Dunnocks *Prunella modularis* which peak when most arthropod vectors are most active.

Data from over 4300 Hippoboscids, collected by citizen scientists, as part of my "Mapping the UK's Flat Flies Project", are used throughout this thesis to update our knowledge of their ecology, and avian pox is used as a model for exploring disease transmission.

I begin by attempting to resolve the confusion around the species in the genus *Ornithomya* by focusing on *Ornithomya fringillina*, using both morphometric analysis and DNA sequences to show that it has several morphotypes, and is arguably the same species as the North American species *O. bequaerti*. Additionally, I include a cytochrome c oxidase subunit I (COX1) DNA sequence for *Pseudolynchia garzettae*, which like many Hippoboscids has no previously published DNA sequences available to help with identification by "DNA barcoding".

Secondly, I describe the current biogeography and host associations of the UK Hippoboscidae. I provide evidence that three species, previously known only as vagrants, *Ornithomya biloba*, *Pseudolynchia canariensis* and *P. garzettae*, are now breeding here. I show major polewards range expansion of *O. avicularia* and *O. fringillina,* and range contraction of *O. chloropus* at the southern part of its range, since the 1960's, and explore the increasingly complex network of interactions between the Hippoboscidae and their host species which could facilitate the spread of disease.

I then switch my focus to the epidemiology of APV in Dunnocks, using data from a 15 year study of Dunnocks in my garden on Exmoor, to explore survival rates, the seasonality of the disease and to estimate its incubation period, from the timing of the growth of primary feathers in Dunnock fledglings. Finally, I combine these results with those from DNA sequencing, and the phenology of Hippoboscids on Dunnocks, to conclude that APV is

probably mechanically vectored by Hippoboscidae, and propose the use of Hippoboscidae as a non-invasive method for monitoring disease in wild bird populations.

Figure: A Dunnock *Prunella modularis* from the study population.

GLOSSARY

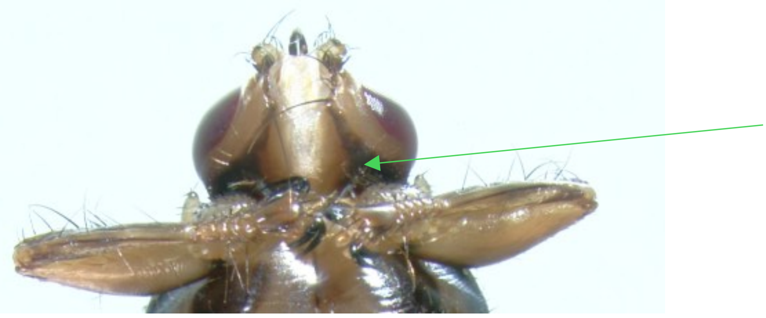
Adenotrophic viviparity: reproductive method in which eggs hatch within the female's uterus and the larvae are fed from special milk glands, until they mature when they are released immediately before pupation. A characteristic of the superfamily Hippoboscoidea.

Crataerina pallida: Swift Louse Fly, found on Common Swift *Apus apus* and occasionally on hirundines.

Euryxenous: of a parasite, having a wide range of hosts.

Flat flies: United Kingdom (UK) name for the group of Hippoboscidae found on birds, known as louse flies elsewhere in the world.

Gena: ventral area of the head of a dipteran, seen below the compound eye when a live insect viewed from the front. Dark markings in this area are considered important in distinguishing *Ornithomya chloropus* from other species in the same genus.



Dark marking
on the gena of
Ornithomya chloropus
(photograph Dave Brice)

Glossinidae: Tsetse flies, a family in the superfamily Hippoboscoidea.

Hippobosca equina: the (New) Forest Fly, a ked, found on horses and occasionally on cattle. Current UK range appears to be restricted to the New Forest and Dartmoor, but it used to be frequent throughout most of England and Wales with occasional records from Scotland.

Hippoboscidae: family of Diptera containing the louse (flat) flies and keds, and according to some authorities the bat flies.

Hippoboscoidea: superfamily of Diptera (two-winged flies) containing the Glossinidae (Tsetse flies), Hippoboscidae (louse/flat flies and keds) and Nycteribiidae and Streblidae (Bat Flies).

***Icosta minor*:** vagrant species of louse fly in the UK.

Keds: group of Hippoboscidae found on mammals.

***Lipoptena cervi*:** the Deer Ked, found on Cervids throughout the UK, population probably increasing with the increasing deer population.

Louse flies: worldwide name for Hippoboscidae found on birds, usually known as flat flies in the United Kingdom and Ireland.

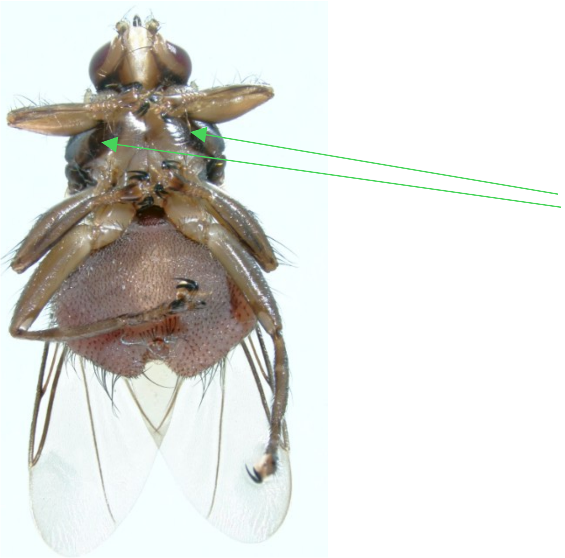
Melophagus ovinus: the Sheep Ked. Almost certainly extinct throughout the United Kingdom mainland following compulsory dipping for sheep scab. Still present on a few of the more remote Scottish Islands.

Neotype: a specimen selected to replace the existing holotype (or syntypes) when these have been destroyed or lost.

Nycteribiidae: family of bat flies found mostly in temperate regions.

Puparium: the final instar larval skin which hardens to protect the pupa inside it.

Mesothoracic basisternum: largest plate on the ventral thorax (also called mesobasisterum in some texts). Dark colouration in this area is an important feature for identifying *Ornithomya chloropus*.



Dark markings on the mesothoracic basisternum of *Ornithomya chloropus* *(photograph Dave Brice)*

Melophagus ovinus**:** the Sheep Ked. UK range now restricted to a few Scottish Islands where sheep dipping was not compulsory, believed extinct on the mainland.

Microtrichia: small hairs, in the *Ornithomya* species the arrangement of these hairs on the wings is an important means of identification for most species.

Monoxenous: of parasite, only using one host.

Nycteribiidae: family of bat flies, mostly found in the Old World regions apart from a few species in the Neotropics. Some authorities place the Nycteribiidae and Streblidae as sub-families within the Hippoboscidae.

Ornithomya**:** genus of mostly generalist louse flies, sometimes spelt Ornithomyia in older publications.

Ornithomya anchineuria**:** North American species, similar in appearance to *Ornithomya fringillina*.

Ornithomya avicularia**:** Bird Louse Fly or Common Louse Fly, the largest of the UK *Ornithomyae*, generalist, previously published UK range suggests a southerly distribution.

Ornithomya bequaerti**:** A small north American species, similar in appearance to *Ornithomya fringillina*. Named by Tsing-Chao Maa, when she split the species, in honour of Joseph Bequaert, an entomologist who believed that all the smaller *Ornithomyae* in the Northern Hemisphere were a single species!

Ornithomya biloba**:** Swallow Louse Fly, found on Swallows *Hirundo rustica*. Vagrant in the UK until recently.

Ornithomya chloropus**:** Grouse Louse Fly, a medium-sized *Ornithomya* species, previously published UK range suggests a northerly distribution.

Ornithomya fringillina**:** Finch Louse Fly, smallest of the UK *Ornithomya*, previously published UK range suggests a southerly distribution.

Ornithomya lagopodis**:** old name for *Ornithomya chloropus*.

Pseudolynchia canariensis**:** Pigeon Louse Fly, first reported from the United Kingdom in 2021.

Pseudolynchia garzettae**:** Nightjar Louse Fly, previously considered a vagrant in the UK.

Scutellar bristles: bristles on the scutellum, usually refers to the arrangement of those bristles in a line towards the posterior edge of the scutellum.

Scutellum: shield shaped, posterior part of the dorsal thorax.

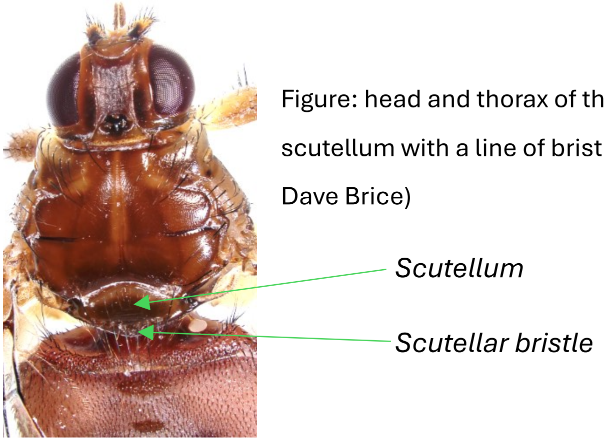


Figure: head and thorax of the louse fly *Ornithomya avicularia* showing the scutellum with a line of bristles adjacent to its posterior edge. (Photograph Dave Brice)

Stenepteryx hirundinis: Martin Louse Fly, also known as *Crataerina hirundinis*, found on House Martins *Delichon urbica* and occasionally on other hirundines.

Stenoxenous: of parasite, having a narrow range of hosts.

Streblidae: family of bat flies found mostly in tropical regions.

Syntype: each one of a group of specimens on which an original species description was based, as opposed to a holotype or single specimen.

Tergite: Hard plate (or sclerite) on the dorsal part of the abdominal segment of an insect.


Tergites of a male
Ornithomya fringillina
(photograph Dave Brice)

CHAPTER 1

Avian ectoparasites and vectored diseases: could the Hippoboscidae vector avipoxvirus?

CHAPTER 1: Introduction

Avian ectoparasites and vectored diseases: could the Hippoboscidae vector avipoxvirus?

Abstract

Birds are host to a range of arthropod ectoparasites including haematophagous species that are known to vector disease. Vectors are important in the transmission of disease but, despite birds being a well-studied taxon, most vectors of bird diseases are infrequently studied and not subject to long-term monitoring, which is increasingly important as climate change alters their geographical ranges and phenology, and hence their interactions with other species, potentially leading to an increased risk disease transmission.

The louse flies (Diptera: Hippoboscidae) are part of the superfamily Hippoboscoidea, which also contains the Tsetse Fly, the vector of African Sleeping Sickness. Research has shown that the louse flies vector some diseases, but other avian diseases with the potential to be vectored have not been studied: avipoxvirus is one such disease.

Introduction

Birds are a well-studied taxon, but their diseases and parasites are less frequently studied, this is in part due to the difficulties of sampling wild populations, compounded by the often low prevalence of the parasites, together with the sporadic nature of disease outbreaks and the difficulty in detecting them. There have been few studies of some vectors, and even for the relatively well studied groups such as ticks, there are few long-term datasets (Nuttall, 2021) which makes it difficult detect changes in biogeographic and host ranges which may be necessary to provide warnings of potential disease outbreaks.

As climate change, global travel and changing patterns of land use leading to human-wildlife conflict, increase the risk of emergent diseases, the study of wildlife diseases and their vectors becomes more important and requires collaboration between those working in different fields (WHO, 2022).

Avian diseases can jump species, for example, *Trichomonas gallinae* transferred to Greenfinches *Chloris chloris* in 2005 from pigeons or doves (Lawson, Robinson, et al., 2012), and some diseases seen in birds are zoonotic. Birds can act as reservoirs of these zoonotic diseases (Kurtenbach et al., 1998). These diseases include, protozoa, such as *Cryptosporidium parvum* a cause of diarrhoea (Wells et al., 2019), and bacterial infections such as *Borrelia burgdorferi* sensu lato (sl) which causes Lyme Disease (Newman et al., 2015), and multiple causes of human gastroenteritides, such as *Salmonella* spp., *Escherichia coli* serovars, *Campylobacter jejuni* and *C. coli*, (Benskin et al., 2009; Cody et al., 2015). Viruses accounting for 20% of all known viral zoonoses (Woolhouse et al., 2012), and 17% of the zoonotic RNA viruses, many of which are virulent emergent diseases in humans, such as the flavivirus, West Nile Virus (WNV) are also found in birds (Woolhouse & Brierley, 2018).

Parasites

By definition, parasites cause harm to their hosts, organisms which live on another species without causing harm being defined as commensals or, if both species benefit, symbionts. Parasites may have a range of direct and indirect effects on their individual hosts depending on their lifecycle, feeding habits and the anatomical site at which they feed. One example of a direct effect of an avian ectoparasite is that of feather mites, which may cause damage resulting in loss of thermal insulation or a reduction in the quality of flight feathers (Freed et al., 2008). Blood-loss from biting insects may cause decreased or delayed growth and death of nestlings from loss of nutrients, but the rate of fatalities varies widely between host-parasite systems. The larvae of the native fly *Passeromyia longicornis* were found to kill 81% of Forty-spotted Pardalotes *Pardalotus quadragintus* nestlings but far lower numbers of the sympatric Striated Pardalote *Pardalotus striatus* nestlings in south-eastern Tasmania, Australia (Edworthy et al., 2019). The introduced fly *Philornis downsi* was shown to have a greater effect on the fledging rate of one of Darwin's Finches, the Medium Ground Finch, *Geospiza fortis*, than on Galapagos Mockingbird *Mimus parvulus*. This was despite similar levels of infestation and the older Mockingbirds having a 40% lower haemoglobin titre in infested nests than those in nests which had been fumigated. The difference in survival was due to increased begging by the Mockingbird nestlings leading to increased provisioning, which did not occur in the finches (Knutie et al., 2016). However, the Hippoboscid fly, *Crataerina pallida*, a parasite of the Common Swift *Apus apus*, has been shown not to decrease the survival of nestlings (Walker & Rotherham, 2010) with no evidence of increased parental investment in response to parasite loads (Walker & Rotherham, 2011b). In the UK, the Dipteran, *Protocalliphora azurea*, a blow fly, is a nest parasite of birds, the larvae of which suck the blood of nestlings. Usually, there is little long-term physical damage to the nestlings from these larvae, but in California, a species of *Protocalliphora* has been shown to cause permanent deformity including bill deformities after feeding in the nasal cavity, and loss of digits (McClure, 1962).

Indirect effects of parasites include the trade-offs between growth and the need to mount an immune response against the parasite, with the weakest chicks least able to mount a strong immune response (Christe et al., 1998), the need to preen to remove ectoparasites and the energy used to do so (Freed et al., 2008), the risk of predation during preening or the energy expended in moulting to shed parasites (Clayton et al., 2014).

Vectors

If a parasite moves from one host to another it may have the capacity to transmit other organisms between hosts. Phoresy is a commensal relationship in which one organism, a phoront, uses another for transport or dispersal, mammals may act as phoronts dispersing plant seeds which stick to their fur, and the Hippoboscidae, which parasitise birds, do so by carrying various mites and lice (Adly et al., 2020; Corbet, 1956b; Hill et al., 1967; Lee et al., 2022), although there is evidence that mites in the genus *Myialges* are hyperparasitic feeding on haemolymph of their hosts (Goater et al., 2018; Hill et al., 1967).

Figure: Chewing louse attached to the abdomen of *Ornithomya chloropus*. (photographed by Dave Brice)

More importantly organisms, known as vectors, can transmit pathogens when moving between hosts, for example, birds carrying spores of *Phytophthora ramorum* on their feet between trees (Dadam et al., 2019). In order to be successfully transmitted by a vector, a pathogen needs to be able to attach itself to a vector in a place or form which will survive the journey. Mechanically vectored disease agents only need to survive the transfer, whereas other pathogens are able to reproduce within their vectors (biological vectors), and some species of protozoa and nematodes have complicated lifecycles involving primary and secondary hosts with amplification occurring in one or both, and the secondary host acting as a vector.

Most larger organisms have a protective external layer, such as a waxy cuticle of leaves, bark of trees, or the skin or scales of animals, which makes it harder for parasites and diseases to reach their vital internal structures. Parasites that are able to overcome these defences by biting or chewing are able to gain more resources than organisms that live on the surface, which are often forced to have a detritivore lifestyle feeding on dead skin cells and other waste. Diseases transmitted by biting parasites are able to bypass part of the innate immune system, as they are delivered directly into blood or interstitial fluid. While the biting parasites have the greatest potential to vector diseases, non-biting insects, such as the chewing lice in the insect order Phthiraptera (previously known as the Mallophaga), have the potential to act as mechanical vectors, transmitting parasites on their bodies between one host and another.

Biting bird ectoparasites fall within two classes of the phylum Arthropoda, the Insecta and Arachnida, and are reported vectors of a wide range of diseases, although the level of evidence provided varies, from being found on sick birds (Obanda et al., 2016; Surrey Dane, 1948) to experiments on live birds (Baker, 1956a, 1963; Cepeda et al., 2019; Ross, 1898). Koch's postulates, proposed in 1890, have long been considered the gold standard test for whether an organism causes a disease. These require that that the putative pathogen is present in every case of the disease, that it is not found in healthy organisms and that it can cause disease in healthy hosts (and ideally that it can be re-isolated from the newly infected hosts). Similar standards should apply to a putative vector. It is necessary to show that the pathogen is present within the vector and that it transmits the disease when transferred from one host to the next, as Ross did to first demonstrate that Malaria was vectored by mosquitoes (Ross, 1898). In addition, a true biological vector must naturally move between hosts, not just experimentally in laboratory settings.

However, animal experiments not only present the researcher with an ethical dilemma, but are also complicated and costly to perform. More recently researchers have used molecular techniques to explore the relationship between candidate vectors and disease, for example, confirming the presence of closely related DNA sequences in both vectors and a host species (Yeo et al., 2019).

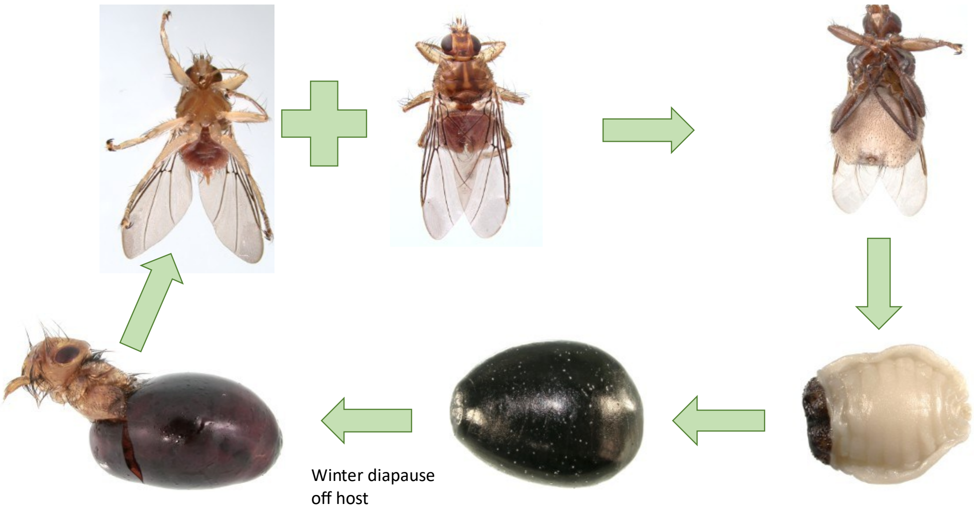
The Hippoboscidae

The Hippoboscidae are a family of dipteran obligate haematophagous ectoparasites of mammals (keds) and birds. They are part of the same superfamily, the Hippoboscoidea, as the Tsetse Flies, *Glossina* spp., that are competent vectors of Trypanosomes which cause African Sleeping Sickness in humans and animal trypanosomiasis. There are over 200 species worldwide (Dick, 2018), with a number of species currently being described from areas where they have not been previously studied in any detail, for example, *Ornithoctona zootherae* from southern Russia (Yatsuk et al., 2023), *Ornithomya strigilis* from the far east of Russia (Nartshuk et al., 2022), *Ornithomya helvipennis* from Southern Siberia (Yatsuk et al., 2024a), and *Icosta korzuni* from Vietnam (Yatsuk et al., 2024b). However, despite the increasing number of new species, many have no published DNA sequences available to aid their identification by researchers without expert knowledge of taxonomy wishing to study their roles are disease vectors.

The Hippoboscidae are generally divided into those that parasitise mammals (keds) and those that are found on birds (louse flies, generally known as flat flies in the United Kingdom and louse flies throughout the rest of the world) but this division is somewhat artificial as host switches have occurred on multiple occasions throughout their evolution and the phylogeny does not fully support the division (de Moya, 2019). For example, the genus *Ortholfersia* is found on Macropodidae (kangaroos) and the most closely related genus *Pseudolynchia* is found on birds, and *Struthiobosca struthionis*, a parasite of ostriches *Struthio* spp., sits within the subfamily Hippoboscinae, which are parasites of mammals.

The Hippoboscidae have an unusual lifecycle amongst Insects. They are viviparous (Hutson, 1984), which could possibly facilitate their ability to transmit infections, with prolonged maternal contact promoting vertical transmission. After her eggs are fertilised by a male, the female allows one at a time to enter the uterus, where the larva is fed from a specialised milk gland. The final instar larva is released on maturity and immediately the exoskeleton begins to harden to form a puparium (Hutson, 1984). The puparia of the Sheep Ked *Melophagus ovinus* remain tangled in the fleece but those of other species drop off the host and generally emerge the following year to seek out hosts. Some species such as the Deer Ked *Lipoptena cervi* and the Forest Fly *Hippobosca equina*, synchronise their emergence and can form swarms. Some species shed their wings after finding a host and others are dealate or have reduced, non-functional wings. Most louse flies die either with the death of their hosts – if they are unable to find another – or by being eaten by their hosts during preening.

Figure 1. The lifecycle of a louse fly. After her eggs are fertilised by a male, the female allows one egg at a time to enter the uterus, where the larva is fed from a specialised milk gland. The final instar larva is released on maturity and immediately the exoskeleton hardens to form a puparium. Most species in the UK undergo a winter diapause (photographs Dave Brice).



In the United Kingdom and Ireland there are 15 species in the family Hippoboscidae which occur naturally, of which three are keds, the Deer Ked *Lipoptena cervi* (found on Cervids, including Reindeer *Rangifer tarandus* and Moose *Alces alces* in other parts of Europe), Sheep ked *Melophagus ovinus* (found on sheep) and the Forest Fly *Hippobosca equina* (which is usually found on horses and occasionally on cattle) (Hutson, 1984). Another ked, *Hippobosca longipennis*, has been recorded as an accidental import on Cheetahs *Acinonyx jubatus* from Namibia in Dublin Zoo in 1982 (O'Connor & Sleeman, 1987). The other species are all bird parasites. Eight are breeding species and the rest (*Icosta ardeae*, *I. minor*, *Olfersia spinifera* and *Ornithophila metallica*) are vagrants (Chandler, 2024; Hutson, 1984; Wawman, 2024). Additionally, *Ornithophilia gestroi,* has been accidently imported to the UK twice: it was found on captive Red-billed *Leiothrix Leiothrix lutea* in

Yorkshire in 1965 and on Ring-necked Parakeet *Psittacula krameria* in 1975 at London Airport (Chandler, 2024; Hutson, 1984) .

The avian parasites in the group are divided between monoxenous and more generalist (euryxenous) species. Of the eight resident species in the UK, three species in the genus *Ornithomya* are generalist on a wide range of bird species, and individual flies are known to switch hosts (Corbet, 1955). A fourth species in the genus *Ornithomya*, *O. biloba*, which is monoxenous on Swallow *Hirundo rustica* and sometimes found on other hirundines has rapidly colonised the UK in recent years (Wawman, 2024). *Crataerina pallida* is monoxenous on the Common Swift *Apus apus* but is occasionally found on Hirundines, and *Stenepteryx hirundinis* (also known as *Crataerina hirundinis*) is found on House Martin *Delichon urbicum* and Sand Martin *Riparia riparia*. Two recent colonists are also monoxenous within the UK, *Pseudolynchia garzettae* on Nightjar *Caprimulgus europaeus* and *P. canariensis* on feral pigeon *Columba livia domestica* (Wawman, 2024) although both have a range of other hosts in other countries (Haeselbarth et al., 1966; Maa, 1969).

Until now, the most recent comprehensive studies of the ranges of the common resident species of louse flies in the UK and Ireland were done in the 1950's and 1960's. They used some specimens collected from a few sites at the time of the studies, but relied heavily on previous reports (Thompson, 1953, 1954a, 1954b, 1955a, 1955b), or museum specimens of varying ages, some of which were decades old (Hill, 1962a). A major taxonomic change within the genus *Ornithomya*, splitting *Ornithomya chloropus* from *Ornithomya fringillina* (Hill, 1962b; Smart, 1939), was not widely adopted amongst entomologists, making all records of *Ornithomya fringillina* prior to the mid-1960's uncertain, unless they are known to be those identified by a small group of entomologists who accepted the taxonomic split.

The Hippoboscidae as disease vectors

A wide range of pathogens have isolated from Hippoboscidae, but their roles as vectors have not been clearly established for most of these pathogens (Bezerra-Santos & Otranto, 2020). Keds have been studied more frequently than louse flies, because they infest livestock, and species such as *L. cervi* are more inclined to bite humans than other species. *Melophagus ovinus* has been shown to transmit Bluetongue virus (BTV) between sheep (Luedke et al., 1965). In other parts of the world, *Bartonella* spp. have been isolated from the all of the UK native species of ked, L. *cervi*, *M. ovinus* and *H. equina* (Dehio et al., 2004; Halos et al., 2004; Szewczyk et al., 2017), and although they have not been proven to be competent vectors of this gram-negative bacterium, *Bartonella schoebuchensis* has been shown to localise in the midgut of L. *cervi* and is thought to have a role in the aetiology of Deer Ked dermatitis, a human skin condition which occurs following a bite from a Deer Ked, due to an immune mediated response (a type IV delayed hypersensitivity reaction), rather than the response to a pathogen. However, as Deer Keds shed their wings after finding a host, it is highly unlikely that an individual fly could vector a disease unless by vertical transmission of the pathogen in the parasite. *B. schoebuchensis* has been shown to be vertically transmitted in *L. cervi* (de Bruin et al., 2015). Other pathogens, such as *Anaplasma* spp. and *Rickettsia* spp., (de Bruin et al., 2015) have also been found in Deer Keds. Infective larva of the filarial worm *Acanthocheilonema* (*Dipetalonema) dracunculoides* were found in *Hippobosca longipennis* on dogs in Kenya (Nelson, 1963) and the Camel Ked *Hippobosca camelina* has been shown experimentally to transmit an *Anaplasma* sp. from Camels to Rabbits (Bargul et al., 2021). Trypanosomes have also been shown to be vectored by Sheep Keds *Melophagus ovinus* but infection only occurs when the ectoparasites are ingested by their hosts (Baker, 1967; Hoare, 1923a, 1923b; Theodor, 1928).

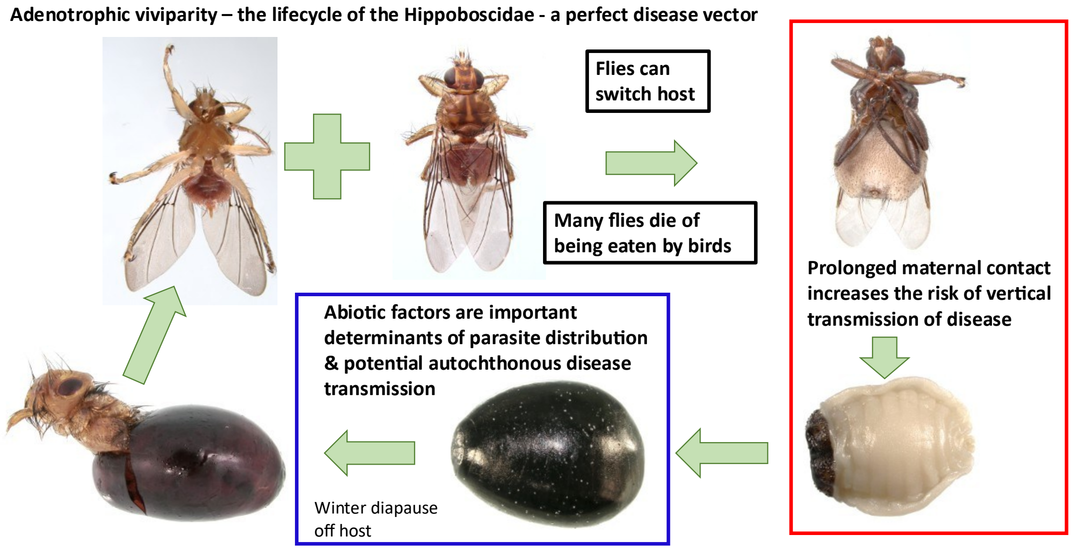
Most diseases vectored between birds by louse flies are either caused by protozoa, bacteria or enveloped RNA viruses, but the current evidence is often weak, for example, the flavivirus West Nile Virus, WNV, which was found in the louse fly I*costa americana* from WNV infected raptors (Farajollahi et al., 2005) and in an outbreak of disease caused by the Paramyxovirus, Newcastle Disease Virus, NDV, an unidentified Hippoboscid was considered a potential vector when found in association with NDV infected Laughing Doves *Streptopelia senegalensis* (Obanda et al., 2016).

The best evidence for the Hippoboscidae acting as vectors, is for species of avian haemoparasites and the early work is thoroughly reviewed by Baker (Baker, 1967). Bennet, working in Canada, described multiplication of *Trypanosoma avium* in hindgut of a species of louse fly identified as *Ornithomya fringillina* (Bennett, 1961, in Baker, 1976), a species which is no longer considered to be a North American species (Valerie Levesque-Beaudin, pers. comm.). *T. avium* has been shown to develop in crithidia in the mid-gut and hind-gut of *Ornithomya avicularia* and then to develop into infective metacyclic trypanosomes, and many wild caught individual louse flies are naturally infected and some birds became infected after ingesting infected parasites (Baker, 1956b).

Haemoproteus columbae, from an infected Woodpigeon *Columba palumbus,* was found to undergo sporogony in *Ornithomya avicularia* (Baker, 1957) and it was shown that *O. avicularia* was a competent vector, capable of maintaining the parasite in wild birds (Baker, 1963). Another species of louse fly, *Pseudolynchia canariensis*, only recently recorded from the UK (Harrow, 2021; Wawman, 2024), has been widely shown to transmit this parasite (Baker, 1957; Cepeda et al., 2019).

Several factors in the lifecycle of the Hippoboscidae could increase their potential for disease transmission. Prolonged maternal contact with the larva may increase the risk of vertical disease transmission, compared to other non-viviparous insects in which pathogens can only be transmitted transovarially and by external contact between the egg and the adult female during and after larviposition. Flies switch hosts (Corbet, 1956a): presumably either in search of a mate, or if their host dies; or in the example of nest parasites such as *Crataerina pallida* move between individual nestlings, adults and other nests (Walker & Rotherham, 2011a). Many Hippoboscids are ingested by their hosts while preening (Hutson, 1984) providing the route for transmission of pathogens such as trypanosomes (Baker, 1967).

Figure 2. Several factors in their lifecycle potentially could increase the risk of louse flies transmitting disease. Including prolonged maternal contact due to adenotrophic viviparity, switching host and being eaten by preening hosts. However, other abiotic factors that determine parasite distribution are also important determinates of the potential for autochthonous disease transmission (photographs Dave Brice).



Avian Pox

APV is an enveloped double-stranded DNA virus. It has recently been reclassified, becoming a genus, *Avipoxvirus*, with seven recognised species (ICTV, 2024). Fowl pox virus (FPV) *Avipoxvirus fowlpox* is most widely studied because of its impact on commercial poultry (Van Riper & Forrester, 2007). Many species or groups of related species of birds have their own strains of APV which vary in pathogenicity, but these may switch species (Buenestado et al., 2004; Fukui et al., 2016).

In the UK, APV has been recorded in wild birds since the 1900's (Harris, 1965) and in Dunnocks *Prunella modularis* since 1949 (Edwards, 1955). In 2006, virulent forms of Avian Pox appeared in Paridae in the UK (Lawson, Lachish, et al., 2012) and Corvidae in Japan (Fukui et al., 2016).

In the United Kingdom, endemic Avian Pox seems to occur with some degree of seasonality (Lawson, Lachish, et al., 2012), as does Paridae Pox in Great Tits *Parus major* (Lachish et al., 2012), however, researchers in Spain did not find any temporal variation in the prevalence of avian pox in House Sparrows *Passer domesticus* which occurred in about 3% of birds (Ruiz-Martínez et al., 2016).

APV can be transmitted by direct contact between birds, fomites and arthropods. It is known to remain viable on the proboscis of *Culex tarsalis* for up to 28 days (DaMassa, 1966). Proven experimental vectors of FPV are: mosquitoes *Aedes* and *Culex* spp. (Akey et al., 1981; Kligler et al., 1929), midges (Lee et al., 2017) Common Red Mite *Dermanyssus gallinae* (Huong et al., 2014; Shirinov et al., 1972) and Stable Flies *Stomoxys calcitrans* (Alehegn et al., 2014). The mosquito, *Culex nigripalpus* (Forrester, 1991) and fleas (Smits et al., 2005) are natural vectors of APV. Evidence suggests that all of these species are acting as mechanical rather than biological vectors (Carn, 1996).

A 15 year study of Dunnocks in Somerset, UK, found a temporal association between the presence of Hippoboscid flies of the genus *Ornithomya* and the peak of Avian Pox infections (Wawman, unpublished data), with the peak in avian pox lagging a few weeks behind the peak in louse flies. There is a similar temporal lag between peak mosquito abundance and peak prevalence of Paridae Pox (Lachish et al., 2011). There may be a causal association between Hippoboscids and avian pox in Dunnocks but it could be due to other factors such as the presence of other vectors or large numbers of immunologically naïve juvenile birds in the population.

Conclusion

There are large gaps in our knowledge of bird diseases and their vectors. The Hippoboscidae are known vectors of some diseases, with the potential to vector a large range of diseases, but the currently available data on their UK ranges and host distribution is based on work done in the 1950's and 1960's.

A comprehensive study into the role of the Hippoboscidae as vectors in the UK will first require a study to determine the species currently present in the region, their biogeography, host distributions and phenology. This may rule out certain Hippoboscids as vectors of certain diseases, for example, avian pox in Dunnocks is not expected to be vectored by *Crataerina pallida* which is normally found on Swifts, and other species which are found on Dunnocks may not share their ranges with that of disease outbreaks. Further studies will use molecular techniques, such as PCR, to look for pathogens in Hippoboscids, with an initial focus on avian pox.

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CHAPTER 2

Louse fly taxonomy

Introduction

In order to establish the relationships between potential vectors and their hosts it is first necessary to be able to define which vector species are where, when, and on which hosts. This requires the ability to identify both host and vector species. While the taxonomy of birds is largely fixed, apart from the definition of some subspecies and occasional splits into separate species, and they are generally relatively easy to identify, with comprehensive field guides available, the taxonomy of the Hippoboscidae, especially that of the louse flies, has been a source of disagreement and continues to be a source of confusion.

Some entomologists, such as T. C. Maa, have favoured splitting the louse flies into multiple species on the basis of slight variations in chaetotaxy and the shape of the tergites, while others including Joseph Bequaert have considered some of these features to be inconsistent and have concluded some groups, such as the smaller *Ornithomya* species in the Northern Hemisphere, were all a single species. Additionally, assumptions about geographical boundaries which may form a barrier to other species, may be partially overcome by species whose hosts are migrant bird species, for example, the Swift Louse Fly *Crataerina pallida's* range, while mostly restricted to Europe and west Asia, also includes South Africa where the Swift *Apus apus* overwinters (GBIF, 2023a). This, together with the possible human introduction of species to new areas, has resulted in species being given different names in different regions, for example *Ornithomya variegata* (Bigot, 1885) described in Australia and New Zealand, is now considered to be the same species as *Ornithomya fringillina* (Curtis, 1836) (GBIF, 2023b).

Hopefully, DNA sequencing will eventually sort out the confusion around species identification in this family, but progress has been far slower than in many other taxa. Of the full species listed in the most recent checklist of Hippoboscidae (Dick, 2018), after exclusion of those Carl Dick considered *incertae sedis* and the fossil species *Ornithomya rottensis* (Statz, 1940) only 19.3% (38/197) have a published cytochrome oxidase 1 (COX1) sequence in the NCBI GenBank database and only 0.6% (11/197) have a full mitochondrial sequence. Only one species of Hippoboscid, the Swift Louse Fly, has a full genome sequence available (Wawman et al., 2023).

In this chapter, I combine the two techniques commonly used to describe species, morphology and DNA. Firstly, I look at the wing morphology of *Ornithomya fringillina*, comparing the three morphotypes previously described within the United Kingdom (Hill, 1962; Smart, 1939), and attempt to determine whether they are all a single species by using both principal component analyses of these and biogeographical factors, and COX1 sequences as “DNA barcodes”. The second part of this chapter aims to contribute to the development of a DNA library of COX1 sequences for the Hippoboscidae, by publishing a sequence from a properly vouchered specimen of the Nightjar Louse Fly, *Pseudolynchia garzettae*, collected as part of the Mapping the UK’s Flat Fly Project.

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2.1

Clarifying the taxonomy of the Finch Louse Fly *Ornithomya fringillina* (Curtis) (Diptera: Hippoboscidae) – an analysis of morphotypes.

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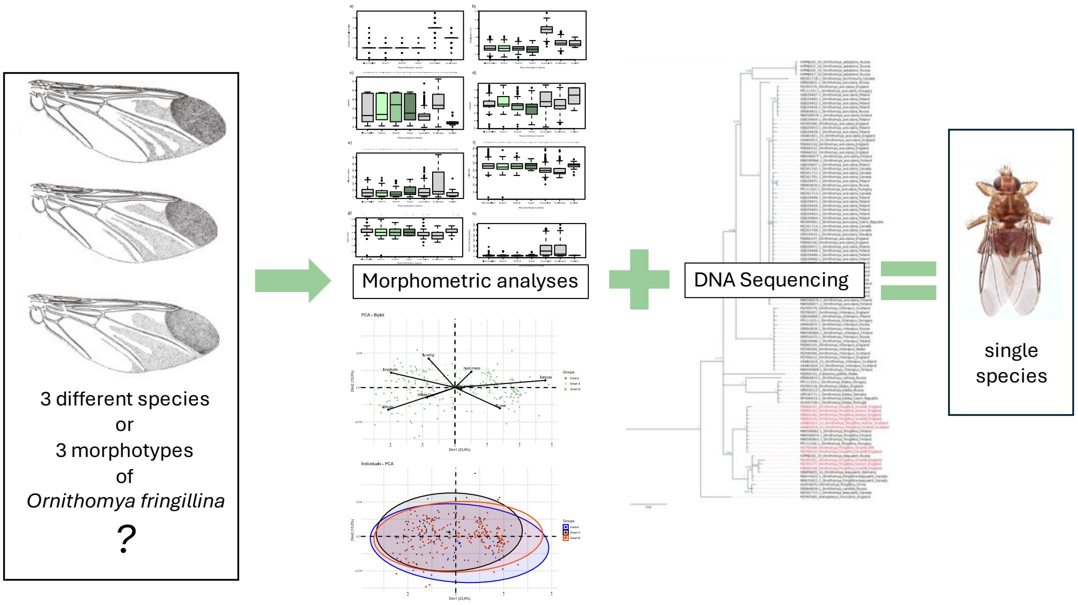
GRAPHICAL ABSTRACT



- The taxonomy of the smaller louse flies in the genus *Ornithomya* has often been disputed. Three morphotypes of *Ornithomya fringillina,* similar to species elsewhere, exist in the United Kingdom.
- Morphometric analyses and COXI DNA sequencing indicated that these morphotypes are all one species.
- Further work is needed to confirm whether *Ornithomya bequaerti* and *Ornithomya candida* are also morphotypes of *O. fringillina* or full species.

ABSTRACT

The louse flies in the genus *Ornithomya* are avian ectoparasites. The patterns of alar microtrichia on the wings of the Ornithomyae are commonly used to help distinguish the various species, with the patterns in most species found to be constant between individuals. The Finch Louse Fly *Ornithomya fringillina* (Curtis) in the United Kingdom, Ireland and the Isle of Man, is unusual in that the several patterns have been described. Consequently it has a complicated taxonomic history and there is some confusion about species identification. Louse flies were collected by licensed bird ringers and an analysis of the simple morphological features, phenology and geographical distribution of these traits was performed. No significant differences were found between the three main types, and it was concluded that the differences were not due to sexual dimorphism and did not provide evidence that the different forms were separate species. Analysis of COX1 DNA sequences confirmed this result and proved that these are indeed morphotypes and not distinct species. There was no geographical separation between COX1 sequences from the United Kingdom and those from flies sampled in other parts of the world. The molecular analysis also suggested that *Ornithomya bequaerti* (Maa) and *Ornithomya candida* (Maa) may not be valid species, but represent morphotypes of *O. fringillina*.

Key Words: taxonomy; phylogeny; morphometric analysis; louse fly; ectoparasite;

INTRODUCTION

The genus *Ornithomya* belongs to the family Hippoboscidae, which are ectoparasites of birds and mammals. Worldwide around 30 species are recognised in the genus (Dick, 2018; Yatsuk, Nartshuk and Matyukhin, 2024), of which four species are found within the United Kingdom (UK), Ireland and the Isle of Man (hereafter called “the region”) (Hutson, 1984; Wawman, 2024). While the recent UK colonist *Ornithomya biloba* (Dufour) is generally considered to be monoxenous on Barn Swallow *Hirundo rustica,* and is sometimes found on other hirundines, and occasionally on the raptors which predate them (Hill, Hackman and Lyneborg, 1964; Hutson, 1981, 1984; Wawman, 2024), the other three species are more generalist, being found on a range of bird hosts (Hill, 1962a; Hutson, 1984). The Bird Louse Fly or Common Louse Fly *Ornithomya avicularia* (Linnaeus) is the largest of the group and is sympatric in the region with the smallest, *Ornithomya* *fringillina* (Curtis), both have a more southerly and lower altitudinal distribution than the Grouse Louse Fly *Ornithomya chloropus* (Bergroth) (Hill, 1962a; Wawman, 2025).

Ornithomya fringillina is found in across the Palearctic Region, and into Africa North of the Sahara (Maa, 1964). It is also found in East Asia; Korea (Iwasa and Choi, 2013) and Japan (Maa, 1969a). It may also occur in North America (Bequaert, 1954b) and Iceland (Messersmith, 1982) but in both of these cases it was not distinguished from other species such as *O. chloropus*.

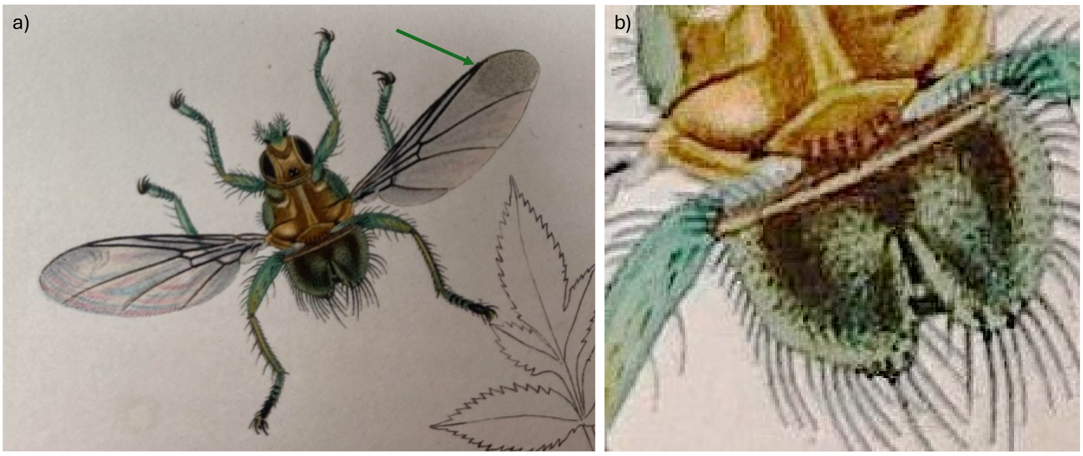
The taxonomy of *Ornithomya fringillina* and the other similar species of the genus *Ornithomya* was a source of disagreement between entomologists for many years in the twentieth century and remains a source of confusion today. The key historical events for these species in the Northern Hemisphere, excluding Asia, are summarised in Table 1 and briefly summarised here. In Europe, *O. fringillina* and *O. chloropus* were initially considered to be the same species, *O. fringillina* (Curtis, 1836). *Ornithomya chloropus* was first described in Finland by Bergroth in 1901 (Hill, 1964). In 1907, Sharp, working in England, separated the smaller *Ornithomya* spp. in the region into *Ornithomya fringillina* and *O. lagopodis* (Sharp) (Hill, 1962b) and Smart also recognised these two species (Smart, 1939). *O. lagopodis* was later shown to be conspecific with *O. chloropus* (Hill, Hackman and Lyneborg, 1964). In the 1940's and 1950's Bequaert, working in America (Bequaert, 1954) and with Leclercq in Belgium (Bequaert & Leclercq, 1947), and Thompson working in Great Britain and Ireland (Thompson, 1954) recognised only one small species in the genus *Ornithomya* across the northern hemisphere until Hill revised the genus in the British Isles (Hill, 1962b), reviewed specimens from Northern Europe (Hill, Hackman and Lyneborg, 1964) and described a neotype of *O. chloropus* – the original syntypes having been lost (Hill, 1964). In North America *Ornithomya anchineuria* (Speiser), which was initially described from America as *Ornithomya pallida* (Say) in 1823, was renamed by Speiser due to another species having the same name (Speiser, 1905). Maa concluded that *Ornithomya anchineuria* should be considered a subspecies of *Ornithomya chloropus* as they were so closely related but also described *O. bequaerti* from Canada (Maa, 1969b). Later, Maa seems to have accepted *O. anchineuria* as a valid taxon and considered it to be one of two species present in North America, the other being *O. bequaerti* (Maa and Petersen, 1987). *Ornithomya anchineuria* was confirmed as a separate species by mitochondrial cytochrome oxidase I (COXI) DNA sequencing of a specimen from Canada (Levesque-Beaudin and Sinclair, 2021). However, the same study found that other specimens from both Europe and North America, morphologically identified as *O. fringillina*, fell into a group with *O. bequaerti*, considered by the authors to be distinct from *O. fringillina* (Levesque-Beaudin and Sinclair, 2021) despite a relatively small phylogenetic distance calculated from a single short DNA sequence from a fly identified as *O. bequaerti*.

Table 1. Timeline showing the major events in the classification of the smaller species of louse flies of the genus Ornithomya in Europe and North America. Each species is indicated by a colour: *O. fringillina*, green; *O. chloropus*, mauve; *O. anchineuria*, light brown; *O. bequaerti*, yellow. The morphotypes of *O. fringillina* are given separate columns for each species, and there are separate columns for Europe and North America.

Year	**Authority**	**Location**	***Ornithomya fringillina***				***Ornithomya chloropus***		***Ornithomya anchineuria***	***Ornithomya bequaerti***	
				Smart type A	**Smart type B**	**Hutson/Hill**					
			North America	**Europe**				**North America**	**North America**	**North America**	**Europe**
1823	Say	North America							As *Ornithomya pallida*		
1836	Curtis	Oxfordshire, England		Described a single species, *Ornithomya fringillina*							
1901	Bergroth	Finland		🟩			*O. chloropus*				
1905	Speiser	(Germany)							renamed *O. anchineuria*		
1907	Sharp	England		🟩			As *O. lagopodis*				
1939	Smart	England		Smart A	Smart B		As *O. lagopodis*				
1947	Bequaert & Leclercq	North America & Belgium		🟩							
1954	Bequaert	North America	Single species *Ornithomya fringillina*								
1954	Thompson	England		Having examined Curtis's syntype							
1962	Hill	British Isles				🟩	🟪				
1964	Hill	Europe				🟩	neotype of *O. chloropus*				
1964	Hill, Hackman & Lyneborg	Fennoscandia, Denmark, Iceland		noted variation in cell 3m - 3 tracts of microtrichia		2 tracts of microtrichia in cell 3m	🟪				
1969	Maa	Worldwide		🟩			*O. anchineuria* subspecies of *O. chloropus*			*O. bequaerti* (Canada)	
1984	Hutson	British Isles				🟩	🟪				
1987	Maa & Petersen	Canada							*O. anchineuria*	?2nd of 2 spp.	
2007	Petersen et al	Denmark		chloropus-like type	intermediate-type	fringillina-type	🟪				
2007	Petersen et al	Worldwide		🟩	🟩	🟩	🟪		🟫		
2018	Goater et al	Canada							🟫	🟨	
2021	Levesque-Beaudin & Sinclair	Northern hemisphere		some redetermined as O. *bequaerti from COI DNA sequences*			🟪		🟫	🟨	Redetermined from *O. fringillina*
2024	GBIF	Worldwide	🟩				in Greenland		form of *O. fringillina*	🟨	
2024	This study	United Kingdom		Smart type A	Smart type B	Hutson type	🟪				

The Global Biodiversity information Facility (GBIF) website currently lists records of *O. fringillina* in North America and Australia, but considers *O. anchineuria* (Speiser), a North American species, and *O. variegata* (Bigot), an Australasian species, as synonyms of *O. fringillina* (*GBIF*, 2022). "*Ornithomya pallida* Say 1823*",* is also listed as a synonym of *O. fringillina* on the GBIF website, whereas "*Ornithomya pallida* Latreille 1812", is a synonym for the Swift Louse Fly *Crataerina pallida* (Latreille). *Ornithomya candida* (Maa), a species described from Japan (Maa, 1967) is also considered a valid species in GBIF (GBIF, 2023).

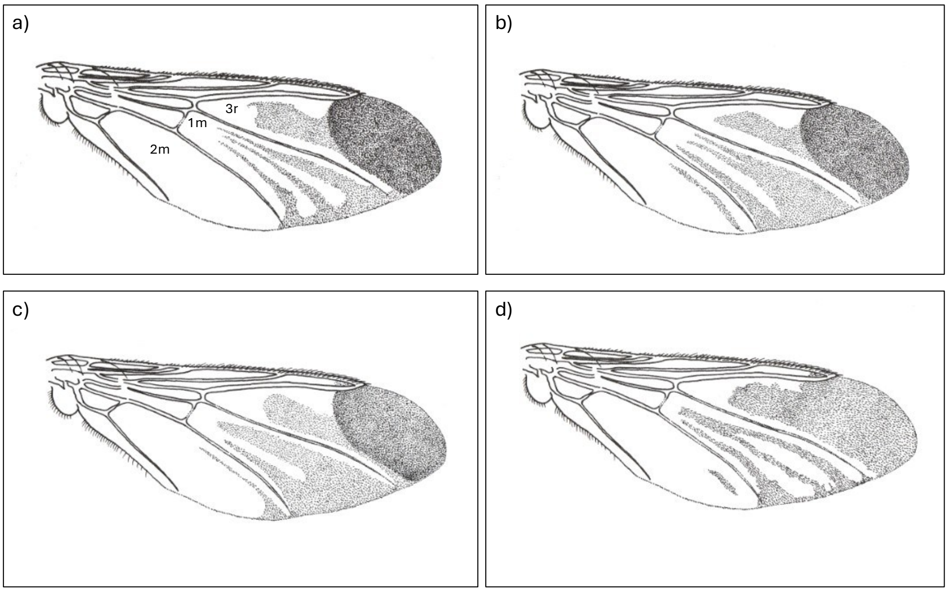
Fig. 1. Images of the original illustration from John Curtis's description of *Ornithomya fringillina* (Curtis, 1836): a, dorsal habitus, the right wing of which lacks a clear area adjacent to where the most distal vein reaches the costa (arrow) and the left wing appears to have been drawn to indicate iridescence; b) Close up of the scutellum, showing six strong bristles.



Part of the confusion would appear to lie with the brevity of the original written description of *O. fringillina*, its illustration (Fig. 1) (Curtis, 1836) and the chosen type specimens, from Robin *Erithacus rubecula*, Great Tit *Parus major* and Yellowhammer *Emberiza citrinella*, collected at Weston-on-the-Green, near Oxford in the United Kingdom. Assuming there were three syntypes, one from each host species, two would appear to be lost and the third is now at the Melbourne Museum in Australia. Photographs of this extant syntype show a female fly (Fig. 2), with a reported wing length of just under 5 mm (Simon Hinkley, Museums Victoria, pers. comms.), that has sadly suffered some damage over the years making further redetermination difficult. It has acquired an undated additional determination label by the Russian entomologist Paramonov of "*Ornithomyia fringillina*" (sic), presumably between 1947 and 1967 when he was working in Australia (*Sergy Paramonov (entomologist)*, 2024). *Ornithomyia* and *Ornithomya* have both been used as the name for the genus (Maa, 1965). This syntype was examined by Thompson, in the UK, who had the specimen posted from Australia, and his illustration (Thompson, 1954) is of a wing with three lines of microtrichia in wing cell 1m (See Fig. 3a for the cell numbers used), and a pattern of microtrichia in cell 3r part way between those seen in the two species *O. fringillina* and *O. chloropus*, which he thought “agreed in every respect with the common, smaller species of *Ornithomyia* (sic), described by Bergroth as *O. chloropus* and Sharp as *O. lagopodis*” (Bequaert, 1954a).

Fig. 2. The syntype of *Ornithomya fringillina* held at Museums Victoria, Melbourne, Australia as photographed by Simon Hinkley, Museums Victoria, on 16th January 2023. a, dorsal habitus; b, left wing; c, distal part of left wing, with no clear area at the distal end of the vein adjacent to the costa; d, ventral abdomen; e, head and thorax; f, specimen labels.

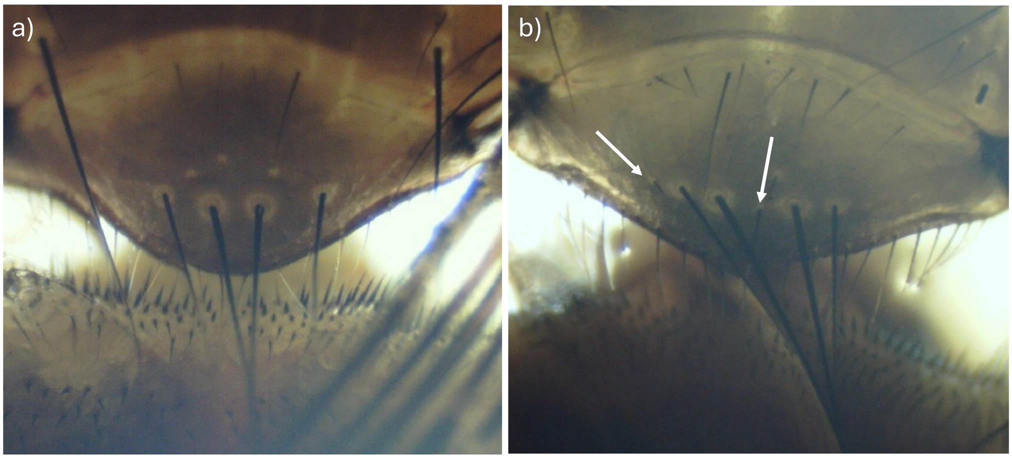
Fig. 3 a-c. Wings of *Ornithomya fringillina*. a, b, redrawn from Smart (1939) showing three tracts of microtrichia in cell 1m, referred to as Smart A and Smart B in the text; c, redrawn from a combination of from Hutson (1984) and Hill (1962b) showing only two tracts of microtrichia in cell 1m; d, *Ornithomya anchineuria* redrawn from Maa (1969).



The illustration in the original description (Curtis, 1836), shows a fly (Fig. 1) with six scutellar bristles – as are normally found in *O. chloropus* (Hutson, 1984), and with no area clear of microtrichia in cell 3r towards the end of the veins at the leading edge of the wing, which is also a feature of *Ornithomya chloropus*. It should be noted that John Curtis was known for his skill as an illustrator and engraver and for the accuracy of his work (French, 2022). Note was made in his obituary of his attention to detail, reporting his complaint to an illustrator that there were only 12 hairs on a fly's tail not 13 (*John Curtis (entomologist)*, 2024). Thus it is likely that the illustration is an accurate rendering of the actual fly and it may be that two species were present amongst the group of syntypes.

Taxonomic confusion between the two species has continued, despite the advent of DNA sequencing techniques. DNA sequencing has produced different results to the morphological identification of some individual specimens (Levesque-Beaudin and Sinclair, 2021) probably because many morphological features exist across a range rather than as two distinct groupings (Petersen, Damgaard and Meier, 2007). The number of scutellar bristles may be difficult to define due to the missing bristles and the presence of weaker ones (Fig. 4) - and dark marks on the inferior surface of the head and thorax - have a tendency to fade over time, especially if specimens are preserved in ethanol (Hill, Hackman and Lyneborg, 1964).

Fig. 4. Scutellar bristles of *Ornithomya fringillina*. a, clearly has 4 bristles along the posterior edge of the scutellum, but b, has two additional small bristles, indicated by arrows. Most entomologists would only count the stronger bristles, following Hutson (Hutson, 1984), but some bristles can be ambiguous.



The patterns of small hairs, variously called microtrichia or setulae, on the wings of the *Ornithomya* spp. have long been considered an important identification feature (Smart, 1939; Hill, 1962b, 1964; Maa, 1964, 1969b; Hutson, 1981, 1984) and are considered to be one of the two most important features by some current researchers in North America (Valerie Levesque-Beaudin, pers. comm.), together with the shape of the tergites on the female which may not be well preserved in specimens (Levesque-Beaudin and Sinclair, 2021). Amongst the Ornithomyae in the region, the patterns of alar microtrichia are almost constant between individuals of each of three species, *O. avicularia, O. chloropus* and *O. biloba*, but highly variable in the fourth species, *O. fringillina*. In England, Smart (Smart, 1939) described two patterns of microtrichia in *O. fringillina,* both with three tracts of microtrichia towards the proximal end of cell 1m, (Fig. 3a, b) but others described a different form (Hill, 1962b; Hutson, 1984) with only two tracts (Fig. 3c). One of the wing forms of *O. fringillina* described by Smart (Smart, 1939) is very similar, to that described for the North American species *O. anchineuria* (Maa, 1969b) (Fig. 3d), with only slight variations in wing cell 3r which seems to be quite variable.

When checking morphologically separated *O. chloropus* and *O. fringillina* from Denmark, Petersen found a grouping of specimens, considered to be *O. fringillina*, which were genetically distinct from *O. chloropus* and had three wing types, described as "fringillina-type, chloropus-type and intermediate" (Petersen, Damgaard and Meier, 2007), that would appear to correspond to the types Hutson, Smart A and Smart B, respectively. Doubt has been cast upon the identification of some of Petersen's specimens (Levesque-Beaudin & Sinclair, 2021) used to produce a phylogeny (Petersen *et al.*, 2007), with

Petersen's *O. anchineuria* now grouped with *O. chloropus* and his *O. fringillina* now classed as *O. bequaerti* (Maa) in Levesque-Beaudin's phylogeny.

The issues around the patterns of alar microtrichia have been further complicated by a key published in 2022 from work in Slovakia, which states that *Ornithomya fringillina* has four longitudinal stripes of microtrichia in the hind part of the wing, while *Ornithomya chloropus* has three (Oboňa *et al.*, 2022), which contradicts earlier work and, when taken with other features in the key, would render a large number of Ornithomyae in the region unidentifiable.

This study aims to determine whether the variations amongst flies identified as *Ornithomya fringillina* on the basis of previously published accounts of the morphology of *Ornithomya fringillina* in the region (Smart, 1939; Hutson, 1984), are morphotypes of the same species or separate species, by examining a variety of morphological, ecological and biogeographic data, alongside DNA sequence analysis.

MATERIALS AND METHODS

The specimens of *Ornithomya fringillina* were obtained between 2020 and 2024 from UK licensed bird ringers collecting louse flies for the "Mapping the UK's Flat Fly Project". The collection methods have been previously published (Wawman, 2024).

The louse flies were provisionally identified to species level using a key (Hutson, 1984) and additional information as required (Smart, 1939; Hill, 1962b, 1964; Maa, 1969b; Petersen, Damgaard and Meier, 2007). The number of strong scutellar bristles was recorded. The wing length of each fly was measured to an accuracy of 0.1mm with callipers, with the fly positioned on its back to straighten the wings. Notes were made of characteristics such as dark markings, on the mesothoracic basisternum, other areas of the ventral thorax, or on the lateral gena, medial to the eye, which have been used to separate *Ornithomya chloropus* from *Ornithomya fringillina* (Hill, 1962b; Hutson, 1984; Petersen, Damgaard and Meier, 2007). Although indistinct triangular markings on the lateral gena were not considered to be significant, and only those which were clearly defined were considered specific for *Ornithomya chloropus* by Petersen, these were recorded separately from clearer markings. Where possible the sex of each fly was recorded, by examination of the external genitalia or the darker patterns made by the tergites on the dorsal abdominal segments including the shape of tergite six.

Flies identified as *Ornithomya fringillina* were analysed on the basis of two classifications. All flies identified as *Ornithomya fringillina sensu lato (s.l.)* were divided into two groups, with either two or three tracts of microtrichia at the proximal end of cell 1m. Additionally, from 1st August 2022 onwards, *Ornithomya fringillina s.l.* were divided into three groups, Smart type A, Smart type B and Hutson/Hill types based on those authors' illustrations of the species (Smart, 1939; Hill, 1962b; Hutson, 1984). The Hutson/Hill type will be referred to as the Hutson type as Hutson's guide is freely available and widely used.

All grid references were checked using the website, Curaera (*Curaera*, 2022), and Ordnance Survey grid references were converted to latitude and longitude using the website, Batch Convert Tool (*Batch Convert Tool*, 2022) for Great Britain and the Isle of Man, and Batch Coordinate Converter (Hunter, 2022) for Ireland. The masses of host species were obtained from the British Trust for Ornithology's "BTO Ringers Info App" (BTO IS and Demography Team, 2016).

The results were analysed in R version 4.1.2 (R Development Core Team, 2022). Initial data checking and the addition of Julian Day and separate columns for day, month and year took place using the packages dplyr (Wickham, Francois, *et al.*, 2023) and lubridate (Grolemund and Wickham, 2011). Principal component analyses (PCAs) were performed and the results plotted using the R packages factoextra (Kassambara and Mundt, 2020), MASS (Ripley *et al.*, 2024), and ggplot2 (Wickham, Chang, *et al.*, 2023).

Two separate sets of analyses were performed. The first compared two groups of louse flies, those with two and three tracts of microtrichia in cell 1m, with the number of tracts being counted at the proximal end of the wing, thus combining morphotypes Smart A and Smart B. The second set of comparisons was made between all three described morphotypes (Smart A, Smart B and Hutson). The groups of flies were compared on the basis of simple morphological features (wing length and number of scutellar bristles), the sex of the fly, and biogeographical and ecological factors (latitude, longitude, altitude, phenology (Julian Day of collection), and host species body mass). The variables were not transformed. Flies were excluded from these analyses if the wings were too damaged to be classified into morphotypes, the patterns of microtrichia were ambiguous (for example, if its two wings were different morphotypes) or if some of the data were missing.

For each PCA the data were sorted into suitable datasets and all non-numeric columns were removed, leaving just those listed above. Sex was coded as a categorical variable and the analyses were run twice: with sex included, because PCA may not be effective with categorical variables as they lack a variance structure. Rows with missing values were excluded and the PCA was performed using a correlation matrix method with scaled data. PCA plots were checked for evidence of clustering of individual flies of the various morphotypes into groups.

Mitochondrial COXI sequences were obtained from a selected sample of flies collected by the project. Table 2 gives details of the accession numbers, species and morphotypes, host species, date and place of collection for all the specimens.

The genome of one specimen of *Ornithomya fringillina* was fully sequenced (Wawman *et al.*, 2025) by the Darwin Tree of Life Project (DToL) (Blaxter *et al.*, 2022).

Table 2. Details of the specimens sequenced, including accession numbers, species, sex and morphotype, host species, date and location of collection, name of collector and laboratory where the flies were sequenced. UKBoL = UK Barcode of Life Project, DToL = Darwin Tree of Life Project, APHA = Animal and Plant Health Agency, Oxford = Department of Biology, University of Oxford.

Study specimen number	**Accession number**	**Species & wing morphotype**	**Sex**	**Host species**	**Date**	**Site**	**Collector**	**Sequenced by**
5366	Bold Systems UKAN1813-23	*Ornithomya avicularia*	♀	Starling *Sturnus vulgaris*	26.vi.2021	England, Norfolk, Thetford	Jo Lashwood	UKBoL
5371	Bold Systems UKAN1821-23	*Ornithomya avicularia*	♂	Starling *Sturnus vulgaris*	28.vi.2021	England, Norfolk, Thetford	Jo Lashwood	UKBoL
7979	Bold Systems UKAN1820-23	*Ornithomya chloropus*	♀	Meadow Pipit *Anthus pratensis*	8.ix.2021	Scotland, Highland, Carse of Ardersier	Hugh Insley	UKBoL
4152	Bold Systems UKAN1816-23	*Ornithomya chloropus*	♂	Siskin *Spinus spinus*	25.vi.2021	Scotland, Skye, Portree	Jonathan Jones	UKBoL
7755	Bold Systems UKAN1815-23	*Ornithomya fringillina* Hutson	♂	Goldcrest *Regulus regulus*	17.vii.2022	Scotland, Highland, Carse of Ardersier	Hugh Insley	UKBoL
5994	Bold Systems UKAN1819-23	*Ornithomya fringillina* Smart A	♀	Treecreeper *Certhia familiaris*	18.ix.2021	Scotland, Skye, Portree	Jonathan Jones	UKBoL
FF154	GenBank CAXBTB000000000.1	*Ornithomya fringillina* Hutson	♂	Great Tit *Passer domesticus*	16.vi.2022	England, Somerset, Minehead, Bratton	Denise Wawman	DToL
FF233/OF048	GenBank PQ068340	*Ornithomya fringillina* Hutson	♂	Blue Tit *Cyanistes caeruleus*	20.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
FF260/OF080	GenBank PQ066342	*Ornithomya fringillina* Hutson	♀	Great Tit *Parus major*	21.viii.2023	England, Somerset, Withiel Florey	Denise Wawman	APHA
FF213/OF028	GenBank PQ066339	*Ornithomya fringillina* Smart B	♂	Robin *Erithacus rubecula*	15.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
FF258/OF078	GenBank PQ066341	*Ornithomya fringillina* Smart B	♀	Goldfinch *Carduelis carduelis*	21.viii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
FF194/OF009	GenBank PQ066338	*Ornithomya fringillina* Smart B	♂	House Sparrow *Passer domesticus*	7.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
LIZZ/CP060	GenBank PQ066331	*Crataerina pallida*		Swift *Apus apus*	23.vii.2023	Wales, Powys, Hay on Wye	Lizzie Harper	APHA

FF199/OC014	GenBank PQ066335	*Ornithomya chloropus*	♂	House Sparrow *Passer domesticus*	7.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
FF234/OA049	GenBank PQ066337	*Ornithomya avicularia*	♀	Great Tit *Parus major*	20.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
FF223/OA038	GenBank PQ066336	*Ornithomya avicularia*	♀	Blackbird *Turdus merula*	18.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
HJ247/OA057	GenBank PQ066333	*Ornithomya avicularia*	♂	Jackdaw *Coloeus monedula*	24.vii.2023	England, Lancashire, Mellor, Reaps	Hugh Jones	APHA
FF196/OA011	GenBank PQ066334	*Ornithomya avicularia*	♀	House Sparrow *Passer domesticus*	7.vii.2023	England, Somerset, Minehead, Bratton	Denise Wawman	APHA
JT01/OA101	GenBank PQ066332	*Ornithomya avicularia*	♀	Dunnock *Prunella modularis*	14.vii.2023	England, Merseyside, Wirral, Hoylake	Jane Turner	APHA
5291	GenBank PQ785575	*Crataerina pallida*	♂	Sparrowhawk *Accipiter nisus*	06.vii.2022	England, Yorkshire, Shirebrook Valley	Bryn Roberts	Oxford
1077	GenBank PQ785576	*Ornithomya avicularia*	♀	Chaffinch *Fringilla coelebs*	21.vii.2022	England, Lincolnshire, Owmby	Jenny Dunn	Oxford
1571	GenBank PQ785577	*Ornithomya fringillina Hutson*	♀	Whitethroat *Sylvia communis*	06.viii.2022	England, Northamptonshire, Stanford Reservoir,	Stanford Ringing Group	Oxford
5295	GenBank PQ785578	*Ornithomya biloba*	♀	Swallow *Hirundo rustica*	01.ix.2022	England, Derbyshire, Avenue Washlands Nature Reserve,	Bryn Roberts	Oxford
3235	GenBank PQ785579	*Ornithomya chloropus*	♀	Wren *Troglodytes troglodytes*	29.ix.2022	Scotland, Argyllshire, Glen Euchar	Rob Lightfoot	Oxford
Study specimen number	**Accession number**	**Species & wing morphotype**	**Sex**	**Host species**	**Date**	**Site**	**Collector**	**Sequenced by**
H926	GenBank PQ785580	*Ornithomya avicularia*	♂	Robin *Erithacus rubecula*	12.vii.2022	England, East Sussex, Icklesham	Rye Bay Ringing Group	Oxford
1073	GenBank PQ785581	*Ornithomya fringillina Smart B*	♀	Whitethroat *Sylvia communis*	15.vii.2022	England, Lincolnshire, Owmby	Jenny Dunn	Oxford
H106	GenBank PQ785582	*Stenepteryx hirundinis*	♂	House Martin *Delichon urbica*	09.vii.2023	England, Northamptonshire, Lamport Hall	Northants Ringing Group	Oxford
A29	GenBank PQ799306	*Ornithomya chloropus*	♂	Red Grouse *Lagopus scotica*	04.viii.2022	Scotland, Angus, near Glen Esk	Anon.	Oxford
1003	GenBank PQ799307	*Ornithomya chloropus*	♂	Merlin *Falco columbarius*	25.vi.2022	England, County Durham	Y. Townsend	Oxford
SB37	GenBank PQ799308	*Ornithomya fringillina Smart A*	♀	Robin *Erithacus rubecula*	11.vii.2022	Ireland, Kerry, Killarney National Park	Sam Bayley	Oxford
7091D	GenBank PQ799309	*Ornithomya chloropus*	♀	Kestrel *Falco tinnunculus*	09.vii.2023	Wales, Montgomeryshire, Llanerfyl, Wern-Fach	Mid Wales Ringing Group	Oxford
X352	GenBank PQ799310	*Ornithomya fringillina Smart B*	♂	Robin *Erithacus rubecula*	10.viii.2023	England, Devon, Bridford	Samuel Gray	Oxford
1011	GenBank PQ799312	*Ornithomya chloropus*	♂	Merlin *Falco columbarius*	02.vi.2022	England, County Durham	Y. Townsend	Oxford

The COXI gene from six louse flies, two of each of *Ornithomya avicularia*, *Ornithomya chloropus* and *Ornithomya fringillina* - one with two tracts of microtrichia(Hutson type) and one with three (Smart A type) - were sequenced as part of the UK Barcode of Life Project (UKBoL) (*UK Barcode of Life*, 2022).

One specimen of *O. chloropus*, five specimens of *O. avicularia* and five specimens of *O. fringillina* and one *Crataerina pallida*, that had been preserved in RNAlater, were sequenced by BPJ using shotgun Illumina NGS sequencing at the Animal and Plant Health Agency laboratories (APHA). The fly was prepared by washing in phosphate buffered saline (PBS) to remove the RNAlater, then in 5% sodium hypochlorite solution to remove contaminants, and finally twice more in PBS to remove the sodium hypochlorite. DNA and RNA were isolated separately from the fly using the QIAgen AllPrep DNA/RNA MiniKit (Qiagen, Manchester, United Kingdom). Briefly, the fly was homogenized in 300µl RLT buffer using a single 5mm steel bead in a TissueLyserII (Qiagen) for 5 minutes at 30Hz. After this, manufacturer's instructions were followed and DNA was eluted into 60µl buffer EB and RNA was eluted into 50µl RNase-free water. Sequencing libraries were prepared using Nexetra XT kits (Illumina, Cambridge, UK) and sequencing using a Nextseq sequencer (Illumina, Cambridge, UK). Illumina) to generate 2 x 150 base paired-end reads. The raw data were filtered to remove adaptors and low quality reads using the programs fastp version 0.23.4 (Chen *et al.*, 2018) and multiqc v 1.19 (Ewels *et al.*, 2016). The sequences were aligned and non-Dipteran sequences removed in the program Bowtie2 (Langmead and Salzberg, 2012). Sequences were assembled using MEGAHIT (Li *et al.*, 2015). Taxonomic classification was carried out using the program Kracken2 (Wood, Lu and Langmead, 2019), with the program Bracken (Lu *et al.*, 2017) to estimate species abundance and facilitate removal of poor quality and low abundance sequences. Sequences identified using these methods were isolated and the identity was confirmed using BLAST+ (Camacho *et al.*, 2009).

The DNA from the legs of a further 12 specimens, preserved in 70% ethanol, was extracted in Oxford by ASB and SRF. The legs were disrupted under liquid nitrogen and DNA was extracted using the Qiagen Blood and Tissue kit, as per the manufacturer's instructions.

The COXI gene fragments were amplified by PCR using primers LEPF1 ATT CAA CCA ATC ATA AAG ATA TTG G and LEPR1 TAA ACT TCT GGA TGT CCA AAA AAT CA (Integrated DNA Technologies, Belgium) (Herbert, et al, 2004) at the manufacturer-recommended concentration of 0.5uM, on an Applied Biosystems Veriti PCR machine, using the following cycling conditions, 5 minutes at 98°C, 40x(30 seconds at 98°C; 30 seconds at 60°C; 30 seconds at 72°C) then 7 minutes at 72°C.

PCR products were visualised after separation on a 1% agarose gel, purified using the Qiagen PCR Clean up kit according to manufacturer's instructions and then Sanger sequenced by Source BioScience, UK, using the same primers as for amplification.

Additional sequences for the *Ornithomya* species, were obtained from NCBI GenBank and BoldSystems with the addition of the moth *Cabera pusaria* as an outgroup. The relationships between the species were initially explored using the R packages: seqinR (Charif and Lobry, 2007), ape (Paradis and et al, 2023), adegenet (Jombart, 2008), viridis (Garnier, 2024), RSQLite (Muller *et al.*, 2023) and DECIPHER (Wright, 2014), and a phylogeny produced from a 446 base pair alignment using MrBayes (Ronquist *et al.*, 2012) with 1,000,000 MCMC under HKY + G model (determined by ng-modeltest).

The final phylogeny was produced using a reduced number of the *Ornithomya avicularia*, retaining only the most distantly related sequence (OR064831 from Russia) and new sequences from the United Kingdom, to show the overall width of the clade. This final phylogeny was produced from sequences aligned and trimmed in R using the package DECIPHER and imported into MEGA version 12 (Kumar et al, 2024). The analysis used three computing threads, 1000 replicates and the standard bootstrapping setting to produce a maximum likelihood tree, using a nearest neighbour interchange (NNI) and uniform rates in the Tamura-Nei model (Tamura and Nei, 1993) of nucleotide substitutions.

RESULTS

A total of 848 *Ornithomya fringillina* were collected. Details of the specimens examined are given in Table S1 in the Supplementary Results. A summaries of the results for each group in the two analyses (using either two morphotypes or three morphotypes) are presented separately below.

Flies with two tracts of microtrichia at the proximal end of cell 1m (Hutson type) were less frequently observed than those with either three tracts of microtrichia (Smart A or Smart B types) being 15.4% of the total (116/753). There was no significant difference between the wing lengths, number of scutellar bristles, Julian Day and peak month of capture, or capture site characteristics of altitude, latitude and longitude, or host mass between either the two morphotypes (two and three tracts of wing microtrichia) or the three morphotypes (Smart A, Smart B and Hutson). To allow comparisons with the clearly defined species in the genus, the other species of *Ornithomyae* identified in the study are also included in the boxplots illustrating these results.

Teneral flies of all three morphotypes were identified from a single site (Table 3), and flies of different morphotypes were observed on the same host species, and frequently found together on the same bird.

Table 3. Teneral *Ornithomya fringillina* examined.

Specimen number	Species	Sex	Site	Date	Host Species	Morphotype
FF265	*Ornithomya fringillina*	♀	Bratton, Minehead, Somerset, UK	25.viii.2023	Unknown	Smart B
FF261	*Ornithomya fringillina*	♀	Bratton, Minehead, Somerset, UK	25.viii.2023	Dunnock *Prunella modularis*	Smart A
FF262	*Ornithomya fringillina*	♀	Bratton, Minehead, Somerset, UK	25.viii.2023	Dunnock *Prunella modularis*	Smart B
FF423	*Ornithomya fringillina*	♂	Bratton, Minehead, Somerset, UK	10.vii.2024	House Sparrow *Passer domesticus*	Hutson
FF424	*Ornithomya fringillina*	♀	Bratton, Minehead, Somerset, UK	10.vii.2024	House Sparrow *Passer domesticus*	Smart B
FF425	*Ornithomya fringillina*	♂	Bratton, Minehead, Somerset, UK	10.vii.2024	Great Tit *Parus major*	Hutson
FF428	*Ornithomya fringillina*	♂	Bratton, Minehead, Somerset, UK	12.vii.2024	Unknown	Smart B

Comparison of two versus three tracts of microtrichia in cell 1m

A total of 512 flies were included in this analysis, 266 were excluded from the PCA because of missing data and four because one wing had three tracts of microtrichia and the other two. The two groups' means, ranges (Table 4) and medians, variance and interquartile ranges (as seen in the boxplots Figure 5) were similar. PCA (Figure 6, Table S2 and Figure S1) confirmed that the groups had similar means and overlapping concentration ellipses. There was no evidence that sexual dimorphism was responsible for the observed differences.

Table 4. Results of the morphometric, biogeographic and phenological analysis of two morphotypes of *Ornithomya fringillina* with either two or three tracts of microtrichia in wing cell 1m.

	Two tracts of microtrichia	Three tracts of microtrichia	Total both groups
Number in sample	112	400	512
Fly wing length (mm)	4.6 (3.6 - 5.9)	4.8 (3.6 - 6.1)	4.7 (3.6 - 6.1)
Number of Scutellar Bristles	4 (3 -6)	4 (2 - 8)	4 (2 - 8)
Latitude	53.57 (50.23 - 57.64)	53.98 (50.25 - 57.64)	53.89 (50.25 - 57.64)
Longitude	-3.82 (-9.01 - 0.64)	-3.58 (-9.56 - 1.23)	-3.63 (-9.56 - 1.23)
Altitude (metres)	81 (0 - 265)	72 (0 - 258)	74 (0 - 265)
Julian Day	232 (163 - 348)	230 (162 - 339)	230 (162 - 348)
Host mass (grams)	18 (5 - 101)	17 (5 -101)	17 (5 - 101)
Proportion of females	0.67	0.44	0.62

Fig. 5. Boxplots showing the results of the analyses for two morphotypes of *Ornithomya fringillina*, that is, those with two and three tracts of microtrichia in wing cell 1m. a, number of scutellar

bristles; b, wing length; c, latitude of capture site; d, longitude of capture site; e, altitude of capture site; f, Julian Day on which the fly was taken; g, month; h, host mass.

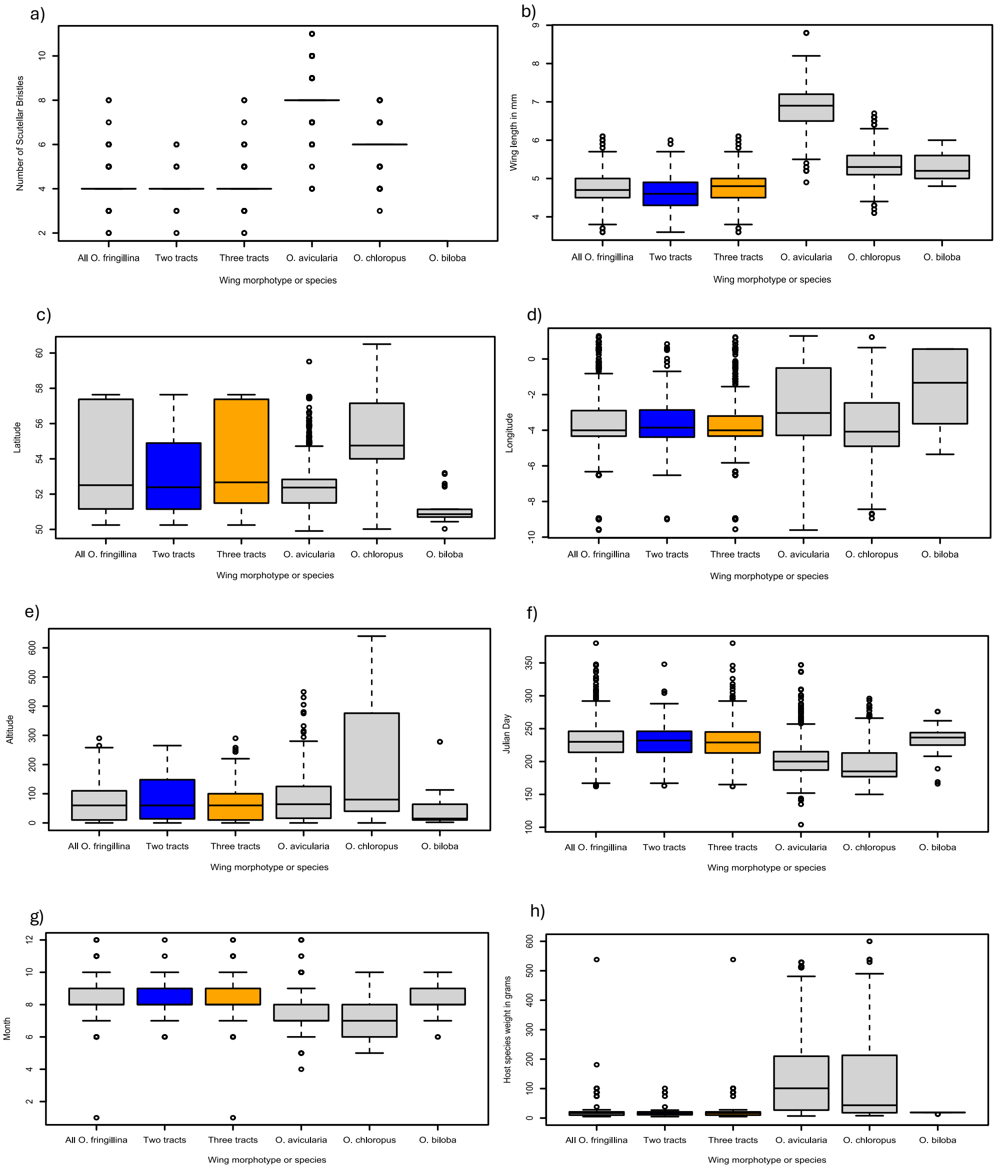
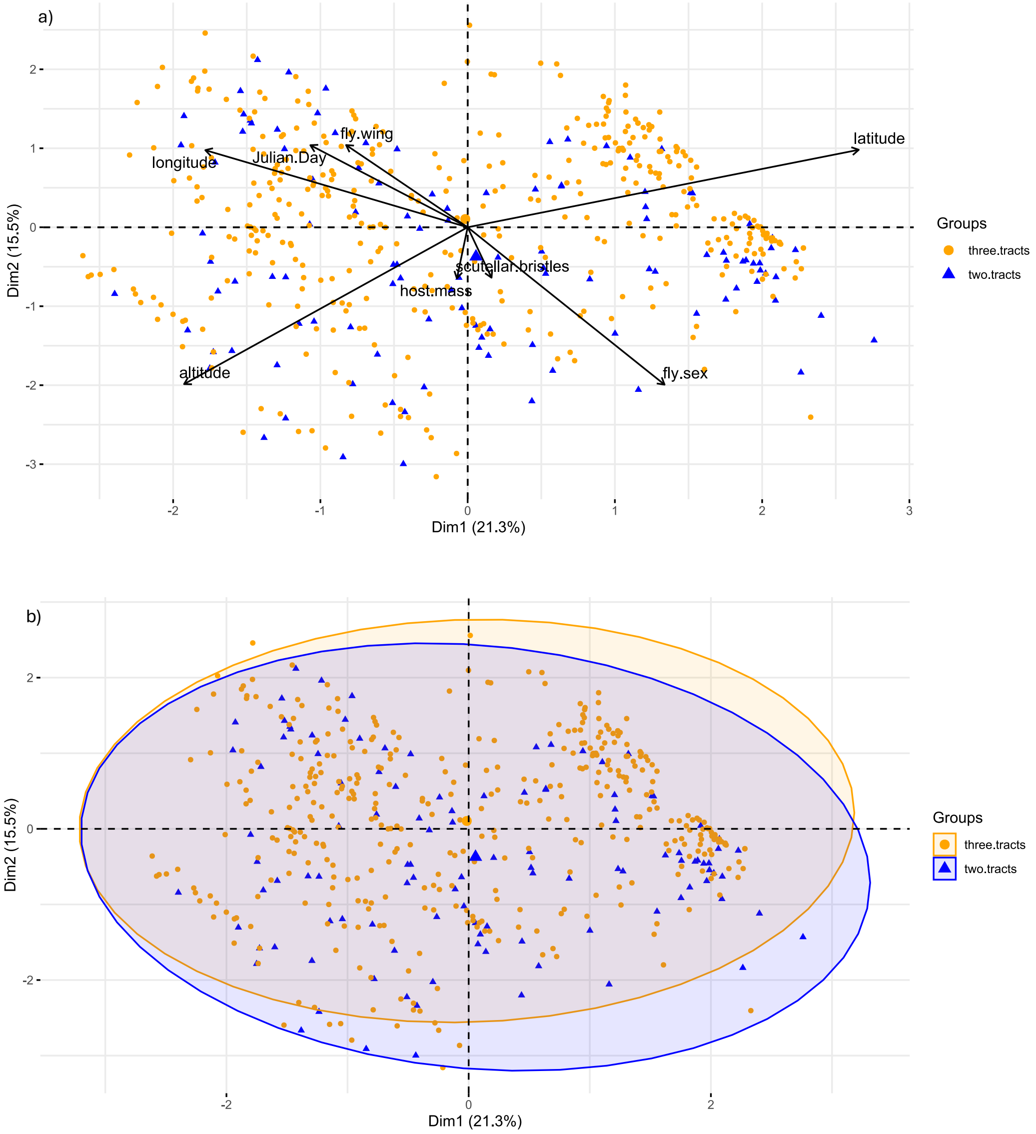


Fig. 6. Results of the PCA comparing two morphotypes of *Ornithomya fringillina*, those with two and three tracts of microtrichia in wing cell 1m. a, PCA biplot showing the relationship between the vectors representing the original variables and the first two principal components; b) individuals

PCA, with group means represented by the larger symbols and concentration ellipses showing the similarity between the two groups.



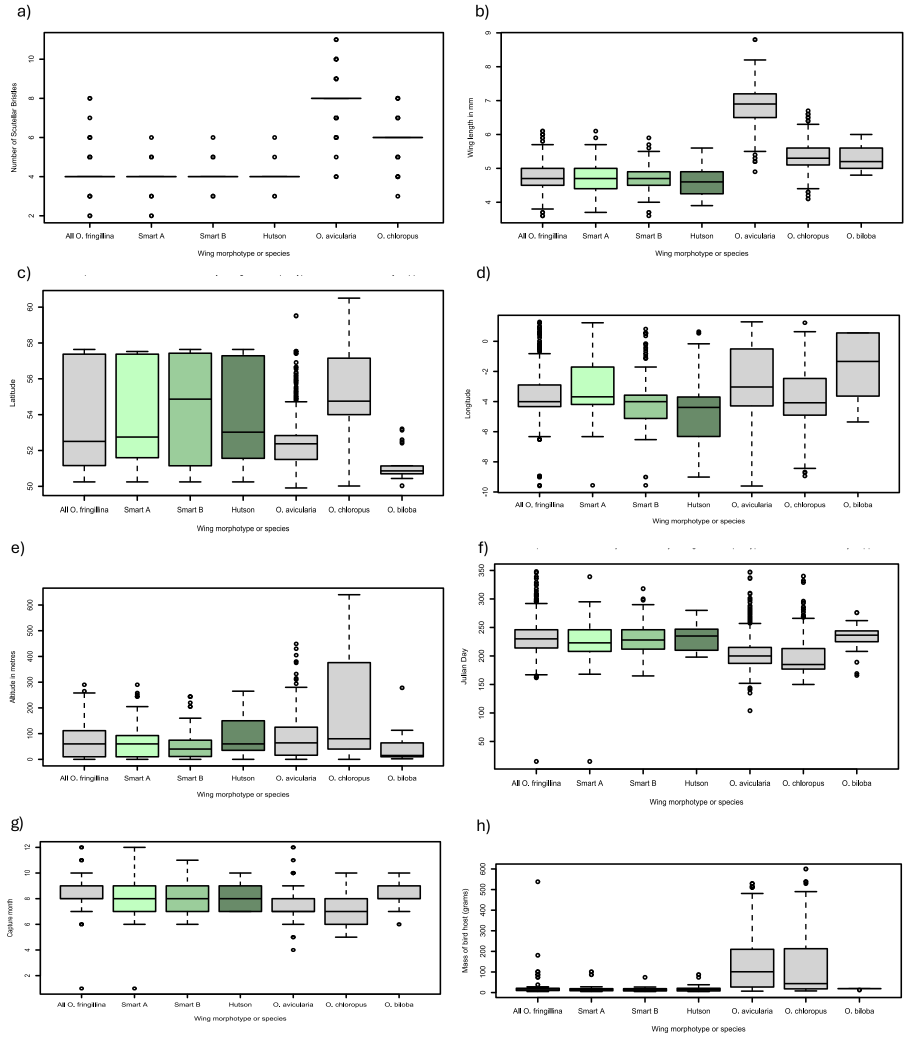
Comparison of three patterns of microtrichia as described by Smart (1939) and Hutson (1984)

A total of 299 flies were used in this analysis. 24 flies were excluded because of missing data and two because they had one wing of the Hutson morphotype and one of the Smart B morphotype. Morphometric analysis found no detectable difference between these morphotypes. The three groups' means, ranges (Table 5) and medians, variance and interquartile ranges (as seen in the boxplots Figure 7) were similar. PCA (Figure 8, Table S3 and Figure S2) confirmed that the groups had similar means and overlapping concentration ellipses. There was no evidence that sexual dimorphism was responsible for the observed differences.

Table 5. Results of the morphometric, biogeographic and phenological analysis of the three morphotypes of *Ornithomya fringillina* based on the descriptions of the tracts of microtrichia in wing cell 1m by Smart (1939) and Hutson (1984).

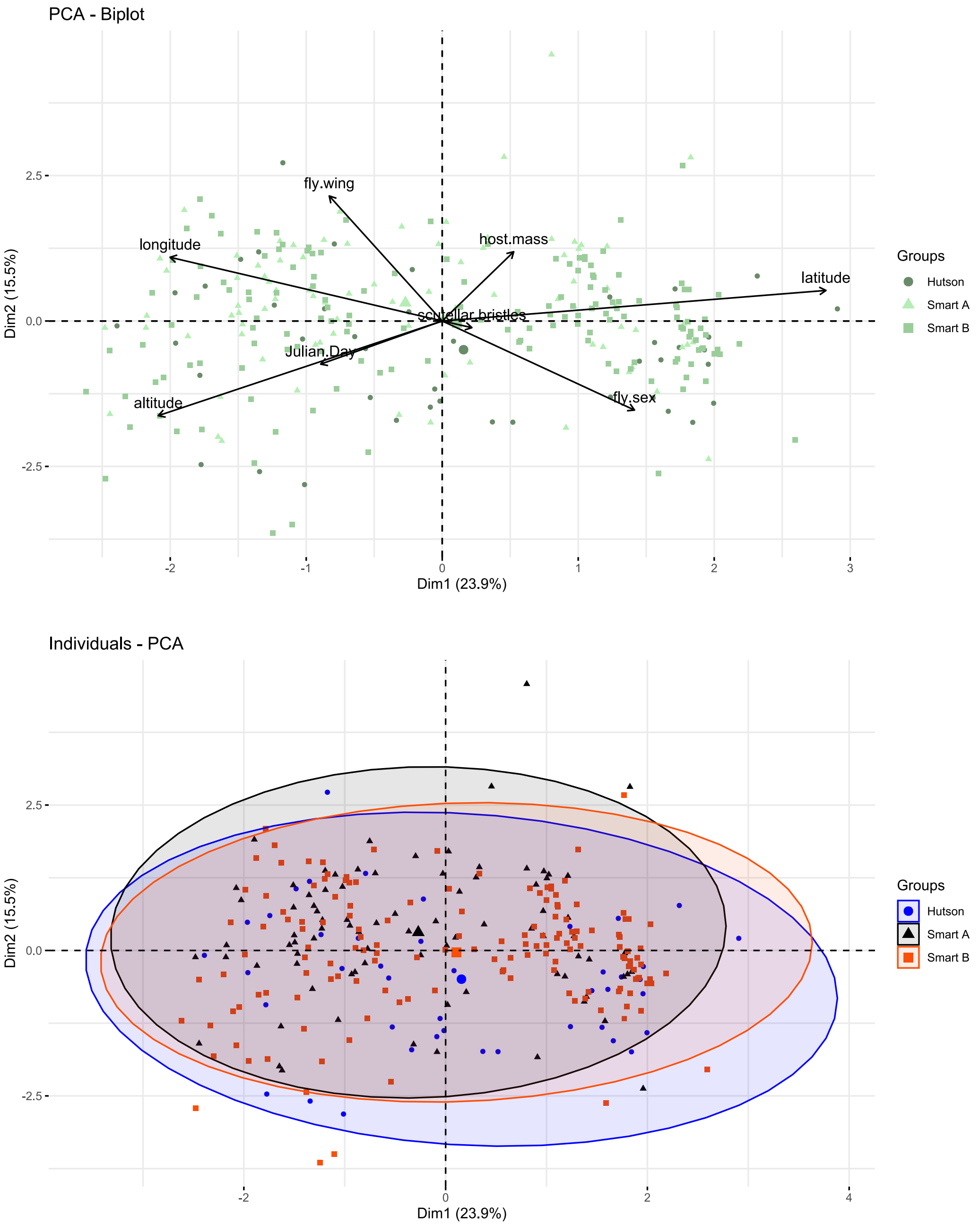
	Hutson	**Smart A**	**Smart B**	**Total**
Number in sample	44	96	159	299
Fly wing length (mm)	4.6 (3.9 - 5.6)	4.7 (3.7 - 6.1)	4.7 (3.6 - 5.9)	4.7 (3.6 - 6.1)
Number of Scutellar Bristles	4 (3 - 6)	4 (2 - 6)	4 (3-6)	4 (2 - 6)
Latitude	53.92 (50.25 - 57.64)	53.99 (50.25 - 57.52)	54.42 (50.25 - 57.64)	54.21 (50.25 - 57.64)
Longitude	-4.25 (-9.01 - 0.64)	-3.69 (-9.56 - 1.23)	-3.8 (-9.56 - 0.81)	-3.76 (-9.56 - 1.23)
Altitude (metres)	94 (0 - 265)	59 (0 - 258)	68 (0 - 244)	72 (0 - 265)
Julian Day	232 (198 - 280)	227 (168 - 339)	230 (165 - 318)	230 (165 - 339)
Host mass (grams)	15 (5 - 87)	15 (5 - 101)	13 (5 - 74)	16 (5 - 101)
Proportion of females	0.41 (n=44)	0.79 (n=88)	0.64 (n=86)	0.65 (n=284)

Fig. 7. Boxplots showing the results of the analyses for three morphotypes of *Ornithomya fringillina*, that is, those with two and three tracts of microtrichia in wing cell 1m. a, number of scutellar



bristles; b, wing length; c, latitude of capture site; d, longitude of capture site; e, altitude of capture site; f, Julian Day on which the fly was taken; g, month; h, host mass (capped at 600g).

Fig. 8. Results of the PCA comparing three morphotypes of *Ornithomya fringillina*, with different tracts of microtrichia in wing cell 1m as described by Smart (1939) and Hutson (1984). a) PCA biplot showing the relationship between the vectors representing the original variables and the first two principal components; b) individuals PCA, with group means represented by the larger symbols and concentration ellipses showing the similarity between the three groups.



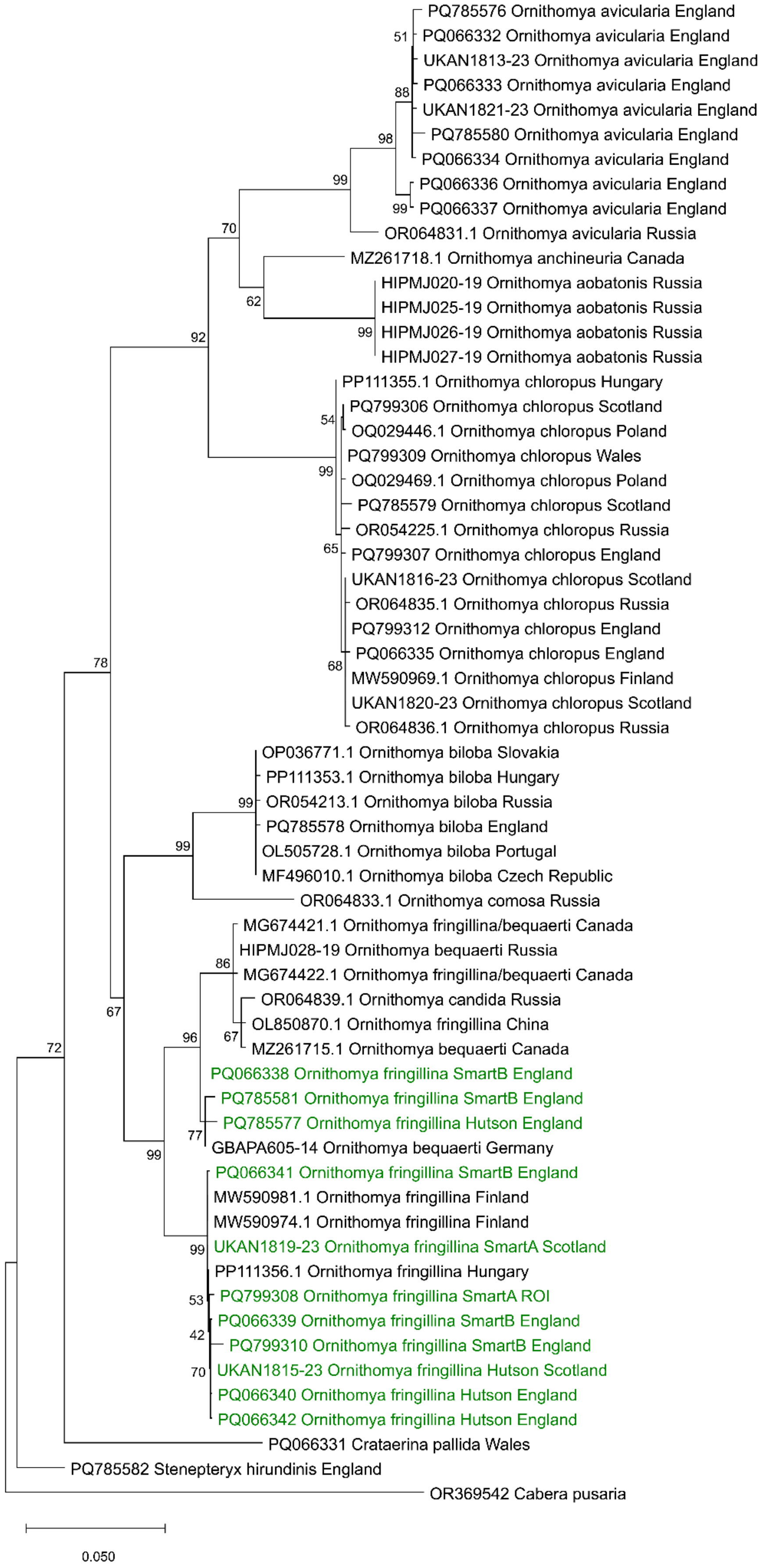
Analyses of DNA sequences

A phylogenetic analysis (Fig. 9) showed that the COX1 sequences obtained all the

Ornithomya fringillina morphotypes lay within a single clade, with less than 2% variation between the sequences, and no clustering of the morphotypes, or by geographical location. Within this main clade, there are two subclades, one containing only *O. fringillina* (but including all three morphotypes), and the second containing specimens (n=3) identified as *O. bequaerti*, two initially identified as *O. fringillina* but later redetermined as *O. bequaerti*, *O. candida* and two of the morphotypes (Hutson and Smart B) from the United Kingdom. It should be noted that only two specimens of the Smart A morphotype were successfully sequenced, so no conclusions can be drawn from their absence from the second clade. *Ornithomya anchineuria* falls within a different distinct clade.

Fig. 9. Phylogeny of the genus *Ornithomya*, produced from the COXI sequences, showing the morphotypes of *Ornithomya fringillina* (in green), other species from the United Kingdom and Ireland, compared to other sequences of the *Ornithomya* sp. from across their ranges. The nodes are labelled with the bootstrap values and the scale bar shows the percentage difference between sequences. The moth *Cabera pusaria* included as an outgroup.

This phylogeny was produced from sequences aligned in R using the package DECIPHER and imported into MEGA version 12 (Kumar et al, 2024) for analysis, using three computing threads, 1000 replicates (500 burn in) and the standard bootstrapping setting to produce a maximum likelihood tree, using a nearest neighbour interchange (NNI) and uniform rates in the Tamura-Nei model (Tamura and Nei, 1993) of nucleotide substitutions The tree with the highest log likelihood of -50,313.95 is shown.


PQ785576 Ornithomya avicularia England
51
PQ066332 Ornithomya avicularia England
UKAN1813-23 Ornithomya avicularia England
88
PQ066333 Ornithomya avicularia England
UKAN1821-23 Ornithomya avicularia England
98
PQ785580 Ornithomya avicularia England
PQ066334 Ornithomya avicularia England
99
PQ066336 Ornithomya avicularia England
99
PQ066337 Ornithomya avicularia England
70
OR064831.1 Ornithomya avicularia Russia
MZ261718.1 Ornithomya anchineuria Canada
HIPMJ020-19 Ornithomya aobatonis Russia
62
HIPMJ025-19 Ornithomya aobatonis Russia
99
HIPMJ026-19 Ornithomya aobatonis Russia
92
HIPMJ027-19 Ornithomya aobatonis Russia
PP111355.1 Ornithomya chloropus Hungary
PQ799306 Ornithomya chloropus Scotland
54
OQ029446.1 Ornithomya chloropus Poland
PQ799309 Ornithomya chloropus Wales
99
OQ029469.1 Ornithomya chloropus Poland
PQ785579 Ornithomya chloropus Scotland
OR054225.1 Ornithomya chloropus Russia
65
PQ799307 Ornithomya chloropus England
UKAN1816-23 Ornithomya chloropus Scotland
OR064835.1 Ornithomya chloropus Russia
PQ799312 Ornithomya chloropus England
PQ066335 Ornithomya chloropus England
78
68
MW590969.1 Ornithomya chloropus Finland
UKAN1820-23 Ornithomya chloropus Scotland
OR064836.1 Ornithomya chloropus Russia
OP036771.1 Ornithomya biloba Slovakia
PP111353.1 Ornithomya biloba Hungary
99
OR054213.1 Ornithomya biloba Russia
PQ785578 Ornithomya biloba England
99
OL505728.1 Ornithomya biloba Portugal
MF496010.1 Ornithomya biloba Czech Republic
OR064833.1 Ornithomya comosa Russia
MG674421.1 Ornithomya fringillina/bequaerti Canada
HIPMJ028-19 Ornithomya bequaerti Russia
86
MG674422.1 Ornithomya fringillina/bequaerti Canada
OR064839.1 Ornithomya candida Russia
67
OL850870.1 Ornithomya fringillina China
96
67
MZ261715.1 Ornithomya bequaerti Canada
72
PQ066338 Ornithomya fringillina SmartB England
PQ785581 Ornithomya fringillina SmartB England
PQ785577 Ornithomya fringillina Hutson England
77
GBAPA605-14 Ornithomya bequaerti Germany
99
PQ066341 Ornithomya fringillina SmartB England
MW590981.1 Ornithomya fringillina Finland
MW590974.1 Ornithomya fringillina Finland
99
UKAN1819-23 Ornithomya fringillina SmartA Scotland
PP111356.1 Ornithomya fringillina Hungary
53
PQ799308 Ornithomya fringillina SmartA ROI
PQ066339 Ornithomya fringillina SmartB England
42
PQ799310 Ornithomya fringillina SmartB England
70
UKAN1815-23 Ornithomya fringillina Hutson Scotland
PQ066340 Ornithomya fringillina Hutson England
PQ066342 Ornithomya fringillina Hutson England
PQ066331 Crataerina pallida Wales
PQ785582 Stenepteryx hirundinis England
OR369542 Cabera pusaria
0.050

DISCUSSION

Smart described two wing forms of *Ornithomya fringillina* (Smart, 1939) which were similar to those of the North American species, *Ornithomya anchineuria* described by Maa (Maa, 1969b) whereas Hill and Hutson described one contrasting pattern (Hill, 1962b; Hutson, 1984). This study looked at the differences between these three morphotypes and between flies with either two or three tracts of microtrichia in wing cells 1m and found no significant difference in their other morphological features, nor in their ecological or biogeographical traits. Louse flies of different morphotypes were found on the same host species and on the same individual birds. The wing length, number of scutellar bristles, geographic and altitudinal distributions and phenology are almost identical. The wing differences were not due to sexual dimorphism and teneral flies of all three morphotypes were caught at a single site suggesting that the differences were not due to either wing wear or geographical variation. Six flies had one wing of one morphotype and the other of a different morphotype. The morphotype COX1 sequences grouped together in the phylogenetic tree further supporting that these are variants of a single species (based on 12 flies: two of the Smart A, five of Smart B and five of the Hutson morphotypes).

It is known that the wings of flies of some species wear as they age, for example, the related Tsetse flies *Glossina* spp. (Hargrove, 2020). The wing fray of flies such as *Lucilia sericata* has been used as a technique to calculate the post-mortem interval in forensic pathology (Beutler, Hart and Hall, 2020). Differential patterns of wear, could result in the loss of microtrichia from some areas of the wing, resulting the appearance of morphotypes, from the Hutson-type, via Smart type B, to Smart type A, and some older flies appear to have bald patches (Wawman, pers. obs). However, the absence of differences in the phenology between the various morphotypes, together with teneral flies being caught of all three morphotypes, is good evidence that the differences are not due to wear.

Taken together, the results of the analyses of morphological features (the number of scutellar bristles and wing length), phenology (Julian Day of capture) and geographical distribution (latitude, longitude and altitude of capture site), all of which showed no significant difference in this study, would support the hypothesis that the flies with three patterns of microtrichia are morphotypes of the same species, *Ornithomya fringillina*, and not separate species, and this was confirmed by DNA barcoding. This makes *Ornithomya fringillina* unusual amongst the other species in the genus Ornithomya which have more consistent patterns of wing microtrichia.

Although based only on very short sequences, the results of DNA sequencing suggested that the North American taxon *Ornithomya bequaerti* and the Japanese species *Ornithomya candida* may not be separate species. Further research is needed to confirm this observation, perhaps including more comprehensive sequence data (e.g. full mitochondria or whole genome), and dissection of male genitalia of multiple specimens, all of which is beyond the scope of this study.

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Ringing groups (RG): Belvide RG, Borders RG, BTO Wetland & Marine RG, Clyde RG, East Dales RG, Gordano Valley RG, Gower RG, Isle of Wight RG, Kenfig RG, Llangorse RG, Lundy Field Society, Merseyside RG, Mid-Wales RG, Northants RG, Northern England Raptor Group, Peak District Raptor Monitoring Group, Rye Bay RG, Shropshire RG, Stanford RG, Steyning RG, Tay RG, Watchtree RG, Wicken Fen RG,
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AUTHOR CONTRIBUTIONS

Conceptualisation DCW; investigation DCW; methodology DCW, BJP, ASB & SRF; project administration DCW; species and morphological determination DCW; data curation DCW; formal analysis DCW; validation DCW; visualization DCW; writing – original draft DCW; writing – review and editing DCW, BJP, SRF, ALS, NJ; DNA extraction ASB, SRF, BPJ; resources DCW, ALS, NJ ; supervision ALS.

SUPPORTING INFORMATION

Table S1. Specimens of *Ornithomya fringillina* examined

Table S2. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of two morphotypes of *Ornithomya fringillina*

Table S3. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of two morphotypes of *Ornithomya fringillina*

Figure S1. PCA Scree plot for the two morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.

Figure S2. PCA Scree plot for the three morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.

DATA AVAILABILTY STATEMENT

Details of all of the flies examined can be found in table S1.

New DNA sequences are available in GenBank accession numbers PQ066331-42, PQ799306-12 and PQ785575-82. All sequences are listed in Table 2.

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ETHICS APPROVAL STATEMENT

All birds from which louse flies were collected were handled by British Trust for Ornithology licensed bird ringers.

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

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2.2

A first cytochrome c oxidase subunit I (COX1) DNA sequence of the Nightjar Louse Fly *Pseudolynchia garzettae* (Rondani, 1979) (Diptera: Hippoboscidae)

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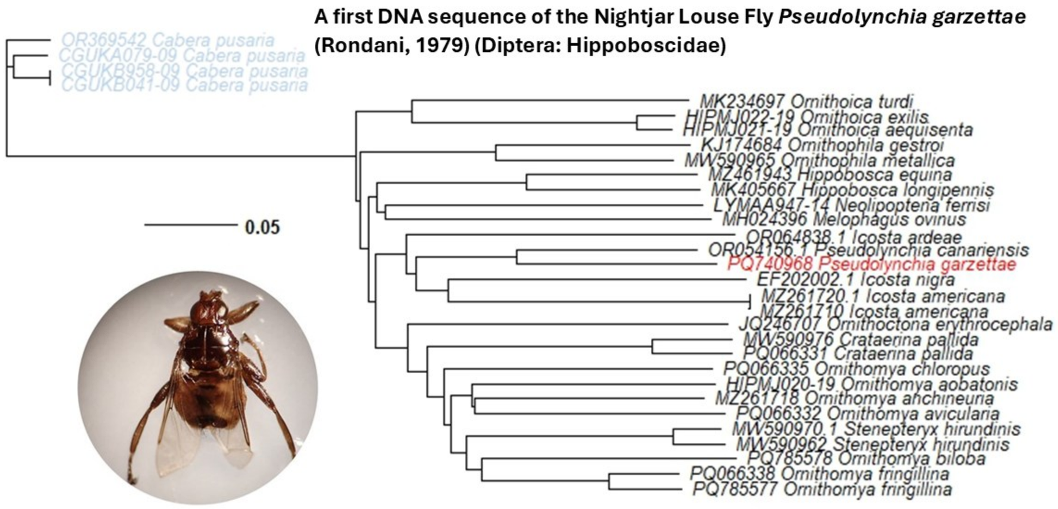
GRAPHICAL ABSTRACT



- *Pseudolynchia garzettae* (Rondani, 1897) has no previously published sequences in either of the two main databases, NCBI GenBank and International Barcode of Life v3 (BOLD)
- We present the first published mitochondrial COX1 DNA sequence for the Nightjar Louse Fly *Pseudolynchia garzettae,* from a gravid female, taken from an adult male European Nightjar *Caprimulgus europaeus* (Linnaeus, 1758), in Wales, United Kingdom.
- A morphological description of the fly is given to aid researchers working with these species.

ABSTRACT

Cytochrome oxidase subunit I (COX1) DNA sequences are widely used as a means of identifying Eukaryotic species, but in some taxonomic groups, such as the louse flies (Diptera: Hippoboscidae), there are many species that have not been sequenced. *Pseudolynchia garzettae* (Rondani, 1897) has no previously published sequences in either of the two main databases, NCBI GenBank and International Barcode of Life v3 (BOLD). We present the first published mitochondrial COX1 DNA sequence for the Nightjar Louse Fly *Pseudolynchia garzettae,* from a gravid female, taken from an adult male European Nightjar *Caprimulgus europaeus* (Linnaeus, 1758), in Wales, United Kingdom. A morphological description of the fly is given to aid researchers working with these species.

Key Words: Sequencing, Hippoboscidae, Louse Fly, Ectoparasite, DNA barcoding

INTRODUCTION

Short sequences of DNA are frequently used as "DNA barcodes" to confirm the identify of species. In Eukaryotic species the mitochondrial cytochrome c oxidase subunit I (COX1) gene sequence is widely used as it has sufficient interspecies variation to be a useful target. DNA sequencing can have major advantages over the traditional methods, using keys and field guides, in that it does not require expertise in species identification and may identify species or cryptic species that are not present in local field-guides, including invasive species. However, to be useful there needs to be a comprehensive library of DNA sequences for comparison (Kress and David, 2012), that do not conflict with morphological classifications (Meier, Lawniczak and Srivathsan, 2025).

The Hippoboscidae are a family of haematophagous ectoparasites that contains some species that are known vectors of trypanosomes in mammals and birds (Hoare, 1923; Theodor, 1928; Baker, 1967) and *Haemoproteus* spp. in birds (Baker, 1957, 1967; Cepeda *et al.*, 2019). Some species of Hippoboscidae have been found to contain many other pathogenic microbes, without conclusive proof that they are acting as vectors (Bezerra-Santos and Otranto, 2020). There are over 200 species within this family, many of which are of uncertain status (Dick, 2018), but many, especially those found in the southern hemisphere, have no published DNA sequences.

The genus Pseudolynchia (Bequaert, 1926) contains five species: *P. serratipes* (Maa, 1966), *P. brunnea* (Latreille, 1812), *P. canariensis* (Macquart, 1840), *P. garzettae* (Rondani, 1879) and *P. mistula* (Maa, 1969) (Dick, 2018). Of these five species, only one, *P. canariensis*, has published COX1 sequences in NCBI GenBank (https://www.ncbi.nlm.nih.gov, last accessed 1st January 2025) and the International Barcode of Life v3 (BOLD) (https://v3.boldsystems.org, last accessed 1st January 2025), however, within the specimens listed for the genus *Pseudolynchia,* there are some that are only identified to the level of genus.

The Nightjar Louse Fly, *Pseudolynchia garzettae*, is a species of central and east Africa and parts of Asia, although it has been found on migrant birds in the United Kingdom (UK), France, Switzerland, Cyprus, Ukraine and Russia (Haeselbarth, Segerman and Zumpt, 1966; Maa, 1969; Palmer, 1987; Nartshuk *et al.*, 2019). In 2022, three females, two of which were gravid, were found in Wales, UK, suggesting that they had established a breeding population (Wawman, 2024). *Pseudolynchia garzettae* is usually found on nightjars (Caprimulgidae) and owls (Strigidae), but has been found on various other species including Spotted Thick-knee (Cape Dikkop) *Burhinus capensis* (Lichtenstein,1823)*,* Burchell's coucal *Centropus burchellii* (Swainson,1838), *Pied Crow Corvus albus (*Müller, 1776), and European Swift *Apus apus* (Linnaeus, 1758) (Haeselbarth, Segerman and Zumpt, 1966).

We present a sequence for the Nightjar Louse Fly *Pseudolynchia garzettae*, from a vouchered specimen (that is one available in a museum reference collection) with a description of the fly, to enable future researchers to quickly review the specimen should conflicts occur with other COXI sequences from Hippoboscids. We compare the sequence to other sequences from the genus *Pseudolynchia*, including published sequences that have only been identified to the level of the genus*,* with the aim of identifying these specimens.

METHODS

A search was performed in NCBI Genbank for the all Hippoboscidae species listed in the checklist (Dick, 2018), after exclusion of the fossil species *Ornithomya rottensis* (Statz, 1940) and species listed as *incertae sedis*, and the available sequences were recorded. Pie charts were plotted from these data using base R v4.3.1 (R Development Core Team, 2022).

The louse flies were collected by British Trust for Ornithology (BTO) licensed bird ringers as part of the Mapping the UK's Flat Flies Project, which has previously been described (Wawman, 2024). They were identified, using a binocular microscope and a key (Hutson, 1984), and a key to the genus *Pseudolynchia* with descriptions of these species (Maa, 1966).

The left middle leg of a fly identified as *Pseudolynchia garzettae* was removed and kept separately in an individually labelled tube, in 70% ethanol. Upon reaching the laboratory, it was stored in a freezer at -80°C, until it could be sequenced. The leg was disrupted under liquid nitrogen and DNA was extracted using the Qiagen Blood and Tissue kit, as per the manufacturer's instructions.

The COXI gene fragments were amplified by PCR using primers LEPF1 ATT CAA CCA ATC ATA AAG ATA TTG G and LEPR1 TAA ACT TCT GGA TGT CCA AAA AAT CA (Integrated DNA Technologies, Belgium) (Herbert, et al, 2004) at the manufacturer-recommended concentration of 0.5uM, on an Applied Biosystems Veriti PCR machine, using the following cycling conditions, 5 minutes at 98°C, 40x(30 seconds at 98°C; 30 seconds at 60°C; 30 seconds at 72°C) then 7 minutes at 72°C.

PCR products were visualised after separation on a 1% agarose gel, purified using the Qiagen PCR Clean up kit according to manufacturer's instructions and then Sanger sequenced by Source BioScience, UK, using the same primers as for amplification.

The sequence was analysed using BLASTN (Altschul *et al.*, 1990) on the GenBank website (https://www.ncbi.nlm.nih.gov/genbank, last accessed 1st January 2025), to compare it against other published DNA sequences, using the standard settings, optimised for "Somewhat similar sequences (blastn)" (https://blast.ncbi.nlm.nih.gov/Blast.cgi, last accessed 1st January 2025).

The tree was rooted, using a COX1 sequences from a moth, the Common White Wave *Cabera pusaria* (Linnaeus, 1758), as an outgroup. The final phylogenies were produced from sequences aligned obtained from the GenBank and BoldSystems websites and trimmed in R v4.3.1 (R Development Core Team, 2022) using the package DECIPHER. These aligned and trimmed sequences were imported into MEGA version 12 (Kumar et al, 2024) for phylogenetic analysis. The analysis was run on three computing threads, for 1000 replicates using the standard bootstrapping setting to produce a maximum likelihood tree, using a nearest neighbour interchange (NNI) and uniform rates in the Tamura-Nei model (Tamura and Nei, 1993) of nucleotide substitutions.

RESULTS

COXI sequences were available in NCBI GenBank for 19.3% (38/197) and full mitochondrial sequences 5.6% (11/197) of the species of Hippoboscid listed in the checklist (Dick, 2018). A range of other mostly partial sequences were available for a few Hippoboscid flies: cytochrome oxidase subunit II (COII), large subunit ribosomal RNA, small subunit ribosomal RNA gene, 12s, 16s, 18s and 28s ribosomal RNA, ribosomal RNA gene, internal transcribed spacer 2, cytochrome b, carbamoyl phosphate synthetase (CAD), trisephosphate isomerase, anayl-tRNAsynthetase (AATS), elongation factor-1 alpha (EF), 6-phosphogluconate dehydrogenase.

The fly used for sequencing was taken from an adult male Nightjar *Caprimulgus europaeus* (Linnaeus, 1758), from the Clocaenog Forest, in Wales, United Kingdom, Latitude 53.03N, 3.49 W, at an altitude of 390 m above sea level, on 11th July 2022.

It was identified a female *Pseudolynchia garzettae*. The genus was determined on the basis of it having fully developed wings with only one cross-vein, whereas the other common fully winged species in the United Kingdom, the *Ornithomya* spp. have three cross-veins. It was distinguishable from *P. canariensis* because the scutellum was approximately three times as wide as it was long with a slightly curved posterior edge (*P. canariensis* has a scutellum approximately four times as wide as it is long, with a straight posterior edge), and it had fewer than twenty dark setae on the dorsal thorax (*P. canariensis* has more than twenty pale setae on the dorsal thorax) (Wawman, 2024). These features are shown in the photographs in Figure 1. The fly has a wing length of 5.2 mm. The other measurements are shown in in Table 1.

Figure 1. Photographs of the specimen of *Pseudolynchia garzettae* that was sequenced: a) dorsal habitus (as seen at x2 magnification) showing the shape of the scutellum; b) ventral habitus (as seen at x2 magnification); c) wing showing only one cross-vein, and the presence of microtrichia on the wing membrane (wing photographed by Dave Brice).

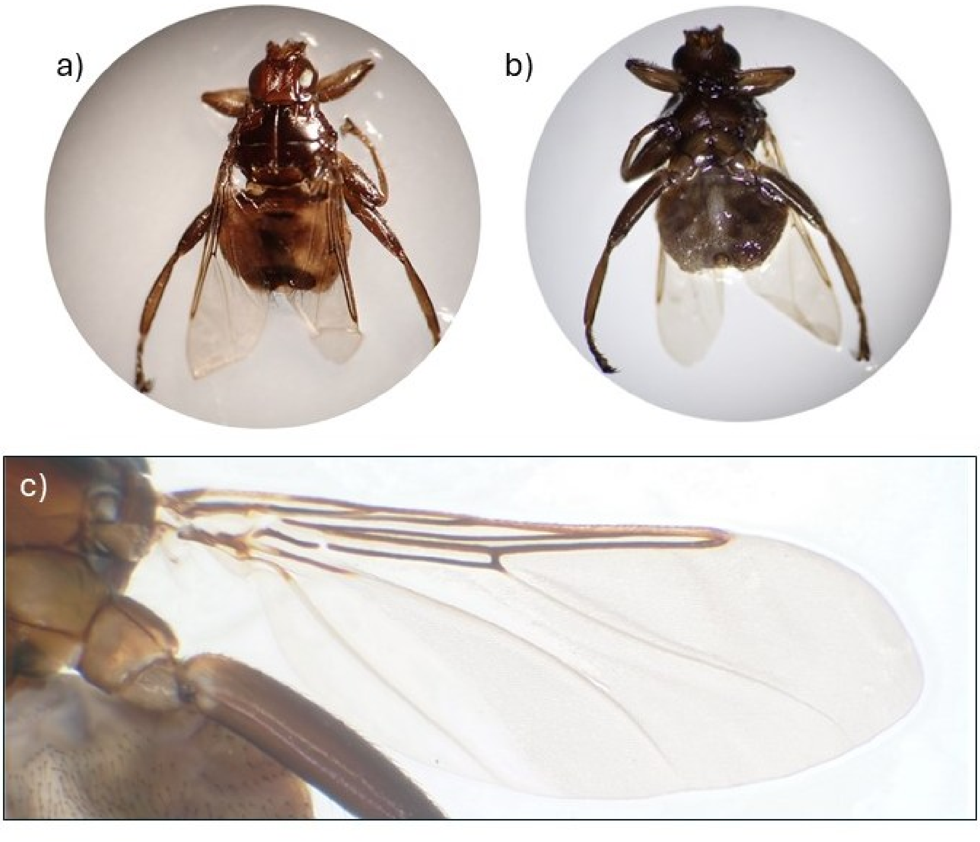


Table 1: Measurements of the specimen of *Pseudolynchia garzettae* that was sequenced.

	Length (in mm)	Maximum width (in mm).
Head	1.2	1.7
Thorax	2.2	2.7
Abdomen	1.5	1.7

DNA sequencing yielded a 662 long base pair consensus sequence (NCBI GenBank accession number PQ740968). The closest match to the sequence found using the BLASTN function in GenBank was a 96% match with *Pseudolynchia canariensis*. The sequences from flies identified only to genus were all a 97.77% or greater match with *P. canariensis,* with all but one of the sequences being a greater than 99.5% match with *P. canariensis*. The phylogeny produced in GenBank can be seen in the Supporting Information, S1.

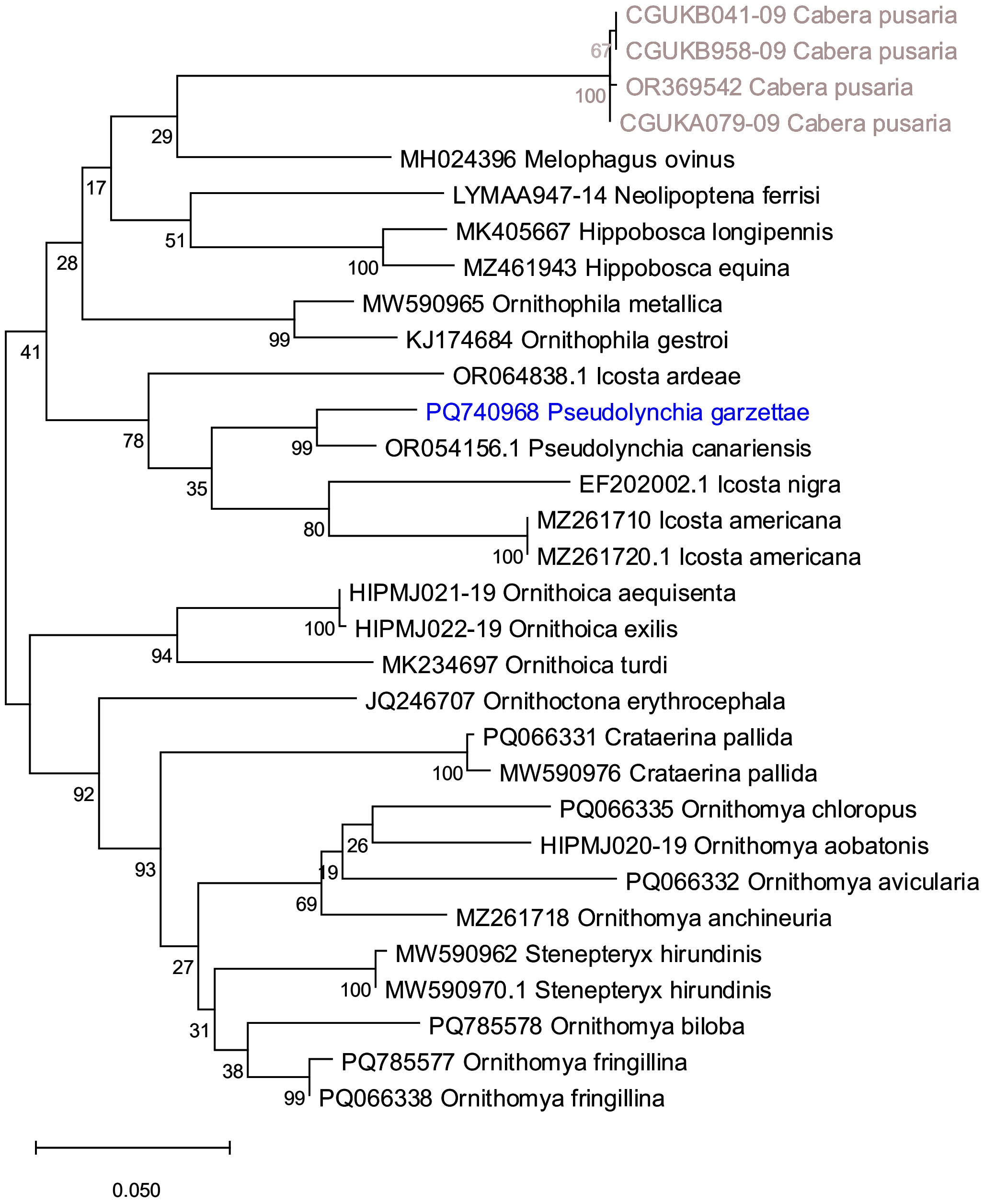
A comparison in GenBank BLASTN with the closest match (*Pseudolynchia canariensis* isolate Pigeon Keds, Pigeon Louse Fly cytochrome c oxidase subunit I (COX1) gene, partial CDS; mitochondrial Sequence ID: OM073981.1) with CDS feature enabled, showed the new COX1 sequence for *Pseudolynchia garzettae* differed by 23 base pairs from the P. canariensis sequence. However, only two of these base substitutions in this short sequence have resulted in a change in the amino acid coded: alanine and valine in *P. garzettae* compared to threonine and methionine in *P. canariensis*.

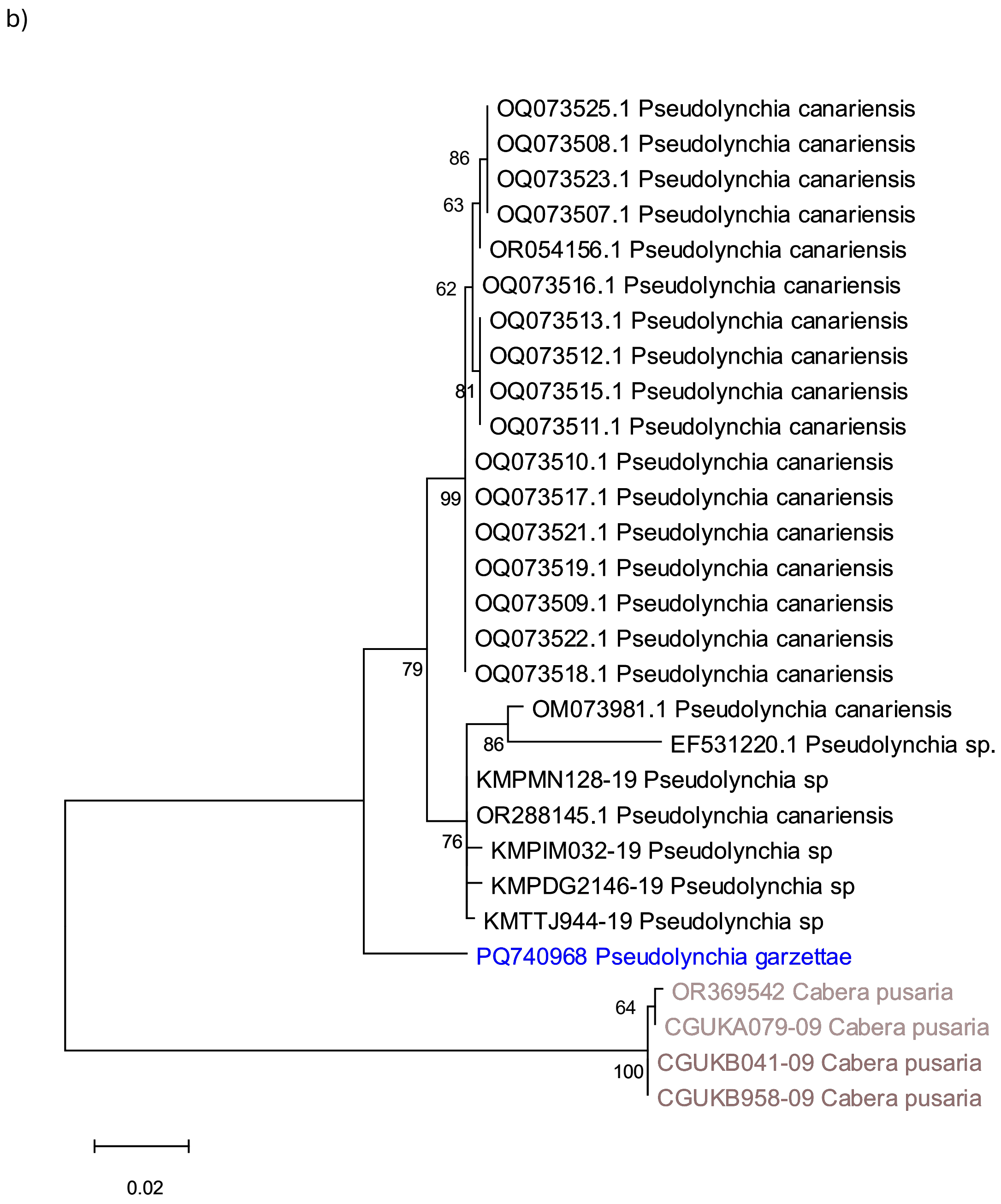
Phylogenies plotted in R, using sequences from GenBank and BOLD, for the Hippoboscidae (Figure 2a) and for the genus *Pseudolynchia* (Figure 2b)) also show that *Pseudolynchia garzettae* is most closely related to *P. canariensis,* and that both species in a clade within the genus *Icosta* (Speiser, 1905), which is large genus represented here by the species, *Icosta americana* (Leach, 1905), *Icosta ardeae* (Marquart, 1835), and *Icosta nigra* (Perty, 1833). However, the bootstrap value supporting this node is low (35).

The second phylogeny also shows that all of the sequences from specimens only identified to the level of the genus *Pseudolynchia* are *P. canariensis.*

Figure 2. Phylogenies including the new sequence, with the moth *Cabera pusaria* as an outgroup, showing the position of *Pseudolynchia garzettae* within a) the *Hippoboscidae* and b) within the genus *Pseudolynchia*. The scale bar indicates the branch length (number of substitutions per site between the nodes).

a)





b)
OQ073525.1 Pseudolynchia canariensis
OQ073508.1 Pseudolynchia canariensis
OQ073523.1 Pseudolynchia canariensis
OQ073507.1 Pseudolynchia canariensis
OR054156.1 Pseudolynchia canariensis
OQ073516.1 Pseudolynchia canariensis
OQ073513.1 Pseudolynchia canariensis
OQ073512.1 Pseudolynchia canariensis
OQ073515.1 Pseudolynchia canariensis
OQ073511.1 Pseudolynchia canariensis
OQ073510.1 Pseudolynchia canariensis
OQ073517.1 Pseudolynchia canariensis
OQ073521.1 Pseudolynchia canariensis
OQ073519.1 Pseudolynchia canariensis
OQ073509.1 Pseudolynchia canariensis
OQ073522.1 Pseudolynchia canariensis
OQ073518.1 Pseudolynchia canariensis
OM073981.1 Pseudolynchia canariensis
EF531220.1 Pseudolynchia sp.
KMPMN128-19 Pseudolynchia sp
OR288145.1 Pseudolynchia canariensis
KMPIM032-19 Pseudolynchia sp
KMPDG2146-19 Pseudolynchia sp
KMTTJ944-19 Pseudolynchia sp
PQ740968 Pseudolynchia garzettae
OR369542 Cabera pusaria
CGUKA079-09 Cabera pusaria
CGUKB041-09 Cabera pusaria
CGUKB958-09 Cabera pusaria
86
63
62
81
99
79
86
76
64
100
0.02

DISCUSSION

The DNA sequence supports the current taxonomy that places *P. garzettae* in the genus *Pseudolynchia* with *P. canariensis*, within the same clade as the genus *Icosta*. All of the other sequences from specimens only identified as *Pseudolynchia* sp. in GenBank and BOLD were confirmed as *Pseudolynchia canariensis*.

This additional sequence may help with the identification of some louse flies by "DNA barcoding". It may be particularly important as this species is increasingly being found in Europe (Nartshuk *et al.*, 2019; Le Guillou, Chapelin-Viscardi and Droz, 2024; Wawman, 2024) and may also be extending its range at its northeastern edge. It will also help to determine the relationship between species in the genus *Pseudolynchia* and be useful the designation of potential new species of louse fly, although the use of longer sequences, and/or whole genome sequencing, would also be useful.

SUPPORTING INFORMATION

Figure S1. Phylogeny for genus *Pseudolynchia* produced from all the specimens in the GenBank database plus the specimen of *Pseudolynchia garzettae*

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AUTHOR CONTRIBUTIONS

Conceptualisation DCW; investigation DCW; methodology DCW; project administration DCW; species identification DCW; data curation DCW; formal analysis DCW; validation DCW; visualization DCW; writing – original draft DCW; writing – review and editing DCW, ASB, SRF, ALS; DNA extraction ASB, SRF; resources DCW, ALS; supervision ALS

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

ETHICAL STATEMENT

The Nightjars were handled by bird ringers licensed by the British Trust for Ornithology.

DATA AVAILABILTY STATEMENT

The DNA sequence is available in NCBI GenBank with Accession Number PQ740968.

The louse fly will be donated to Oxford University Natural History Museum on completion of the study.

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CHAPTER 3

The changing distributions and host associations of the Hippoboscidae of the United Kingdom, Ireland and Isle of Man

Introduction

Human activity is changing the world in a number of ways. The most frequently discussed is climate change, usually in terms of global warming, but some areas may become cooler. and there may be associated changes in changes in precipitation, windspeed, wind direction, and the number and severity of extreme climatic events. These changes may affect the ranges, phenology and interactions between insects (Harvey et al., 2023). While a longer growing season for plants and a longer active period for insects due to increasing temperatures may benefit many species, ranges may contract as the temperature exceeds species' critical thermal limits (Weaving et al., 2023) or those of their food sources. The resulting changes in the balance between prey, predators or competitors, produce changes in the food web (Bartley et al., 2019).

Anthropogenic changes are not limited to climate. Movement of people and livestock may accelerate the movement of diseases and parasites to new areas, and changes in land use, such as urbanisation, bring species into contact that would never previously have met (World Health Organization, 2024). Anthropogenic food sources may lure wild species away from their natural habitats and cause them to congregate in numbers which facilitate disease transmission, as is seen in wild birds on garden bird feeders (Lawson et al., 2018), and species, such as gulls (Laridae), feeding on human refuse and in water sources contaminated with human faeces, facilitating transmission of both pathogens and antibiotic resistant bacteria (Mukerji et al., 2020; Reed et al., 2003; Veldman et al., 2013; Vredenburg et al., 2014).

Changes in the ranges and interactions between hosts and parasites, especially those which cause disease or act as vectors, may have major implications for their hosts, due to increasing parasite prevalence or disease transmission. The risk is not limited to new species of parasite bringing new diseases. Existing vectors may remain active for longer, increasing the duration of disease transmission and, when disease outbreaks occur, increased over-winter survival of vectors may increase the potential for autochthonous disease transmission (Folly et al., 2022; Mansfield et al., 2024).

The Hippoboscidae are proven vectors of avian disease (Baker, 1967; Cepeda et al., 2019), but are also known to harbour a wide range of potential pathogens for which their role as vectors has not been fully determined (Bezerra-Santos & Otranto, 2020). However, the most recent full survey of their UK ranges was in the 1950s and 1960s, and it is likely that with climate change, like other species of insects, their ranges have shifted, and that new species, may have colonised the region.

We are lucky to have a long history of natural history recording in the UK, where even a neglected taxon like the Hippoboscidae has been recorded, although the records are not easily accessible, as most are in the grey literature, such as bird ringing group and local entomological society reports. Many records are within the databases of individual Local Environmental Records Centres (LERCs), or relate to museum specimens which may not be fully catalogued.

The first reliable record of a Hippoboscid in the UK is, perhaps not unexpectedly, one from Gilbert White, of *Stenepteryx hirundinis* in Selborne in 1773 (White, 1789). However, due to the taxonomic disagreements described in Chapter 2.1, many of the earlier records from the genus *Ornithomya* cannot be reliably assigned to a species, so the first reliable records for *O. chloropus* and *O. fringillina* do not appear until after the acceptance of Dennis Hill's revision of the genus (Hill, 1962b). Hill examined 3532 records and specimens, from museums and from his own and other entomologist's collections, of the three species of *Ornithomya* present in the region, to define their ranges and host species associations (Hill, 1962a). For these reasons, and because it predates the period of accelerated global warming (Hansen et al., 2006), in this chapter, I refer frequently to Dennis Hill's work (Hill, 1962a) for information on the ranges and host distributions of the *Ornithomyae* in Great Britain and Ireland in the 1960s. For the other species, I use Tony Hutson's guide (Hutson, 1984) and Peter Chandler's checklist of Diptera (Chandler, 2024) to establish a baseline of species present.

This whole chapter relies on the results of the Mapping the UK's Flat Flies Project, a citizen science project that I set up in 2020. I recruited British Trust for Ornithology (BTO) licensed bird ringers to collect louse flies which left birds during routine ringing sessions, supplied them with collection kits, and asked them to return any flies they caught with the requested metadata at the end of the season. Officially, 286 bird ringing groups, bird observatories and individual bird ringers took part, but many more reported taking part without asking for a kit, but not being able to catch any flies. Hippoboscids are almost impossible to catch if you are outdoors, and can hide very well indoors, often emerging hours later. Entomologists and members of the public also joined in, contacting me via social media and the Hippoboscidae and Nycteribiidae Recording Scheme (https://dipterists.org.uk/hippoboscidae-scheme/home) with offers of flat flies and keds.

In Chapter 3.1, I report that three species of louse fly on the British List (Chandler, 2024), that had only previously been recorded as vagrants, are now breeding in the UK. Of these, one, the Pigeon Louse Fly *Pseudolynchia canariensis* is a proven biological vector of *Haemoproteus columbae* (Cepeda et al., 2019) and another, the Swallow Louse Fly *Ornithomya biloba* has been shown to harbour trypanosomes (Santolíková et al., 2022). There is no research on the vectorial capacity of the third, the Nightjar Louse Fly *Pseudolynchia garzettae* – its first “DNA barcode” being that reported in chapter 2.2.

In Chapter 3.2, I use various techniques to map the ranges of the UK flat fly species, showing pole-ward movement of several species since the 1960s, with three of the *Ornithomya* species significantly expanding their UK and Republic of Ireland (ROI) ranges, and one, *Ornithomya chloropus*, undergoing range contraction at lower altitudes in the southern part of its range.

In Chapter 3.3, I explore the host-parasite interactions of the UK Hippoboscidae, including keds with the louse flies, and compare current host associations of the generalist *Ornithomya* species with those found in the 1960s (Hill, 1962a). With more species of louse fly present, it would be expected that the interaction networks would become more complex with increasing network metrics, purely as a function of increasing the number of nodes in the network (Morris et al., 2014). To avoid this issue, when comparing the current interaction data with that from Hill, for the *Ornithomya* species, I included only the three originally native species of *Ornithomya* and used the same host species list, and used identically similar sized datasets (3532 flies). Despite this the results show a marked increase in the complexity of the host-parasite interaction network, with a notable shift in the host species to include gulls, that is likely to be associated with their colonisation of urban areas, as well as the detection of keds on bird species.

Together, these changes - new breeding species, range shifts and increasing numbers of host-parasite associations – increase the potential for the Hippoboscidae to vector diseases between species. The extent to which this might happen will be dependent on their vector competence and their hosts’ susceptibility to the various diseases, as well as the vagaries of the climate in the region.

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3.1

Ornithomya biloba, Pseudolynchia garzettae and *Pseudolynchia canariensis* (Diptera: Hippoboscidae): three new United Kingdom colonists and potential disease vectors.

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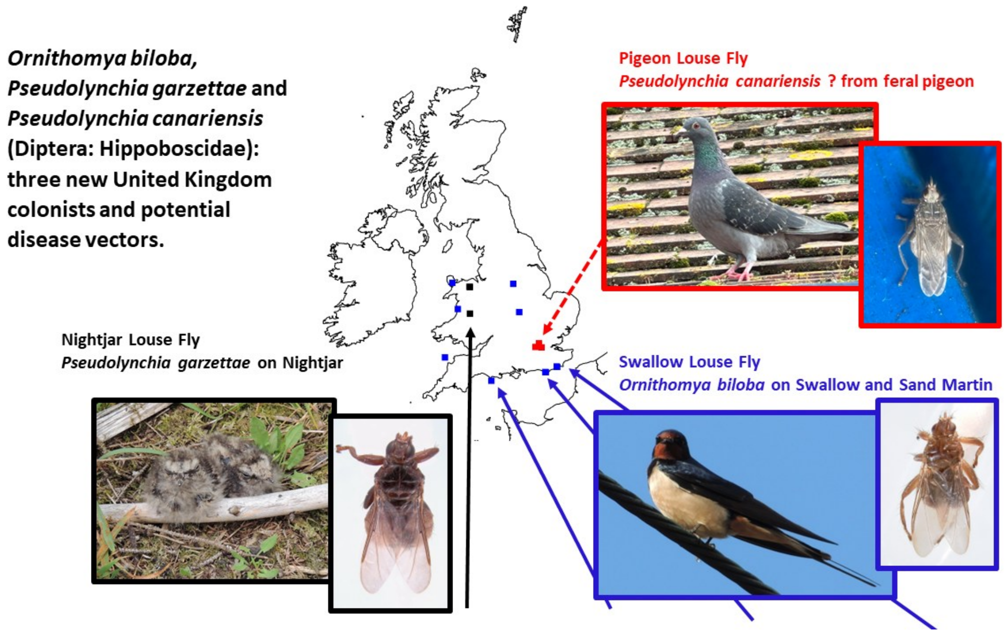
GRAPHICAL ABSTRACT



- A citizen science project found evidence that three species of louse fly, which had previously been considered to be vagrants, are now breeding in the United Kingdom.
- *Pseudolynchia garzettae* was found on Nightjars, *Ornithomya biloba* on Swallows and Sand Martins and free flying *Pseudolynchia canariensis* were found in London.
- The presence of these species may have implications for avian health in the region.

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Ornithomya biloba, *Pseudolynchia garzettae* and *Pseudolynchia canariensis* (Diptera: Hippoboscidae): three new United Kingdom colonists and potential disease vectors

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Abstract

In the northern hemisphere, many species' ranges are shifting northwards with climate change. Here I present evidence, from the first large-scale citizen science study of the Hippoboscidae in the United Kingdom, for the colonisation of the United Kingdom by three species of Diptera in the family Hippoboscidae, which are obligate ectoparasites of birds. The Swallow Louse Fly, *Ornithomya biloba*; the Nightjar Louse Fly, *Pseudolynchia garzettae* and the Pigeon Louse Fly, *Pseudolynchia canariensis* were previously considered to be vagrants from more southerly latitudes but the presence of a pair taken possibly in the act of copulation, gravid females and the increase in numbers of the various species provides good evidence of local breeding activity. I discuss the potential for further northwards range shift and whether the presence of three new species of parasite may have implications for the spread of avian disease within the region. I also include a concise key to the genus *Pseudolynchia* and images of *P. canariensis*, *P. garzettae* and *O. biloba* to aid further identification of these species in the region.

KEYWORDS
avian parasites, citizen science, colonisation, ectoparasites, flat fly, key, louse fly, parasites, range change, range expansion

INTRODUCTION

Colonisation is the establishment of a species where it has not lived previously. Initial colonists generally arrive in small numbers and may fail to reach the numbers required to maintain an established population due to abiotic factors, lack of suitable habitat, the presence of predators and low population density leading to difficulty finding a mate and decreased genetic variability (Chuang & Peterson, 2016; MacArthur & Wilson, 1967). Although the definitions are in many ways artificial (Hoffmann & Courchamp, 2016), species are usually only considered invasive if they were introduced by man and subsequently cause harm. Many insect species have changed their ranges in response to climate change, for example, bumblebees (Soroye et al., 2020) and butterflies (Minter et al., 2020), but changes in parasite ranges, such as ticks, are less often studied and are complicated by their interaction with range changes of their hosts (Nuttall, 2021).

The Hippoboscidae are a neglected taxon of haematophagous ectoparasitic Diptera, which are difficult to study as they are rarely encountered away from their hosts, large mammals and birds. The species found on mammals are known colloquially as keds, whereas those found on birds are known as louse flies in most of the world but as flat flies in the United Kingdom (Hutson, 1984). However, phylogenetic analysis has shown that division by host species is artificial as some of the louse flies found on birds, including *Pseudolynchia canariensis*, are more closely related to the keds on mammals than the other louse flies (Petersen et al., 2007). Here, the terms louse fly and ked will be used to refer to the flies parasitising the different host groups, birds and mammals, respectively, and Hippoboscidae/Hippoboscids to refer to the whole family.

With the exception of some of the keds in the genus *Melophagus*, the Hippoboscidae spend part of their life cycle away from their hosts as puparia, either in abandoned nests of their bird hosts or on the ground. Such a lifecycle means their range is restricted by abiotic factors such as temperature and levels of precipitation: the emergence of louse flies is temperature dependent, with low winter temperatures proving lethal or causing delayed emergence (Corbet, 1956; Kennedy et al., 1975; Klei & Degiusti, 1975; Walker & Rotherham, 2010b), and louse flies of the genus *Ornithoica* were found to be more prevalent on juvenile North Island Robins, *Petroica australis longipes*, in wetter territories (Berggren, 2005). With climate change, some species of Hippoboscidae have expanded their European range. The ked, *Lipoptena fortisetosa*, originally thought to have been introduced on Sika Deer, *Cervus nippon*, was first recorded in the Czech Republic in 1967 and has now spread as far west as Estonia (Kurina et al., 2019), and the Deer Ked, *Lipoptena cervi*, has also shifted its range further north and is now found on Moose *Alces alces* in Finland as well as on several species of deer (Kaunisto et al., 2011).

While some louse flies have little direct effect on their hosts (Walker & Rotherham, 2010a), *P. canariensis* infestation increases the time pigeons spend preening, using energy and reducing the time available for foraging, predator surveillance and courtship (Waite et al., 2012), and may cause emaciation in heavily infested birds (Reeves & Lloyd, 2019). Some louse flies are known to be competent vectors of avian malaria (Baker, 1967; Cepeda et al., 2019) and a range of other pathogens have been isolated from Hippoboscids, including some with zoonotic potential, although in most cases, their status as a specific vector has not been proven (Bezerra-Santos & Otranto, 2020). While most species of louse fly rarely bite humans, bites from *P. canariensis* can cause skin irritation (Reeves & Lloyd, 2019).

In Europe and North Africa, *Ornithomya biloba* (Diptera: Hippoboscidae) is usually found on the Barn Swallow *Hirundo rustica*, rarely on bird eating raptors and occasionally on other Hirundines: House Martin *Delichon urbica*, Sand Martin *Riparia riparia* and Crag Martin *Ptyonoprogne rupestris* (Hill et al., 1964; Hutson, 1981, 1984). It has been found as far north as Skane in Sweden (Hill et al., 1964). This species was recorded in the United Kingdom on four occasions prior to 2020 (Table 1) and was considered a vagrant by Hutson, as it had only been found on early Swallows despite being common on Swallows in France, including at Cap Gris Nez on the English Channel coast (Hutson, 1984), and being recorded on Guernsey in the Channel Islands in 1968 (Guernsey Biological Records Centre, pers. comm.). In one study of *O. biloba* in Czechia, 18.7% were found to contain trypanosomes and were considered to be competent vectors by the authors, although this was not proven (Santolíková et al., 2022).

Despite *P. canariensis* having an almost worldwide distribution in tropical and temperate regions, in association with its main host, the feral or domestic pigeon *Columba livia domestica*, and some of the raptors that prey on them (Haeselbarth et al., 1966; Maa, 1969; Sychra et al., 2020), the first and only previously published record in the United Kingdom was of a fly in Isleworth, London on the 6 October 2020 (Harrow, 2021). This is despite large numbers of feral pigeons living in UK cities, with the most recent reliable estimate suggesting a population of c0.85 million +/−0.2 million in London alone (Taylor, 2013) and there being 42,000 people across the United Kingdom, including in London, who keep and race pigeons (Pigeon Racing UK & Ireland, 2023). *Pseudolynchia canariensis* is a proven vector of *Haemoproteus columbae* (Cepeda et al., 2019).

The main range of *Pseudolynchia garzettae* is central and east Africa, but it has been previously recorded in France, Switzerland, Cyprus, Thailand, Taiwan and the Philippines (Maa, 1969; Nartshuk et al., 2019). It is usually found on nightjars, including the species *Caprimulgus europaeus* (Nightjar) found in the United Kingdom, but has also been found on a range of other species, including owls and buzzards (Haeselbarth et al., 1966). The only previous UK record of *P. garzettae* is that of a specimen found in a museum in Coventry, labelled '31.5.1912, off Nightjar, Hants', which had previously been misidentified as *Ornithomya fringillina* (Palmer, 1987).

Here I provide evidence for colonisation of the United Kingdom by these three species of avian ectoparasites, two of which were collected as part of the Mapping the UK's Flat Flies Project, a study involving British Trust for Ornithology licensed bird ringers, and the third identified from photographs on the internet. I discuss the potential for further range expansion by these species and how this may lead to an increase in avian diseases. I also include photographs of all three species and a simple key to the genus *Pseudolynchia* in the region, as, although these species are included in a recent key to species in Europe (Oboňa et al., 2022), the genus is not comprehensively covered in the commonly used guide to Hippoboscidae in the United Kingdom (Hutson, 1984).

MATERIALS AND METHODS

In 2021 and 2022, following a pilot study in 2020, British Trust for Ornithology (BTO) licensed bird ringers were recruited as expert

TABLE 1 Previous records of *Ornithomya biloba* in the United Kingdom.

Date	Place	Host	References
6 June 1964	Rye Meads, Hertfordshire	Swallow	Lloyd-Evans (1967)
25 May 1970	Spurn, Yorkshire	Swallow	Hutson (1984) Harry E. Beaumont pers. comm.
June 1972	Connel, Argyll	Swallow	Hutson (1984) Hugh Insley pers. comm.
7 October 2007	Icklesham, East Sussex	Paddyfield Warbler *Acrocephalus agricola*	Mark Grantham, pers. comm.

citizen scientists to take part in the Mapping the United Kingdom's Flat Fly Project, via appeals the BTO's publication 'Lifecycle' and on the social media sites Twitter (www.twitter.com, last accessed 25 September 2023) and Facebook (www.facebook.com, last accessed 25 September 2023), as well as direct approaches to bird observatories, ringing groups and individual bird ringers.

Each volunteer was sent a collecting kit containing pots for catching flies, uniquely numbered 2 mL tubes, 70% ethanol (diluted with distilled water and containing no other excipients), pipettes, instructions, recording sheets, a data consent form, a risk assessment for the ethanol and a stamped addressed envelope to return samples. Further supplies were posted to participants as required. Other bird ringers who were not part of the project, including those in Ireland, were also able to submit flies for inclusion in the study.

Collecting was limited to those flies that left birds during normal bird processing due to UK ringing licensing conditions (animal welfare considerations). Ringers were asked to collect all possible flies and return them at the end of the season with the following metadata: site name, Ordnance Survey Grid Reference, altitude and, if known, the species, age, sex and moult status of the host bird, using BTO codes (Redfern & Clark, 2001), and the number of flies seen on and collected from each host.

Louse flies were identified to species level, using a binocular microscope, following a key (Hutson, 1984) with additional information as required (Hutson, 1981; Maa, 1964, 1966; Maa & Petersen, 1987).

Additional records were collected in the author's role as national recorder for the Hippoboscidae as part of a new recording scheme which started in November 2020. The recording scheme uses the website iRecord (https://irecord.org.uk last accessed 25 September 2023) but also receives data from iNaturalist (https://www.inaturalist.org last accessed 25 September 2023). Some records were found on Twitter. The total numbers of Swallows and Nightjars ringed were obtained from the 'BTO online ringing report' (Robinson et al., 2022).

Grid references were checked on the website Curaera (www.cucaera.co.uk/grp last accessed 25 September 2023), and Ordnance Survey Grid References were converted to latitude and longitude using the website Batch Convert Tool (https://gridreferencefinder.com/batchConvert/batchConvert.php, last accessed 25 September 2023), for Great Britain and the Isle of Man and Batch Coordinate Converter (http://ww2.scenictours.co.uk/serve.php?t=WoNlbJvoVlhuJL5405objaa8jVO8atNuwZV, last accessed 25 July 2022) for Ireland.

Graphs and maps were plotted in R version 4.2.1 (R Development Core Team, 2022) with the packages maps (Becker et al., 2022), mapdata (Becker et al., 2018) and scales (Wickham & Seidel, 2022). Kernel densities were calculated and plotted using the package adehabitatHR (Calenge, 2006).

To determine the exact status of the species in the United Kingdom, a literature search, including peer reviewed and grey literature and websites, was performed using each of the terms, '*Ornithomya biloba*', '*Ornithomyia biloba*' (*Ornithomyia* being a previously used spelling for the genus [Maa, 1965]), '*Pseudolynchia*', '*Pseudolynchia canariensis*' or '*Pseudolynchia garzettae*', in combination with each of the following 'United Kingdom', 'Great Britain', 'Ireland', 'England', 'Wales', 'Scotland', 'Northern', 'Ireland', 'British', 'Irish', 'English', 'Scottish' and 'Welsh', using the search engines Google (www.google.com, last accessed 25 March 2023), Google Scholar (https://scholar.google.com, last accessed 25 March 2023) and Bodleian Solo (https://solo.bodleian.ox.ac.uk, last accessed 25 March 2023). Historical data were obtained from Local Environmental Records Centres, museums, GBIF, iRecord, iNaturalist, bird observatory and bird ringing groups' reports. Contact was also made with authors of previous studies to check their current understanding of the status of these species (A.M. Hutson, Harry E. Beaumont, pers. comms.).

RESULTS

A total of 2597 louse flies from 104 species of bird were received from over 140 bird ringers, ringing groups and bird observatories, at sites in 279 unique 10 km squares (Figure 1), across the United Kingdom, Isle of Man and Ireland (the region) as the BTO ringing scheme covers the whole region, and bird ringers in Ireland were keen to take part. This article focuses only on the new breeding species recorded in the region, and the results of the main study will be published in due course.

Ornithomya biloba (Dufour, 1827)

The mapping project yielded 13 new specimens (Table 2 and Figure 2a,b). Unlike the previous records from Hirundines, these all occurred within their hosts' breeding seasons or autumn migrations. Although reverse migration (López-Calderón et al., 2021) of birds from Continental Europe cannot be completely ruled out, it is unusual and most of the bird ringers who caught the specimens at coastal sites were sure, from a combination of weather conditions, local knowledge and the recovery histories of birds controlled on the same day as those caught with ectoparasites, that these were mostly local or UK breeding birds (Clare Buckle, Tony Cross and Phil Jones, pers. comms.). One pair of flies was taken 'tangled together' (Clare Buckle, pers. comms.) possibly in the act of copulation.

Pseudolynchia sp.

There is one UK record of '*Pseudolynchia*' in the records supplied by the Warwickshire Biological Records Centre, from a rural area adjacent to Solihull, from May 2014 to September 2014. Unfortunately, there is no further information, which would allow this record to be verified or determined to species level.

Pseudolynchia canariensis (Macquart, 1839)

Three new records have been added. All were found as misidentified flies on Twitter (one) and iNaturalist (two; Table 3 and Figure 2c). The

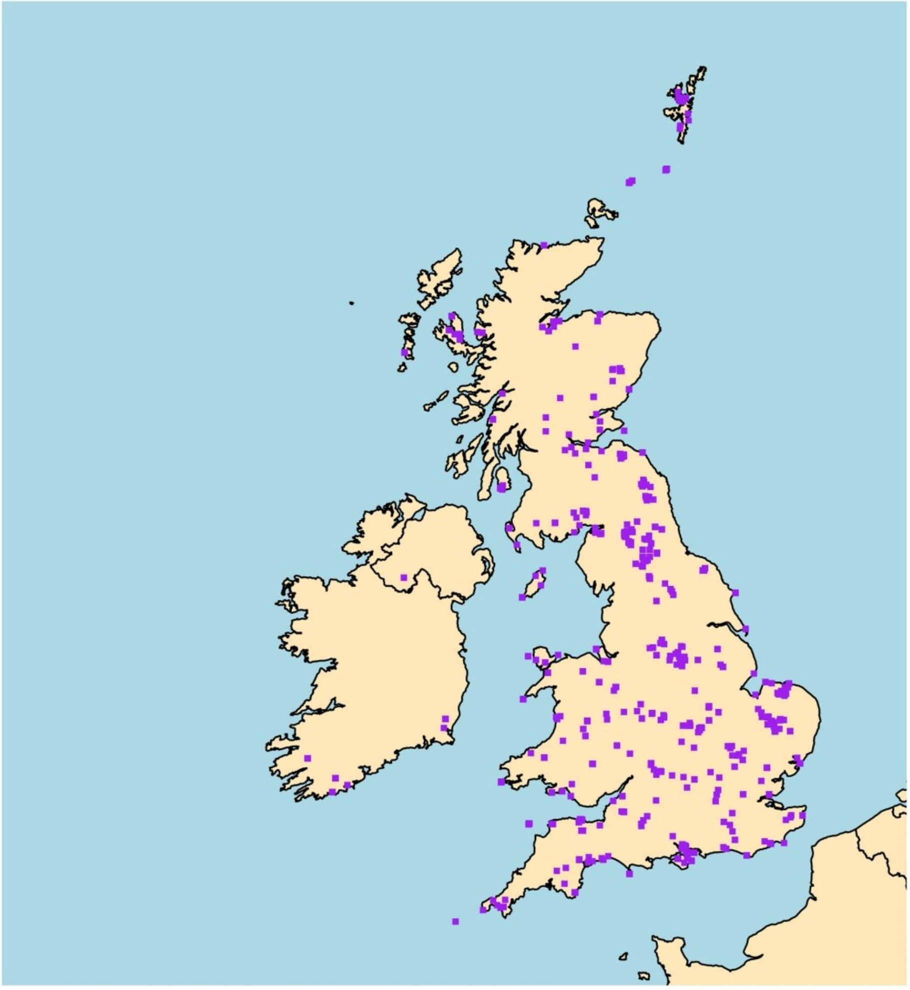

FIGURE 1 Sites at which ectoparasites were collected for the Mapping the UK's flat fly project.

fly found by D.F. Huerta (Figure 6b) has a very rounded, pale abdomen, which may indicate that it is a gravid female but this is impossible to confirm from the photograph.

All records of this species have been of free-flying individuals in the London area, the new records falling within a relatively small area of Inner London. There are no records of flies found in association with a host, usually the feral pigeon or domestic pigeon *Columba livia domestica*. This is not unexpected as pigeon fanciers treat their birds for parasites and feral pigeons are not included in the BTO ringing scheme.

Pseudolynchia garzettae (Rondani, 1879)

The mapping project found three more specimens of *P. garzettae*, all female, two of which were gravid (Table 4 and Figure 2d).

TABLE 2 New records of *Ornithomya biloba* in the United Kingdom.

Date	Place	Host	Finder	Sex/breeding status
8 July 2021	Culverwell, Portland Bill, Dorset	Swallow	Mark Cutts	Female
3 August 2021	Cors Ddyga, Anglesey	Swallow	Rachel Taylor	Female
23 August 2022	Icklesham, East Sussex	Sand Martin	Rye Bay Ringing Group	Male
24 August 2022	Icklesham, East Sussex	Sand Martin	Rye Bay Ringing Group	Female
25 August 2022	Icklesham, East Sussex	Swallow	Rye Bay Ringing Group	Two females on same bird
25 August 2022	Borth Bog, Ynyslas, Dyfed	Swallow	Mid-Wales Ringing Group	Male
26 August 2022	Icklesham, East Sussex	Unknown	Rye Bay Ringing Group	Female
1 September 2022	Avenue Washlands Nature Reserve, Derbyshire	Swallow	Bryn Roberts	Female
19 September 2022	Stanford Reservoir, Northamptonshire	Swallow	Stanford Ringing Group	Female
19 September 2022	Lundy Island, Devon	Swallow	Lundy Field Society	Male
3 October 2022	Hope Bottom, East Sussex	Swallow	Clare Buckle	Male and female? in copula

DISCUSSION

A 2-year study, in which volunteer BTO licensed bird ringers collected bird ectoparasites, found evidence that three species of louse fly, which were previously considered to be vagrants in the United Kingdom, are now breeding in the region. The study added 13 new records of *O. biloba*, including a possible mating pair, to the previous UK total of four. Three new specimens of *P. garzettae*, including two gravid females, were found in Wales, this being a species which had only been recorded once before in southern England. In addition, records from the internet added three new records of *P. canariensis*, from the Inner London area, bringing the UK total to four.

Some of the flies in the genus *Pseudolynchia* have been previously misidentified by recorders, as evidenced by the online records of *P. canariensis* and the historical misidentification of the only previous UK specimen of *P. garzettae* (Palmer, 1987). Misidentification is more likely to occur with flies in the genus *Pseudolynchia* as they are not illustrated in the most widely used identification guide (Hutson, 1984) and this may partially account for some of the recent increase in observations.

As this is the first large-scale study of louse flies in the United Kingdom undertaken at a large number of sites over a short period of time, it is impossible to say whether these species have been present, and have gone undetected, or whether they are recently arrived, although earlier systematic work in the 1950s and 1960s by entomologists and museum curators (see Supplementary Materials), who examined large numbers of louse flies, collected over previous decades, did not find evidence of these species. Neither did smaller more intense studies of single species of flies or single host species nor studies from single sites such as those found in bird observatory annual reports. A list of the important studies reviewed but not cited in this text is included in the Supplementary Materials. It is unlikely that multiple studies in the 1950s and 1960s would have missed species entirely if they were present in significant numbers but small localised populations on infrequently studied species of bird host could have gone undetected, especially as most louse flies are seen by bird ringers who are usually more interested in the host than its parasites.

Pseudolynchia garzettae might easily go unnoticed in the United Kingdom: its main host, the Nightjar, is a crepuscular summer migrant, unlikely to be found near human habitation, and only small numbers are ringed each year (Figure 3), with fewer than 10 ringed in most years before 1965 and recent annual totals of only between 500 and 600 (Robinson et al., 2022). Bird ringers monitoring Nightjars are usually working outdoors, in poor light or in the dark when it would be hard to spot parasites leaving their host and difficult to catch them.

Conversely, *O. biloba* should have been detected if it was present in the United Kingdom. The numbers of its main host, the Swallow, ringed each year are similar now, at roughly 20,000 birds per year, to those ringed during the heyday of UK louse fly studies in the 1960s (Figure 4) and were much higher during the intervening period. *Ornithomya biloba* is relatively easy to distinguish from the other species of *Ornithomya* present in the region (Figures 5a, 6a and 7a) and is illustrated in Hutson's guide (Hutson, 1984), although caution is needed to separate it from other potential vagrants such as *O. roubaudi*, which is yet to be recorded in the United Kingdom. It therefore seems likely that *O. biloba* is a new colonist rather than a previously overlooked species. It also seems unlikely that a major infestation of *P. canariensis* could have gone unreported in domestic pigeons in the United Kingdom for any length of time, but large numbers of ectoparasites could survive undetected on feral pigeons as these are rarely handled. The detection of several free-flying individuals would suggest a much larger population as these flies are rarely seen away from their hosts.

The probability of successful long-term colonisation by a species is proportional to the original population size, birth rate and death rate of the species and carrying capacity of the environment (MacArthur & Wilson, 1967). In the case of parasites, the carrying capacity of the environment is the availability of suitable hosts. Thus further range expansion by *P. garzettae* in the United Kingdom is likely to be limited by the low population density of its main host the Nightjar. In contrast, *P. canariensis* has a readily available supply of its preferred host the feral or domestic pigeon, which is common in urban areas throughout the country, and its wild ancestor, the Rock Dove, found

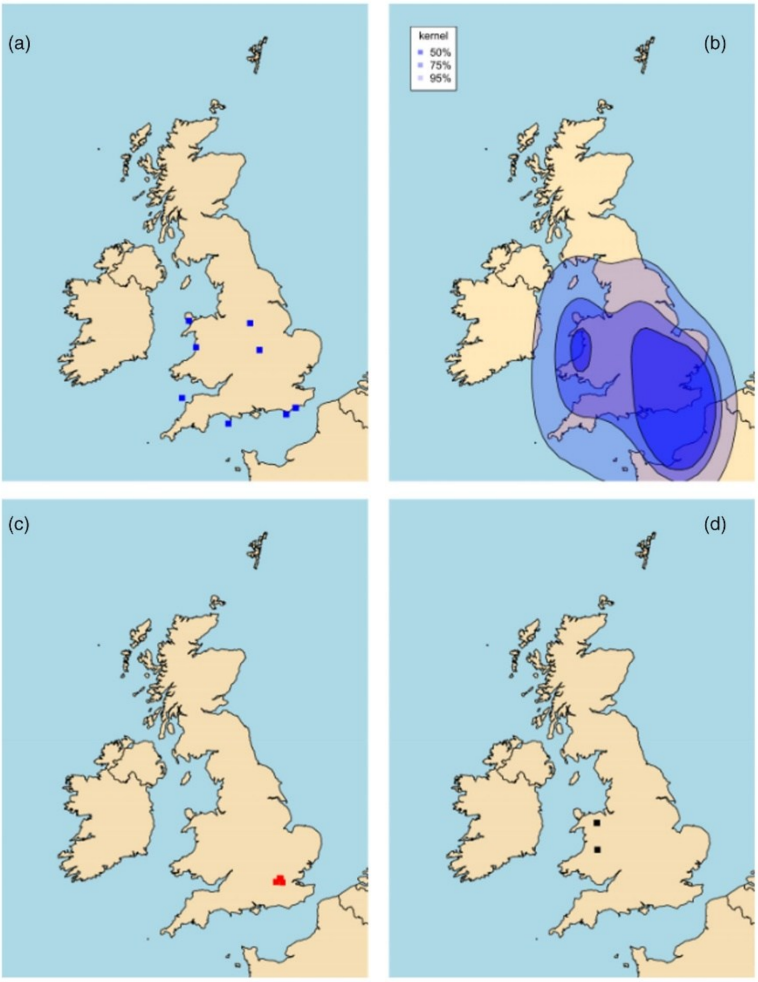

FIGURE 2 Maps showing (a) the locations of new *Ornithomya biloba* specimens and (b) their kernel densities at 50%, 75% and 95% probabilities. (c) Map of new records of *Pseudolynchia canariensis*. (d) Map of the locations of new specimens of *Pseudolynchia garzettae*.

TABLE 3 New records of *Pseudolynchia canariensis*.

Date	Place	Host	Source of data	Finder/Licence
5 September 2022	Waldram Cresent, Forest Hill, Dulwich, Inner London	Free-flying	iNaturalist	David Fernández Huerta CC-BY-NC
28 October 2022	Hampstead, London Borough of Camden, Inner London	Free-flying	Twitter	Rory Dimond
14 November 2022	Camden Square, London Borough of Camden, Inner London	Free-flying	iRecord via iNaturalist	'lamaureen' CC-BY-NC

TABLE 4 New UK records of *Pseudolynchia garzettae*.

Date	Place	Host	Finder	Sex breeding status
11 July 2022	Gors-y-wern. Clocaenog Forest	Nightjar	Mid-Wales Ringing Group	Female
27 July 2022	Clywedog Reservoir, Clocaenog Forest	Nightjar	Mid-Wales Ringing Group	Female Gravid
7 August 2022	Waun Marteg, near Rhayader	Nightjar	Mid-Wales Ringing Group	Female Gravid

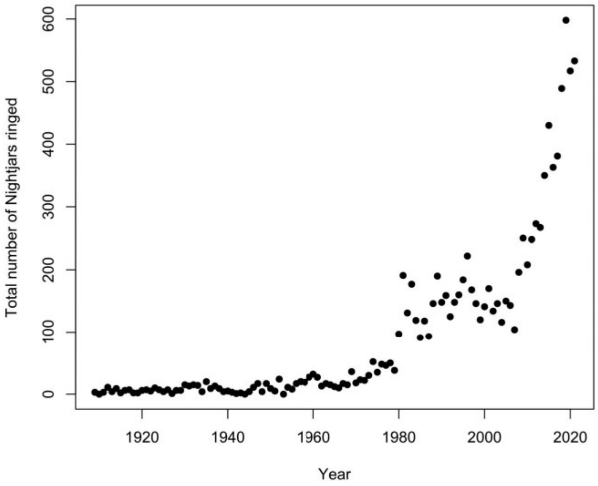

FIGURE 3 Total number of Nightjars ringed in the United Kingdom, Ireland and the Isle of Man, per year. Data from the BTO online ringing and nest recording report (Robinson et al., 2022).

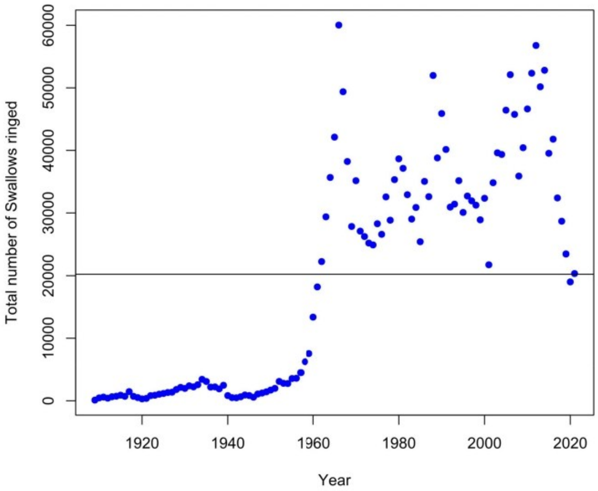

FIGURE 4 Total number of Swallows ringed in the United Kingdom, Ireland and the Isle of Man, per year. The horizontal line represents the total number of Swallows ringed in 2021, the first year of the main study. Data from the BTO online ringing and nest recording report (Robinson et al., 2022).

on remote Scottish Islands (Smith et al., 2022). The Swallow, the main host of *O. biloba*, breeds across the United Kingdom, being absent from only a few areas of central London and northern Scotland (Balmer et al., 2013).

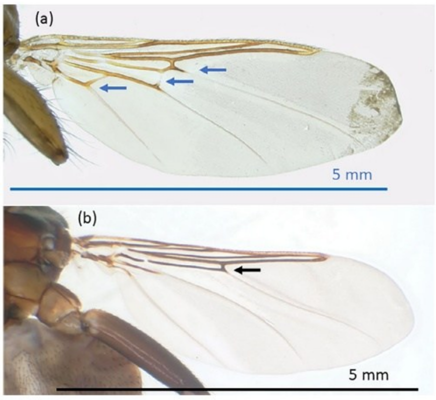

FIGURE 5 (a) Wing of *Ornithomya biloba*: note the three cross-veins, indicated by arrows, one of which rarely fills. This contrasts with the single cross-vein seen in (b) the wing of *Pseudolynchia garzettae*.

However, host ranges place only a partial limitation on the ranges of these species of flies because of their potential to switch host species. Despite its widely used common name suggesting host specificity, the Pigeon Louse Fly *P. canariensis* has been found on many other avian species: Maa reported *P. canariensis* from 33 genera of birds across 13 families (Maa, 1969), and Sychra et al. found it on a further six species of birds in five families in South Africa (Sychra et al., 2020). *Pseudolynchia canariensis* has been found living on urban, but not rural, Woodpigeons *Columba palumbis* in Spain (Gutiérrez-Galán & Martínez-Fernández, 2023) and it is possible that, as Woodpigeons are migrants (Snow, 1953), they could help *P. canariensis* spread across the United Kingdom. Across its range, *P. garzettae* has been found on 14 genera of birds of seven families (Maa, 1969) although it has only been recorded on Nightjar in the United Kingdom. Elsewhere in Europe, *O. biloba* has been recorded on all three species of Hirundine, which breed in the United Kingdom (Hutson, 1981) and on Sparrowhawk *Accipiter nisus* (Hill et al., 1964). In the United Kingdom, it had only previously been recorded on Swallow, with the records presented here from Sand Martin and Paddyfield Warbler *Acrocephalus agricola*, representing new host records for the country.

Although the UK's native species of louse flies undergo a winter diapause (Corbet, 1956; Hill, 1963; Walker & Rotherham, 2010b), which limits them to one generation a year, *O. biloba* has both diapausing and non-diapausing generations (Kennedy et al., 1975), and adult *P. canariensis* emerge after only 25–31 days when kept at laboratory temperature (Coatney, 1931). In good conditions, these shorter

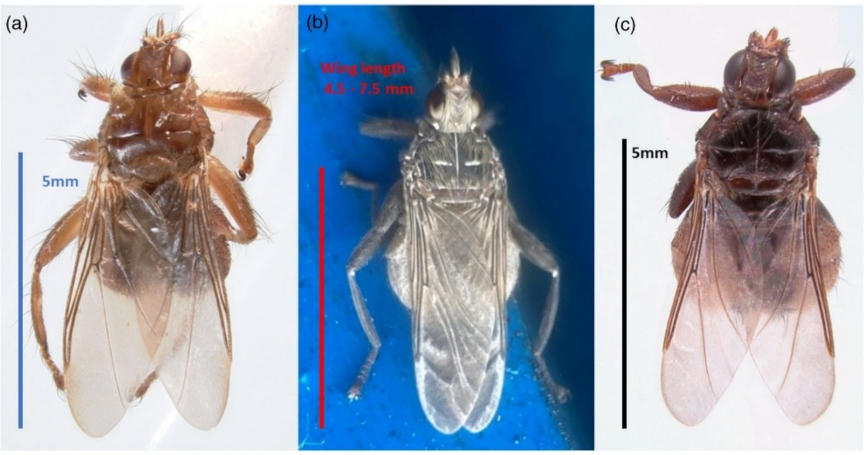

FIGURE 6 (a) *Ornithomya biloba*. Note the presence of multiple bristles on the scutellum, which are not restricted to a single row near the posterior edge as they are in the other species of *Ornithomya* in the region (shown in more detail in Figure 7a). (b) *Pseudolynchia canariensis*. Note the rectangular scutellum and pale bristles on the thorax. The very rounded, pale abdomen suggests that this might be a gravid female, but this cannot be confirmed without a more detailed examination of the specimen. The wing length is indicated as the known range for the species (Maa, 1966) because the specimen was not measured. Image reproduced with permission © David Fernández Huerta, 2022. (c) *Pseudolynchia garzettae*. The scutellum is rounded posteriorly, and the bristles on the thorax appear black in a live fly and are shown in more detail in Figure 7b. All images reproduced with permission.

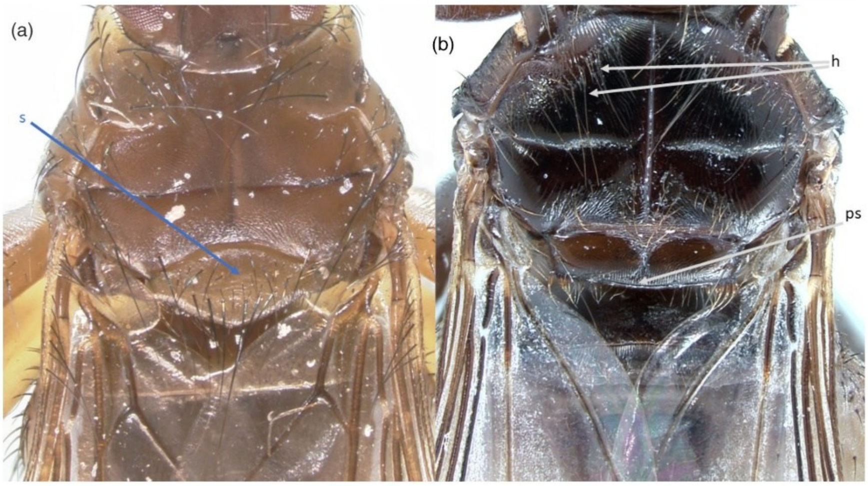

FIGURE 7 Detail of thorax, (a) *Ornithomya biloba* and (b) *Pseudolynchia garzettae* highlighting key identification features. (a) The arrow labelled 's' indicates the scutellum of *O. biloba* with multiple bristles that are not restricted to a single row as they are in the other species of *Ornithomya* in the region. (b) Note the rounded edge to the scutellum of *P. garzettae* indicated by 'ps' and the dark bristles on the anterior thorax 'h'—in real life, these are dark, but the colour has been adjusted to highlight them. Images reproduced with permission.

generation times could allow a rapid increase in numbers, helping these species to establish new populations.

Conversely, factors that decrease survival may prevent further range expansion. *Pseudolynchia canariensis* is likely to be limited by abiotic factors such as winter temperatures in rural areas: the puparia die after more than 20 days at temperatures of 13°C or lower (Klei & Degiusti, 1975), but the puparia could survive in pigeon lofts where pigeon racing enthusiasts keep their birds. Adult flies can survive for up to 86 days, although the mean is only 17 or 18 days (Arcoverde et al., 2009), so it is also possible that small numbers of adult flies could survive cold periods on adult pigeons, either on domestic birds that are not treated for ectoparasites or feral pigeons. The increased temperatures in urban heat islands may help *P. canariensis* to survive in cities, but changes in humidity due to urbanisation (LaDeau et al., 2015) and pollution (Buczek et al., 2014) have been shown to limit the spread of some arthropod vectors within an urban setting and might limit its spread. The puparia of *O. biloba* could survive overwinter in sheltered Swallow nests in buildings, especially as they have been shown to develop most rapidly at 11°C under laboratory conditions (Kennedy et al., 1975).

Combining what is known of these parasites' lifecycles may allow us to predict which of these three species are most likely to successfully expand their ranges in the United Kingdom. The shorter generation times and widespread availability of suitable hosts, that nest in buildings or within urban heat islands, could allow *O. biloba* and *P. canariensis* to rapidly colonise the region, with *O. biloba* having a greater advantage as the puparia survive at lower temperatures. Gaps in our knowledge of the biology of *P. garzettae* make it more difficult to predict the long-term outcome for this species in the United Kingdom, but the lower population density of its hosts that live in rural areas, away from urban heat islands, may limit the spread of this species outside of its main range in Africa.

Even though the Hippoboscidae are unlikely to transfer disease to humans, their role as vectors of avian malaria within bird populations could be important. The presence of additional species of haematophagous ectoparasite might increase the potential for disease transmission, and the risks of emergent avian diseases and zoonoses, especially when their hosts are long distance migrants with large geographical ranges, like Nightjars, Swallows and Sand Martins, or species living in close association with humans such as pigeons. We would do well to continue to monitor the ranges of these ectoparasites carefully and explore their potential as disease vectors, and this will form the basis of future research.

SIMPLIFIED KEY TO THE GENUS PSEUDOLYNCHIA IN THE UNITED KINGDOM

Fully developed wings with one cross-vein (Figure 5b), large eyes. On birds.

> Rectangular scutellum, approximately four times as wide as it is long, with a distinct, straight posterior edge. 20 or more long, pale setae on thorax (Figure 6b). Usually on pigeons.
>
> ***Pseudolynchia canariensis***

Scutellum approximately three times as wide as long, with a slightly curved posterior edge (Figure 7b). Fewer than 20 dark or black setae on thorax (Figure 6c). Usually on Nightjar.

Pseudolynchia garzettae

AUTHOR CONTRIBUTIONS

Denise C. Wawman: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; resources.

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CONFLICT OF INTEREST STATEMENT

The author declares that there are no conflicts of interest. All records have been correctly attributed. With the exception of the photograph of *Pseudolynchia canariensis* (Figure 6b), all photographs and images have been produced by, or commercially for, the author, who wishes to retain copyright of these images. David Fernández Huerta has agreed to the use of his image of *Pseudolynchia canariensis* but wishes to retain the copyright.

DATA AVAILABILITY STATEMENT

The data for the three species discussed are provided in the tables in the main text. These details will be uploaded to the Hippoboscidae and Nycteribiidae Recording Scheme records in iRecord in due course, and published as part of the full data set for the whole Mapping the UK's Flat Fly Project when all the research has been published.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. *Supplementary information: additional references and acknowledgements not included in the main text*. References for original species descriptions. Sources of information checked for species records but not referenced in the main text as no relevant records were found. List of all the people who collected specimens for the project. Data for the three species discussed are provided in the tables in the main text. Full details will be uploaded to the Hippoboscidae and Nycteribiidae Recording Scheme records in iRecord in due course. The BTO ringing totals for the United Kingdom and Ireland are freely available in the online ringing report section of the BTO website: http://www.bto.org/ringing-report. The specimens of *O. biloba* and *P. garzettae* have been retained by the author.

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3.2

Citizen scientists mapping the United Kingdom's flat flies (louse flies) (Diptera: Hippoboscidae) reveal a vector's range shift.

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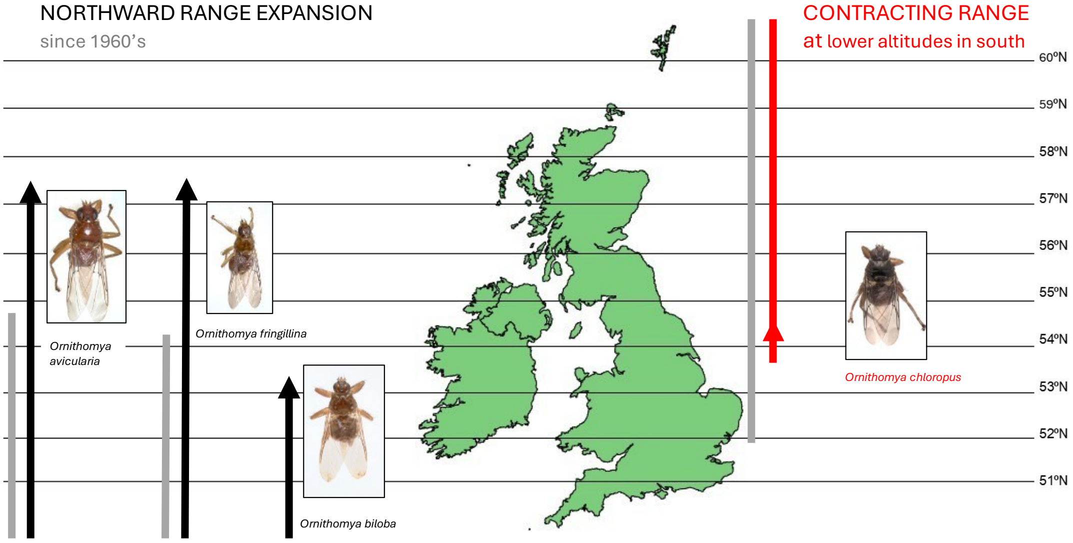
GRAPHICAL ABSTRACT



- The Common or Bird Louse Fly *Ornithomya avicularia*, a vector of Haemoproteus sp. and trypanosomes, has undergone a major northwards range expansion in the United Kingdom since the 1960's.
- The Finch Louse Fly *Ornithomya fringillina* has also expanded its range northwards and the Swallow Louse Fly *O. biloba* is now established in Wales and Southern England.
- The range of the Grouse Louse Fly *Ornithomya chloropus* is contracting at lower altitudes at the southern edge of its range.

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ORIGINAL ARTICLE

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Citizen scientists mapping the United Kingdom's and Republic of Ireland's flat flies (louse flies) (Diptera: Hippoboscidae) reveal a vector's range shift

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Abstract

Changes in climate may cause changes in the ranges, phenology and interactions of insects with other species and lead parasites to switch host species. A study of louse (flat) flies in the United Kingdom, Republic of Ireland and Isle of Man, in which licensed bird ringers acting as citizen scientists collected ectoparasites that left birds during ringing, showed recent range shifts of several species. The Common or Bird Louse Fly *Ornithomya avicularia* (Linnaeus, 1758), a vector of *Haemoproteus* sp. and trypanosomes, has undergone a major northwards range expansion of over 300 km in the United Kingdom (UK) since the 1960s. The Finch Louse Fly *Ornithomya fringillina* (Curtis, 1836) has also expanded its range over 300 km northwards and 400 km westwards into the Island of Ireland, and the Swallow Louse Fly *Ornithomya biloba* (Dufour, 1827) is now established in Wales and Southern England. The Grouse Louse Fly *Ornithomya chloropus* (Bergroth, 1901) has undergone a range contraction at lower altitudes and on the southern edge of its range. Other species of louse fly were detected: *Crataerina pallida* (Latreille, 1812), *Stenepteryx hirundinis* (Linnaeus, 1758), *Pseudolynchia garzettae* (Rondani, 1879) and *Icosta minor* (Bigot, 1858). Some generalist species have shifted their phenology, whereas the more specialist nest parasites of migrant birds have not, as the arrival and breeding dates of their hosts have not changed. The range changes of the generalist species of these ectoparasites may have implications for bird health, especially if they switch to new host species as their ranges shift.

KEYWORDS
birds, climate change, ectoparasites, modelling, prediction, range shift, vectors

INTRODUCTION

Changes in climate, such as those in temperature and seasonality, may affect the ranges, phenology and interactions of insects with other species (Harvey et al., 2023). Range changes are often related to physiological constraints such as thermal limits (Weaving et al., 2023), as well as changes in interactions with other species, in both food webs, with effects on their ability to find suitable food (Bartley et al., 2019), and with competitors (Gilman et al., 2010). While generalist species may be able to change their position in a food web quickly (Bartley et al., 2019), specialist species are generally slower to adapt (Menéndez et al., 2006). Nonstandardised methods of historic data collection complicate the analyses of range shifts (Guzman et al., 2021), but there are few long-term datasets for parasitic arthropods, even for species such as ticks that are known to be important disease vectors (Nuttall, 2021).

The Hippoboscidae are a family of haematophagous ectoparasites of birds and mammals. The species found on birds are known as louse flies in most of the world but are often referred to as flat flies in the United Kingdom (UK), Republic of Ireland (ROI) and Isle of Man (Hutson, 1984), an area collectively historically referred to as the British Isles, and referred to hereafter as 'the region'. In the UK, there are eight breeding species of flat fly (Hutson, 1984; Wawman, 2024), three of these are generalists, although with some niche separation according to host size and local environmental factors (Hill, 1962a; Lehikoinen et al., 2021). These three generalists are in the genus *Ornithomya* species group 'a': *O. avicularia* (Linnaeus, 1758), *O. chloropus* (Bergroth, 1901) and *O. fringillina* (Curtis, 1836) (Dick, 2018). A fourth member of the genus, the relatively recent UK colonist, *O. biloba* (Dufour, 1827), is in group 'b' and has a preference for Swallow *Hirundo rustica* (Linnaeus 1758) as its main host but can be found on other hirundines (Wawman, 2024). Another two fully flighted species have bred in the UK, *Pseudolynchia canariensis* (Macquart 1839), on feral pigeons *Columba livia domestica* (Gmelin, 1789), and *P. garzettae* (Rondani, 1879) on Nightjar *Caprimulgus europaeus* (Linnaeus, 1758) (Wawman, 2024). A further two species are flightless nest parasites: *Crataerina pallida* (Latreille, 1812) prefers to parasitise Swift *Apus apus* (Linnaeus 1758) but may be found on hirundines, and *Stenepteryx hirundinis* (Linnaeus, 1758) (*Crataerina hirundinis* [Linnaeus, 1758]) is found on hirundines, especially on the House Martin *Delichon urbicum* (Linnaeus, 1758) (Hutson, 1984). In Ireland, only five species of louse fly are known to breed: *O. avicularia*, *O. chloropus*, *O. fringillina*, *C. pallida* and *S. hirundinis* (O'Connor & Sleeman, 1987; Smiddy & Sleeman, 2004).

Louse flies reproduce by adenotrophic viviparity. Fertilised eggs are released one at a time into the female's uterus, where the larvae hatch and are fed from a special milk gland. When a third instar larva is mature, parturition occurs and the larva's exoskeleton hardens to form a puparium (Baker, 1967). Flightless females in the genera *Crataerina* and *Stenepteryx* leave their avian hosts to deposit their larvae in their hosts' nests (Hutson, 1984). Females capable of flight in the genus *Ornithomya* may give birth while on their hosts or leave them when they are resting to find a suitable site to larviposit (Corbet, 1956; Hutson, 1984), and female *P. canariensis*, kept on captive domestic pigeons, were observed to deposit their larvae away from both their hosts and their nest material in darkened corners or under objects (Coatney, 1931). The well-established species in the region undergo a winter diapause (Corbet, 1956; Hill, 1963; Walker & Rotherham, 2010b), but the recent UK colonists (Wawman, 2024) have shorter lifecycles: *P. canariensis* emerges from puparia after only 25–31 days when kept at 'laboratory temperatures' (Coatney, 1931); *O. biloba* has both diapausing and non-diapausing generations (Kennedy et al., 1975).

Adults, and thus the eggs and larvae inside females, are protected against environmental extremes when on their homeothermic avian hosts but free-flying adults and overwintering puparia may be exposed to harmful temperature, humidity and precipitation. The ability of flighted adults to find hosts maybe affected by wind speed, and in Poland, counts of the ked *Lipoptena fortisetosa* (Maa, 1965) were negatively correlated with increasing wind speed (Gałęcki et al., 2020). In common with the Hippoboscids found on birds, the puparia of the Deer Ked *Lipoptena cervi* (Linnaeus, 1758) undergo a winter diapause off their hosts and have been shown to freeze at −26°C during diapause, −20°C as developing puparia and −21°C as adults (Harkonen et al., 2012). High temperatures (20°C) during the winter diapause cause a deterioration in the immune-based encapsulation response of diapausing *L. cervi* (Kaunisto et al., 2015). Little is known about the thermal tolerance of louse flies in the region but prolonged temperatures of 13°C or lower, or over 37°C were lethal to the puparia of *P. canariensis*, and colony survival was best between 24.6 and 30°C (Klei & Degiusti, 1975). Adult *C. pallida* successfully emerge from puparia in greater numbers at temperatures of 27–36°C—the temperature range in Swift nests during incubation—although smaller numbers emerged at lower temperatures, and none emerged when they were kept at 4–14°C to simulate winter temperatures (Walker & Rotherham, 2010a).

Thompson reported the presence of *S. hirundinis* in the British Isles from May to October, with numbers reaching a peak in June and *C. pallida* from June to August with maximum numbers in July (Thompson, 1953). Unfortunately, he did not distinguish between *O. chloropus* and *O. fringillina*, but he reported *O. avicularia* as mainly present from May to September, with a few flies in October, and November, and a peak in August (Thompson, 1954), and Hill reported this species as present from June to late November with a peak in August (Hill, 1963). *Ornithomya fringillina* was found from early July to late September at several sites, and *O. chloropus* (reported as *O. lagopodis* [Sharp, 1907]) was seen from July to September in Fair Isle (Hill, 1963). Corbet reported *O. chloropus* (as *O. fringillina* before the *Ornithomya* species were revised and the specimens reviewed [Hill, 1962b]) as present from June to mid-August, and occasionally as late as October on Fair Isle (Corbet, 1956).

Hill reported that *O. avicularia* was, other than accidental records on migrant hosts from Scandinavia, absent from Scotland and the surrounding islands (Hill, 1962a). Whereas earlier authors (Smart, 1939) believed that *O. fringillina* was rare and restricted to south and south-east England, Hill reported it as far north as Lancashire, with a continental distribution only as far north as Southern Sweden and Denmark (Hill, 1962a). *Ornithomya fringillina* was first reliably identified from the Island of Ireland in 1982 (Smiddy & Sleeman, 2004). *Ornithomya chloropus* was distributed in areas favoured by the Red Grouse *Lagopus lagopus scotica* (Latham, 1787), on higher ground bounded by a line that, in the early 1960s, correlated with the '61°F July isotherm' (~16°C) and suggested it was a glacial phase survivor, whereas *O. fringillina*'s and *O. avicularia*'s distributions suggested that they were post-glacial invaders (Hill, 1962a). Other earlier research on the distribution of *Ornithomya* spp. in the region (Thompson, 1954) cannot be compared with records using the current taxonomy because only two species of *Ornithomya* were recognised, instead of three. Suitable avian hosts of the generalist species are present throughout the UK and are unlikely to restrict their ranges.

Thompson suggested that *C. pallida* and *S. hirundinis* would be found throughout the breeding ranges of their hosts, although he had no records from collectors in Scotland and northern England for *C. pallida* or for the northern half of Scotland for *S. hirundinis* (Thompson, 1953). *Ornithomya biloba* was first recorded as a vagrant in the UK in 1964, with only four records up until 2007 (Lloyd-Evans, 1967; Wawman, 2024). Its main host, the Barn Swallow, is also found throughout the UK, with the exception of Central London and the highest parts of the Scottish Highlands (Balmer et al., 2013).

Changes in the ranges of UK Hippoboscidae are expected with climate change, as many species of insect have expanded their ranges towards higher latitudes (Harvey et al., 2023) and range shifts have been seen in other Hippoboscids in Europe. For example, *Lipoptena fortisetosa* expanded its range northwards from the Czech republic, where it was first found in 1967, to reach Estonia in 2014 (Kurina et al., 2019), and *L. cervi* invaded Northern Europe to reach Finland (Kaunisto et al., 2011).

Parasite range changes may have consequences for its hosts, especially when it is a competent vector of microparasites. As a group, the Hippoboscidae are known to harbour a range of disease causing organisms although in many cases, their status as vectors is not proven (Bezerra-Santos & Otranto, 2020). Of the long established UK species, *O. avicularia* is a proven vector of *Haemoproteus* spp. (Baker, 1963) and trypanosomes in the UK, although the latter was only transmitted if the flies were ingested by the host (Baker, 1956). Several studies have also suggested that *Leucocytozoon* sp. may be transmitted by *Ornithomya* spp. that are present in the UK, but having carefully reviewed all available evidence, Baker felt that it was not conclusive (Baker, 1967). In other countries, trypanosomes have been detected in *O. avicularia*, *O. chloropus* and *O. fringillina* but not in *C. pallida* (Santolíková et al., 2022) and several species of *Babesia* have been detected in *O. avicularia* (Čisovská Bazsalovicsová et al., 2023). Of the recent UK colonists, *P. canariensis* is a vector of *Haemoproteus columbae* (Baker, 1967; Cepeda et al., 2019) and trypanosomes were detected in 18.7% of *O. biloba* in a study in Czechia (Santolíková et al., 2022). *Babesia canis* has also been detected in *O. biloba* (Čisovská Bazsalovicsová et al., 2023). *Rickettsia belii* and *Rickettsia monacensis* have been detected in *C. pallida* (Cerutti et al., 2018), but a study failed to detect *Haemoproteus* spp. in either this fly or its host the Swift in Italy (Ilahiane et al., 2023).

The Mapping the UK's Flat Flies Project is an ongoing citizen science project in which licensed British Trust for Ornithology (BTO) bird ringers are asked to collect flat flies that leave birds during their normal ringing sessions, with the aim of determining which species are present in the region, their geographical and host ranges, and the phenology of the species. It has expanded to include Hippoboscidae of all species, across the region made up of the UK, ROI and Isle to Man. This paper considers the geographical ranges and phenology of the louse fly species as revealed by data collected from June 2020 to May 2024. The presence of new species breeding in the UK has been previously discussed (Wawman, 2024), and the host–parasite associations revealed will be the topic of a further study.

METHODS

The Mapping the UK's Flat Flies Project began as a small pilot study in 2020 and is an ongoing study run as part of the UK Hippoboscidae and Nycteribiidae Recording Scheme. BTO volunteer bird ringers were recruited via social media groups, articles in the BTO's 'Lifecycle' magazine and personal communications and were asked to collect louse flies that were seen leaving birds during their normal ringing activities, as current UK animal welfare regulations prevent the use of methods such as 'dust-ruffling' using insecticidal powders (Walther & Clayton, 1997) or a Fair Isle Apparatus (Williamson, 1954). Participants were sent recording forms, tubes and 70% ethanol and asked to return any flies with the metadata at the end of the season.

Volunteers were asked to collect the following metadata: site name, Ordnance Survey Grid Reference, altitude and, if known, the host species, the number of flies both seen on and collected from each host and its age, sex and moult status, using BTO ringing codes (Redfern & Clark, 2001).

Keds were collected by bird ringers, entomologists and interested members of the public, via both the main mapping project and the national recording scheme.

The flies were identified to species, under a binocular microscope, following a published key and descriptions of flat flies in the British Isles (Hutson, 1984). Additional information for rarer species was sourced from a range of publications (Hutson, 1981a; Maa, 1964, 1966, 1969; Maa & Petersen, 1987).

The grid references and site altitudes supplied in the metadata, that were used for the initial analyses, were checked on the website Curaera (www.cucaera.co.uk/grp last accessed 27 May 2024).

The data were analysed in R version 4.2.1 (R Development Core Team, 2022). The packages *dplyr* (Wickham et al., 2023) and *lubridate* (Grolemund & Wickham, 2011) were used to process the data prior to analysis. Graphs were made in base R, and basic maps were plotted using packages *maps* (Becker et al., 2022) and *mapdata* (Becker et al., 2018), with the package *scales* (Wickham & Seidel, 2022). Kernel densities were calculated using the packages *adehabitatHR* (Calenge, 2006) and *rgdal* (Bivand et al., 2023). Bioclimatic data and species data were formatted into rasters and manipulated in R using the package *raster* (Hijmans, 2023). The maps of previously published ranges were replotted using the functions on the website MapChart (https://www.mapchart.net/uk.html, last accessed 10th June 2024). Binomial glms, comparing pairs of the *Ornithomya* sp., and *O. chloropus* with all the other *Ornithomya* in the study were run in R (family = binomial, link = cloglog) with the package *arm* used to validate the models (Gelman & Su, 2022).

Bioclimatic data, for 2022, the middle year of the main study, and most recent year available, were sourced from the HadUK-Grid data (Met Office et al., 2023). The UK altitude, as the mean altitude for each 1 km^2 square, was taken from Intermap (Intermap. NERC Earth Observation Data Centre, 2009), land cover from LCM 2007 (Morton et al., 2011), protected area status from the UNEP-WCMC and IUCN Protected Planet Report 2020 (UNEP-WCMC and IUCN, 2020) and

TABLE 1 Variables used in the Maxent SDMs and the rationale for choosing them and hypotheses to be tested.

Description	Year	Source	Rationale for inclusion in initial models/hypotheses to be tested	Reason for exclusion from final models
Latitude			Initial data exploration suggested this was important, frequently found to be important in similar studies	
Longitude			Initial data exploration suggested this was important, frequently found to be important in similar studies	
Altitude (m above sea level)	2009	Intermap (2009)	Initial data exploration suggested this was important, frequently found to be important in similar studies	
Calcareous bedrock (% cover per square km)	2014	British Geological Survey	Soil pH may affect survival of invertebrates, relevant to species where puparia may be on the ground	Not found to be relevant
Ground frost annual (number of days)	2022	Met Office HadUK-Grid	Prolonged low temperatures may affect survival more than shorter cold spells, potentially represented by minimum temperatures	
Minimum air temperature seasonal (°C)	2022	Met Office HadUK-Grid	May be lower than lower critical thermal range	Highly correlated with other temperature measures
Maximum air temperature seasonal (°C)	2022	Met Office HadUK-Grid	May exceed higher critical thermal range	
Mean air temperature annual (°C)	2022	Met Office HadUK-Grid	May be a suitable proxy for both maximum and minimum temperature which are likely to be highly correlated and allow a reduction in the number of variables	Highly correlated with other temperature measures
Relative humidity annual (hPa)	2022	Met Office HadUK-Grid	Desiccation may decrease survival of puparia	
Wind speed at 10 m—annual—(m s^{-1})	2022	Met Office HadUK-Grid	May affect flighted flies' ability to find a host	
Precipitation seasonal (mm)	2022	Met Office HadUK-Grid	Possibility of puparia drowning, rain may affect flighted species ability to find a host	
Urban land cover (% cover per square km)	2007	2007 UKCEH land cover map	Some species (*Stenepteryx hirundinis*, *Crataerina pallida* and *Ornithomya biloba*) are associated with hosts that nest in buildings. To check for spatial bias in data. Possible urban heat island effects	
Protected area status (proportion per square km)	2020	UNEP-WCMC and IUCN (2020)	To check for spatial bias in data	Not found to be relevant

Abbreviation: SDM, species distribution modelling.

calcareous bedrock from the British Geological Survey's parent material model (British Geological Survey, 2024; Lawley & Rawlins, 2014). The bioclimatic and land cover variables were used in the species distribution modelling, and the rationale for their inclusion are shown in Table 1. It was not possible to obtain data on the same grid scale for some of these variables for the ROI and those which were available were on a different spatial grid and geographical projection, so, as the area was only sparsely sampled, these data were not included in the most complex level of modelling.

As bioclimatic data were not available for some smaller islands and coastal areas with less than 50% land within a 1-km grid square, these were dealt with in one of two ways. Where there was land immediately adjacent to the site (for example, Portland Bird Observatory and Calf of Man Bird Observatory), the bioclimatic data for the most similar adjacent square (north and west respectively) were used. Where there was no adjacent Ordnance Survey Grid Square with available data (for example, Skokholm Bird Observatory), that of the nearest similar land was used (Skomer Island).

Maximum entropy species distribution modelling (Maxent SDM) was performed using the program Maxent version 3.4.1 (Phillips et al., 2024) using the default settings. After removal of highly correlated variables, the best models were chosen on the basis of the area under the receiver operator curve (AUC) and by visual inspection of the maps produced for anomalies. Variables that did not contribute to the model of each species distribution were excluded based on a combination of permutation importance, jackknife plots and response curves. The data were checked for the presence of spatial bias in favour of urban areas, which is known to occur in many citizen science datasets (Bowler et al., 2022; Sumner et al., 2019), and protected areas (Bowler et al., 2022) by modelling the locations of all flies collected against both urban land cover and protected land cover. The maps published here were produced from the mean of five replicates using the final set of variables.

TABLE 2 Total number Hippoboscids collected (louse/flat flies and keds), number of 1 km Ordnance Survey gird squares square (UK and Isle of Man) that were included in the Maxent species distribution models and total number of 10 km grid squares (UK, Isle of Man and Republic of Ireland) where each species was reported. Some specimens were only supplied with a 10-km grid reference. *Icosta minor* is a vagrant, while the other species are known to breed in the region. It was not possible to identify one damaged *Ornithomya* sp. specimen. The keds are included for completeness although they do not form part of the main study of bird parasites and *Pseudolynchia canariensis* is included to highlight the absence of data from this study.

Species	Number of flies	Number of 1 km squares (United Kingdom only)	Total number of 10 km squares
Louse/flat flies			
Swift Louse Fly *Crataerina pallida* (Latreille, 1812)	60	22	21
Icosta minor (Bigot, 1858)*	1	1	1
Common or Bird Louse Fly *Ornithomya avicularia* (Linnaeus, 1758)	1438	249	217
Swallow Louse Fly *Ornithomya biloba* (Dufour, 1827)	30	13	13
Grouse Louse Fly *Ornithomya chloropus* (Bergroth, 1901)	864	136	103
Finch Louse Fly *Ornithomya fringillina* (Curtis, 1836)	848	139	123
Ornithomya sp.	1	1	1
Pigeon Louse Fly *P. canariensis* (Macquart, 1839)	0	0	0
Nightjar Louse Fly *Pseudolynchia garzettae* (Rondani, 1879)	3	2	2
Martin Louse Fly *Stenepteryx hirundinis* (Linnaeus, 1758)	155	30	29
Keds			
New Forest Fly *Hippobosca equina* (Linnaeus, 1758)	3	1	2
Deer ked *Lipoptena cervi* (Linnaeus, 1758)	99	21	18
Sheep Ked *Melophagus ovinus* (Linnaeus, 1758)	4	2	2
All species	3506	463	350

Flies raised from puparia were excluded from the analysis of phenology as these may have emerged earlier than they would have normally due to being kept indoors.

RESULTS

Total of 3506 Hippoboscids, of 11 species, were received from over 170 individual bird ringers and entomologists, bird observatories and ringing groups up until the date of the analysis in May 2024. These came from 350 10-km grid squares across the UK, Isle of Man and ROI. The flies were collected over a 22-year period from 2002 to 2024, with most collected during the main study period from June 2020 to May 2024. The totals included eight species of louse fly and all three UK species of ked. The only UK breeding species that was missing was the Pigeon Louse Fly, *P. canariensis*, as the BTO bird ringing scheme does not include feral pigeons. The total numbers of each species received are provided in Table 2, with a breakdown of the number of 1-km and 10-km grid squares from which they were collected. A map of all the sites at which specimens were collected can be found in the Figure S1.

The Maxent SDM showed that there was no evidence of bias favouring records from urban or protected areas (Figure S2) with an AUC of 0.541 (0.5 is random, range 0 to 1.0) for urban landcover, 0.563 for protected area status and 0.604 for both urban and protected areas combined, suggesting that the overall sampling distribution of the study was close to random in relation to both human population density and protected area status. As might be expected, a kernel density plot made from the locations of all individual flies collected in the study (Figure S3) showed that collection was not even across the region, reflecting both differences in collecting effort, including poor coverage over most of the island of Ireland, and the populations of Hippoboscids.

The distributions of each of the six most common species (*O. avicularia*, *O. chloropus*, *O. fringillina*, *O. biloba*, *C. pallida* and *S. hirundinis*) can be seen as a series of plots in Figures 1–6, which show the location at which specimens were collected, estimates of distribution using kernel densities and Maxent SDMs, together with the previously published distributions (Hill, 1962a) for the generalist *Ornithomya* spp. Only three specimens of *Pseudolynchia garzettae* (the UK's and the region's second, third and fourth) and one *Icosta minor* (the region's and UK's fourth) were received, and this was insufficient to run a Maxent SDM with the number of variables used in the analyses.

Ornithomya avicularia (Figure 1) has increased its UK range approximately 300 km northwards, from the 1960s, when it was rarely found north of latitude 55°N, roughly the latitude of the Isle of Man, to reach Inverness, latitude 57.5°N. It was caught in numbers at

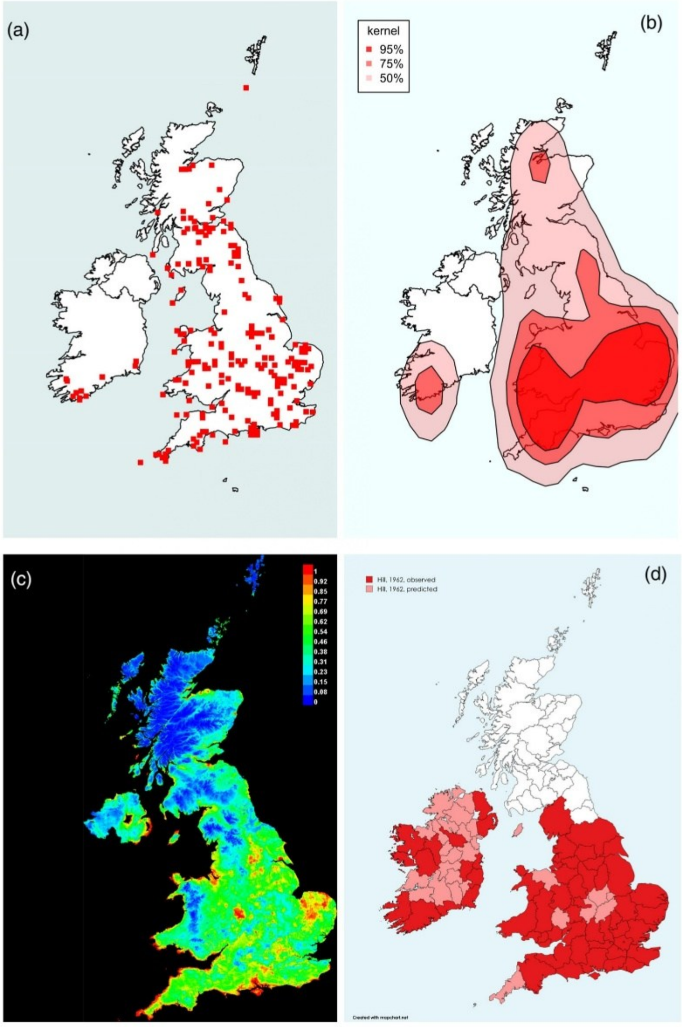

FIGURE 1 Range of the Common or Bird Louse Fly *Ornithomya avicularia* (Linnaeus, 1758). (a) Locations of each 10 km square in which *O. avicularia* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *O. avicularia* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *O. avicularia*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.737). (d) Hill's 1962 ranges for the *O. avicularia*, produced at county level, replotted. The darker red areas are where the species was found: paler areas where he expected it to be present. Note that Hill removed flies found on passage migrant birds from his analysis, whereas they have not been removed from the analyses in this study. AUC, area under the receiver operator curve; SDM, species distribution modelling.

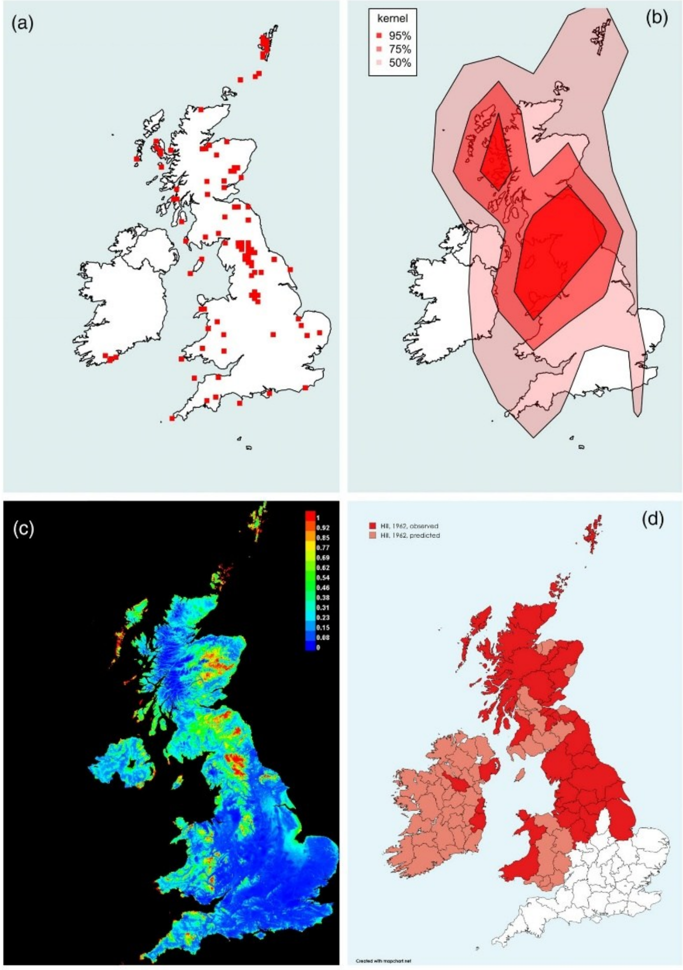

FIGURE 2 Range of the Grouse Louse Fly *Ornithomya chloropus* (Bergroth, 1901). (a) Locations of each 10 km square in which *O. chloropus* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *O. chloropus* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *O. chloropus*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.810). (d) Hill's 1962 ranges for the *O. chloropus*, produced at county level, replotted. The darker red areas are where the species was found: paler areas where he expected it to be present. Note that Hill removed flies found on passage migrant birds from his analysis, whereas they have not been removed from the analyses in this study. AUC, area under the receiver operator curve; SDM, species distribution modelling.

multiple locations (Figure 1a) in the north of England and Scotland where it was not present in the 1960s (Figure 1d). The kernel density plot (Figure 1b) indicates a range covering most of Great Britain, with a concentration of records from England and Lowland Scotland, but does not take altitude and other bioclimatic variables into account. The Maxent SDM (Figure 1c) predicts suitable bioclimatic niches

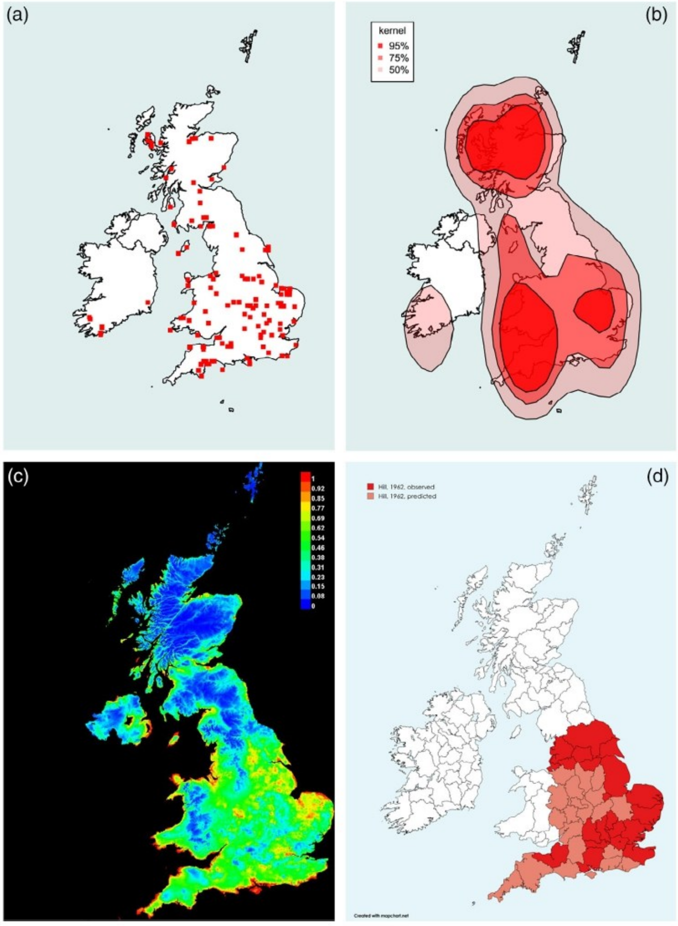

FIGURE 3 Range of the Finch Louse Fly *Ornithomya fringillina* (Curtis, 1936). (a) Locations of each 10 km square in which *O. fringillina* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *O. fringillina* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *O. fringillina*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.738). (d) Hill's 1962 ranges for the *O. fringillina*, produced at county level, replotted. The darker red areas are where the species was found: paler areas where he expected it to be present. Note that Hill removed flies found on passage migrant birds from his analysis, whereas they have not been removed from the analyses in this study. AUC, area under the receiver operator curve; SDM, species distribution modelling.

(shown on the map as green, through yellow, orange and red with increasing probability), corresponding to the sites at which flies were observed. It shows a likely current range throughout the UK, with the exception of the highest ground in England and Wales, and all but the lowest ground in Scotland.

Ornithomya chloropus (Figure 2) may have undergone a slight range contraction at lower altitudes at the southern edge of its range. The few records (Figure 2b) from southern England were mainly on suspected migrant birds near the coast—a set of records that was excluded by Hill (Hill, 1962a) (Figure 2d)—or restricted to higher

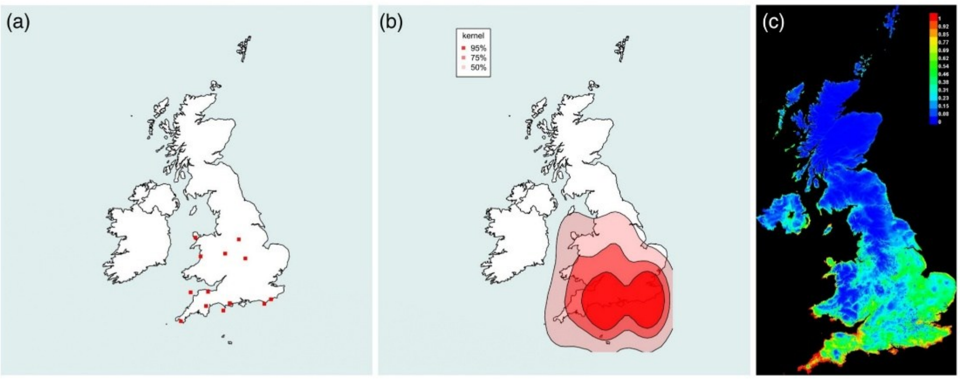

FIGURE 4 Range of the Swallow Louse Fly *Ornithomya biloba* (Dufour, 1827). (a) Locations of each 10 km square in which *O. biloba* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *O. biloba* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *O. biloba*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.805). AUC, area under the receiver operator curve; SDM, species distribution modelling.

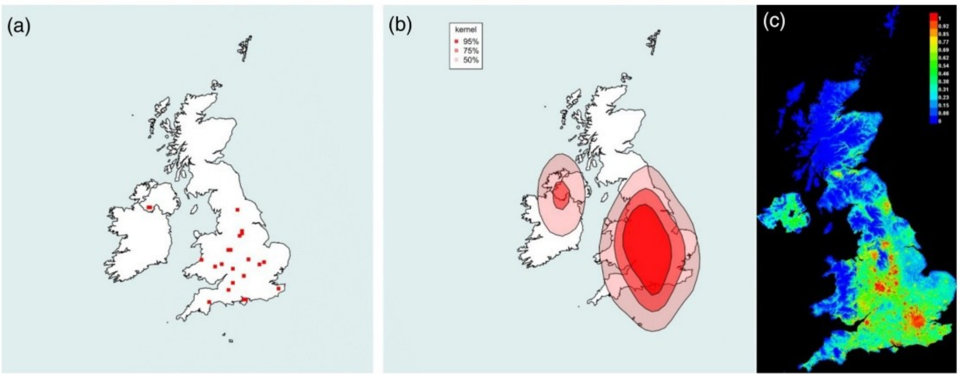

FIGURE 5 Range of the Swift Louse Fly *Crataerina pallida* (Latreille, 1812). (a) Locations of each 10 km square in which *C. pallida* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *C. pallida* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *C. pallida*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.807). AUC, area under the receiver operator curve; SDM, species distribution modelling.

ground on Dartmoor and Exmoor. *Ornithomya chloropus* was also detected on breeding birds on Skokholm Island and Lundy Island off the southern coasts of the UK. *Ornithomya chloropus* has a marked presence along The Pennines—the ridge of hills running north–south in northern England—and is present throughout Scotland. It appears from the map of sites (Figure 2a) and the kernel density plot (Figure 2c) to have been lost from the most southerly part of its former distribution (Figure 2d). The Maxent SDM (Figure 2c) predicts the highest probability of finding areas suitable for *O. chloropus* (red) is at higher altitudes in Scotland, Wales, northern and southwest England, as well as on islands around the coast.

Ornithomya fringillina, in contrast to *O. chloropus* (Figure 3), has, like *O. avicularia*, greatly expanded its UK range. It was mainly restricted to southern England below 54°N, an area south of a line

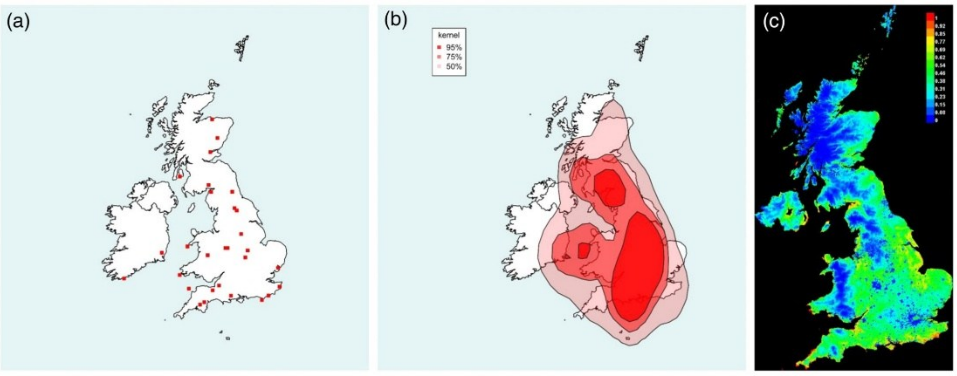

FIGURE 6 Range of the Martin Louse Fly *Stenepteryx hirundinis*. (a) Locations of each 10 km square in which *S. hirundinis* was caught during the study. (b) Kernel density plot at 95% predicted probability (dark red), 75% probability and 50% probability of finding *S. hirundinis* at a given location, based entirely on latitude, longitude and presence data. (c) Maxent SDM, red 100% probability of the environmental niche being suitable for *S. hirundinis*, with orange, yellow and green being increasingly lower probabilities of finding it (green 50% and blue 0%). This plot was produced from five iterations of the Maxent SDM using the final list of bioclimatic variables in Table 1 combined with the presence data from the study (AUC = 0.670). AUC, area under the receiver operator curve; SDM, species distribution modelling.

TABLE 3 The altitude ranges of the *Ornithomya* species in metres.

Species	Altitude range (m)	Mean altitude (m)	Median altitude (m)
Ornithomya avicularia	0–449	84.9	64.0
Ornithomya chloropus	0–640	185.1	80.0
Ornithomya fringillina	0–290	74.7	60.0
Ornithomya biloba	2–278	44.6	20.0
O. avicularia + *O. fringillina* + *O. biloba*	0–449	80.6	64.0

from Blackpool to Leeds, in the 1960s (Figure 3d), but is now seen throughout lowland Scotland to latitude 57.5°N, a distance of over 350 km further north. It has also expanded its range over 400 km westwards into Wales and the ROI. The kernel density plot (Figure 3c) fails to take altitude into account, showing an unlikely distribution over higher ground in Scotland and Wales. The Maxent SDM (Figure 3c) predicts suitable environmental niches present throughout the UK, except at higher altitudes.

Ornithomya biloba (Figure 4) was first recorded as a vagrant in the UK in 1964. Figure 4a shows the location of sites at which it was found; Figure 4b shows the predicted range throughout southern England and all of Wales, south of latitude 53.5°N, using kernel densities; and Figure 4c shows a similar predicted range from a Maxent SDM.

Crataerina pallida (Figure 5) and *S. hirundinis* (Figure 6) were described in the 1950s as being present throughout the region wherever their hosts were found (Thompson, 1953). The sites at which they were recorded (Figures 5a and 6a) were widely dispersed, with the Maxent SDMs (Figures 5c and 6c) suggesting suitable habitat in all lowland areas of the UK, but showing *C. pallida* favouring urban areas and *S. hirundinis* rural areas, in common with their respective preferred avian hosts.

Analyses of the altitude ranges of each species showed that *O. chloropus* is present at higher altitudes than the other species in the genus *Ornithomya* (Table 3; Figure 7). None of the other species were seen above 449 m, whereas *O. chloropus* was seen up to 640 m, and a binomial glm (Figure 7) predicted an increasing probability of finding *O. chloropus*, rather than other species, as altitude increases with a 100% expectation that a fly would be *O. chloropus* at 600 m and above. A boxplot of the altitude ranges of all the species can be found in Figure S4.

The numbers of flies caught per month, of the six most common species are shown in Figure 8 plotted with the results of previous studies. These show that the peaks in the numbers of both *O. avicularia* (Figure 8a) and *O. chloropus* (Figure 8b) now occur a month earlier than previously. *Ornithomya fringillina* peaks a month later (Figure 8c). *Ornithomya biloba* is now found throughout the breeding season of its host, rather than as a vagrant on a few early Swallows. The phenology of *C. pallida* and *S. hirundinis* appears unchanged from the mid-20th century.

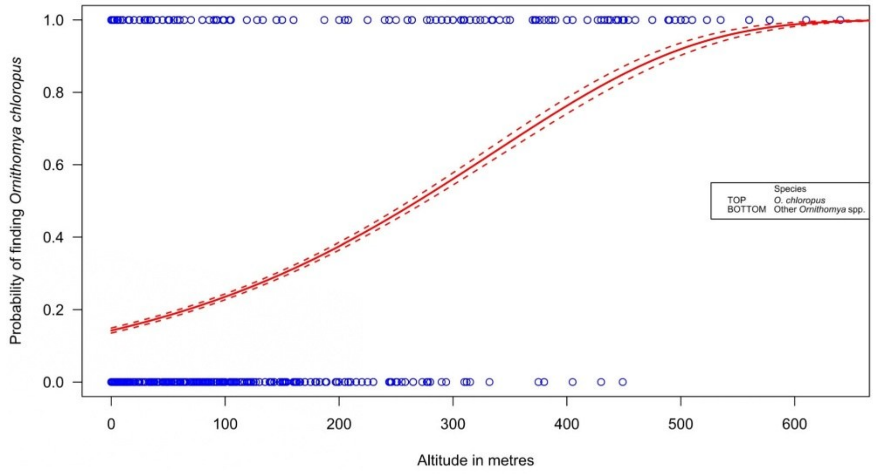

FIGURE 7 The probability of finding a species at a given altitude with standard error lines (dotted) from the output of a binomial glm comparing the altitude at which *Ornithomya chloropus* (top) is found to the that other species in the genus *Ornithomya* (*O. avicularia*, *O. fringillina* and *O. biloba*); probability, $p < 0.001$.

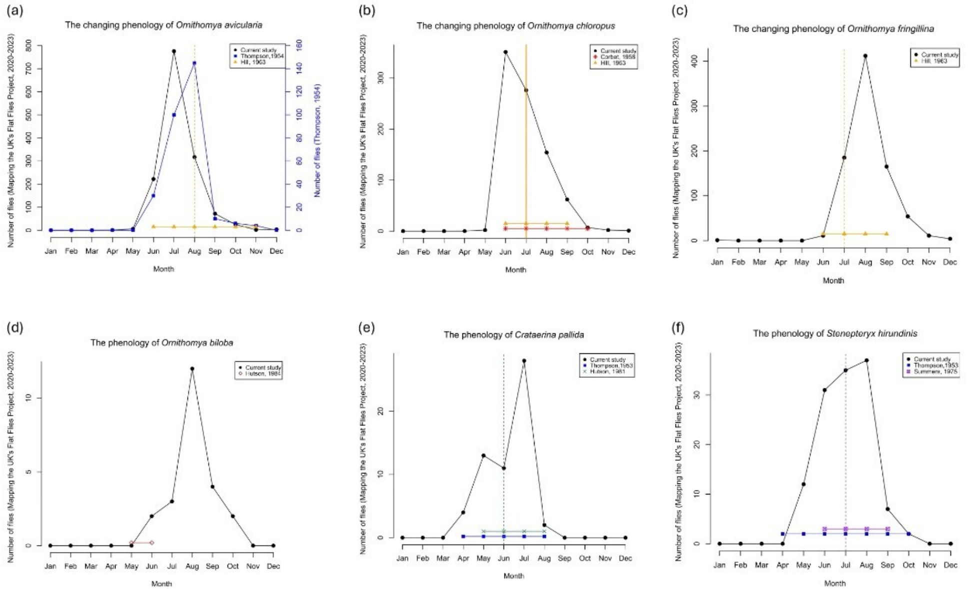

FIGURE 8 The phenology of the UK louse flies. The current study shown in black. With results of previous studies: Thompson (1953, 1954)) in blue, Hill (1963)) in orange, Corbet (1956)) in red, Summers (1975)) in purple, Hutson (1981b)) in green, and Hutson, 1981b) in brown. For most of these studies, only a range is dates and a peak, if one is available, is given, and where this is the case, the months in which the species were reported are plotted as a horizontal line close to zero, with a vertical line to show the reported peak. (a) *Ornithomya avicularia*, (b) *Ornithomya chloropus*, (c) *Ornithomya fringillina*, (d) *Ornithomya biloba*, (e) *Crataerina pallida* and (f) *Stenepteryx hirundinis*.

TABLE 4 Comparison of sample sizes of the *Ornithomya* species between this study and that by Hill (1962a)).

Species	Hill (*n*)	Hill (% of total)	Current study (*n*)	Current study (% of total)
Ornithomya avicularia	1030	29.2	1438	45.2
Ornithomya chloropus	2082	58.9	864	27.2
Ornithomya fringillina	420	11.9	848	26.7
Ornithomya biloba	0	0	30	0.9
Total	3532	100	3180	100

A comparison of the number of flies of each species in genus *Ornithomya* seen in this study with that in the 1960s (Hill, 1962a) suggests that *O. avicularia* may have replaced *O. chloropus* as the most common species across the UK (Table 4).

DISCUSSION

The results of this study suggest that the ranges of *O. avicularia* and *O. fringillina* have undergone significant northward shift in the 60 years since their ranges were last mapped in the 1960s (Hill, 1962a). *Ornithomya avicularia* and *O. fringillina* were both found in significant numbers at sites over 300 km north of their previously published distributions, and Maxent SDMs predicted that there are suitable climatic niches up to the northern tip of Scotland over 100 km beyond their recorded distribution. *Ornithomya fringillina* has also colonised areas over 400 km west of its previously recorded range, in the island of Ireland, where it was first recorded in 1982 (Smiddy & Sleeman, 2004). There are suitable climatic niches for the recent colonist *O. biloba* that could allow it to become widely distributed throughout Wales and Southern England. *Ornithomya chloropus* may have undergone a slight contraction of its range at lower altitudes especially in Yorkshire and around Liverpool and Manchester, and it appears to be less common, but comparisons to this level of accuracy are difficult because Hill's data were only plotted to county level. There was insufficient data, both in terms of published maps and within the current dataset, to thoroughly explore the current ranges of *C. pallida* and *S. hirundinis*. The analyses show shifts in the phenology of the three most common species, with *O. avicularia* and *O. chloropus* reaching peaks in their populations a month earlier than previously and numbers of *O. fringillina* peaking a month later. Despite few specimens of *C. pallida* and *S. hirundinis* being received their phenology has remained fairly constant. The current study also detected differences in the proportions of the *Ornithomya* species compared with Hill (1962a), with *O. avicularia* now the most numerous species, compared with *O. chloropus* in the past.

Many species have shifted their ranges northwards since the 1960s. For example, over a 25-year period, there was a mean northwards range shift of 31–61 km in 275 out of the 329 species studied across 16 vertebrate and invertebrate taxa in Great Britain (Hickling et al., 2006). Many of Britain's larger moths (Lepidoptera) have shifted their ranges northwards by over 200 km between the two recording periods 1968–1990 and 1992–2011 (Fox et al., 2013). British dragonflies (Odonata) have shifted their ranges northwards by a mean of 74 km, between recording periods 25 years apart (1960–1970 and 1985–1995) with the northern most edge of the range of the Common Darter *Sympetrum striolatum* (Charpentier, 1840) moving a further 346 km north (Hickling et al., 2005). Even when the longer duration between the two studies compared in this paper is taken into account, the range shifts suggested by this study would appear to be over a greater distance compared with those of most UK insects. However, other Hippoboscids, have also advanced their ranges northwards at a higher than average rate: *Lipoptena fortisetosa* advanced its European range from Czechia to Estonia, a distance of over 1000 km between 1967 and 2014 (Kurina et al., 2019), and *L. cervi* expanded its range northwards by 1000 km in 50 years. While most species of bird in the UK have only shifted their ranges northwards by an estimated 0.76 km per year (Gillings et al., 2015), generalist parasites such as *O. avicularia* and *O. fringillina* are not tied to a single host species and can switch hosts to rapidly expand their ranges as conditions permit.

Adult Hippoboscids and their larvae on endothermic hosts, such as Cervids or birds, will be protected from extremes of climate during those phases of their lifecycle, but will be more vulnerable as puparia. The puparia of the nest parasites *C. pallida* and *S. hirundinis* are protected from the worst winter weather as they are in the nests of birds, usually within or attached to buildings, but unlike the flighted species, are likely to be slower to colonise a new area as they have to rely entirely on birds or crawling to get to new sites. Flighted species such as the *Ornithomya* spp. are able to colonise new areas by flying to find a host, but with the exception of *O. biloba*, which is a nest parasite, are vulnerable to temperature extremes as puparia. This dual advantage may partially explain how quickly *O. biloba* appears to be colonising the UK.

In Scotland, the specimens of the species that were previously thought of as southerly, *O. avicularia* and *O. fringillina*, are from coastal areas, not on the hills like *O. chloropus* that was previously the only species in more northern parts of the UK. Features such as the aspect of a slope or vegetation cover may also produce fine-scale variation in climatic conditions (de Frenne et al., 2021; Wilson et al., 2015) and areas with suitable microclimates may allow insect species to survive in an otherwise unsuitable area (Minter et al., 2020), as well as allowing some of their bird hosts to achieve a higher reproductive rate (Shutt et al., 2022).

Ornithomya chloropus would appear to have a lower minimum thermal tolerance as it is found at higher altitudes than the other species in the same genus and it may be that it also has a lower maximum thermal tolerance as its range has contracted slightly as temperatures have warmed. A similar effect has been observed with some species of the related tsetse flies *Glossina* spp. that are undergoing range contraction in Zimbabwe, where the extinction probability of *G. morsitans* (Westwood, 1851) has been estimated to be a function of temperature (Are & Hargrove, 2020).

Some of the differences in detection of the various species may be due to different sampling methods between the 1960s and the current study. A lot of the results in the older study were from Bird Observatories in the northern half of the UK which may be expected to have more *O. chloropus* than the other species. Apparent changes in the distributions of the generalist *Ornithomya* spp. compared with earlier ranges may in part be due to the inclusion of flies on migrating birds in this study, as Hill removed records he considered accidental, that is those where the host was a passage migrant, from his maps (Hill, 1962a). In the current study, all records were used to produce the maps, but most of the *O. chloropus* on the south coast were on probable migrant species, such as Meadow Pipit *Anthus pratensis* (Linnaeus, 1758), and this may fully explain their predicted occurrences around The Wash and at other localised sites on the south coast in the Maxent SDM maps.

Another major difference is that the current study relied on the capture of flies that left the birds during routine bird ringing: In the 1960s, sampling was usually done using a knock-down method, with chloroform in a Fair Isle Apparatus (Williamson, 1954), which would have resulted in the removal and capture of a significantly higher proportion, if not all, of the parasites on each bird. Smaller species of fly were generally reported by volunteers to be harder to catch, when relying solely on just the visual acuity and dexterity of the bird ringer, than the larger ones which were easier to see and move more slowly. Larger flies might also be more easily disturbed than smaller ones when a bird is handled and *O. avicularia* is the largest of the three generalist species.

The results of this study, compared with earlier studies of UK louse flies, strongly suggest that the phenology of some of the species has changed. *Ornithomya avicularia* is seen at the same time of year as it was in the 1950s and 1960s (Hill, 1963; Thompson, 1954) as is *O. chloropus* (Corbet, 1956; Hill, 1963) but numbers of both species now peak a month earlier. It may be that the true peak is even earlier, as many volunteers waited until they started seeing louse flies before asking to join the study, resulting in a delay in the start of collecting at the beginning of the season. *Ornithomya fringillina* peaks a month later, and this may be due to its range shift to further north or bias in the previous data sets. For the other three species, there is insufficient data from the study to draw robust conclusions, but it would appear that *S. hirundinis* and *C. pallida* have a similar phenology to that in the mid-20th century (Hutson, 1981b; Summers, 1975; Thompson, 1953). While resident host species, for example, Great Tit *Parus major* (Linnaeus, 1758), are able to track climate changes and advance their laying date (Charmantier et al., 2008), allowing their parasites to also shift their phenology, the dependence of *S. hirundinis* and *C. pallida* on migrant hosts limits their seasonality. Hirundines are arriving an average of 10 days earlier than in the 1960s but Swifts have not significantly changed their arrival dates (Newson et al., 2016). *Ornithomya biloba* is a recent colonist, with only three UK records before 2007, all from Swallows recently arrived from Africa in May and June, whereas now *O. biloba* breeds in the UK (Wawman, 2024) and is seen from June to October when its host the Swallow is present. However, most of the cited previous studies were small, from single sites or only a few sites, often at Bird Observatories in the northern part of the UK, or used previously published records. It might be possible to produce better comparisons by obtaining all possible original data from publications, museum records and local environmental records centres, but historical data are also biased (Boyd et al., 2022; Guzman et al., 2021; Shirey et al., 2023).

In Fennoscandia, in 2013, the overall prevalence of *O. chloropus* in Pied Flycatcher *Ficedula hypoleuca* (Pallas, 1764) nests was found to be 59% (Eeva et al., 2015), whereas, in this study, only one, louse fly, *O. chloropus*, was collected from a Pied Flycatcher nestling, despite large numbers of Pied Flycatchers being ringed by volunteers, and the author examining over 100 nests for puparia, and monitoring and ringing over 500 broods of Pied Flycatchers in Somerset (Wawman, unpublished data). It may be that by breeding earlier, Pied Flycatchers in the UK miss the peak in louse flies: Pied Flycatchers in Southern Sweden usually start laying eggs in the third week in May (Källander et al., 2017), whereas those in Somerset, UK, may begin laying in late April (Wawman, unpublished data). I hypothesise that *O. chloropus* is a partial nest parasite as an adaptation to the colder climate in more northerly regions.

As species shift their ranges, species that may not have associated are more likely to do so, and for parasites, this may mean switches in host parasite relationships, bringing the risk of diseases to new hosts. The host–parasite associations of the UK Hippoboscidae found in this study will be the subject of further research, but with known vectors of avian disease amongst them, there is the potential for them to have an impact on avian health.

AUTHOR CONTRIBUTIONS

Denise C. Wawman: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; resources.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset for this study is available at https://doi.org/10.5061/dryad.zs7h44jkh. On completion of the study, the records will be entered into the database on the website iRecord with the other Hippoboscidae and Nycteribiidae Recording Scheme data.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

FIGURE S1. All sites from which louse flies (Hippoboscidae) were collected for the avian louse fly study (all flies excluding keds). UK sites are plotted as white squares at 1 km^2 resolution and Irish sites in purple.

FIGURE S2. Maps showing the distribution of capture sites for all Hippoboscidae in the study (louse flies and keds), as Maxent model outputs predicting the likelihood of a Hippoboscid in the project being collected at a site, relative to (a) the proportion of urban land-cover in that 1 km^2, (b) the proportion of protected land-cover and (c) the proportions of both urban and protected land-cover. Warmer (redder) colours predict a higher probability that a fly will be found at a site. The areas under the receiver operator curve, and the high proportion of green in these maps indicate that the sites are almost randomly distributed with respect to both urban and protected area land-cover.

FIGURE S3. Kernel densities for all Hippoboscidae in the study. The kernel densities are plotted at 95% predicted probability (dark red), 75% probability and 50% probability of a fly being caught at a given location, during the study, based entirely on latitude, longitude and total count data.

FIGURE S4. Boxplots showing the altitude ranges of all of the species of Hippoboscid received during the study period. *Ornithomya chloropus* occurs over a wider altitude range than the other *Ornithomya* sp.

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3.3

Citizen science reveals host-switching in louse flies and keds (Diptera: Hippoboscidae) during a period of anthropogenic change

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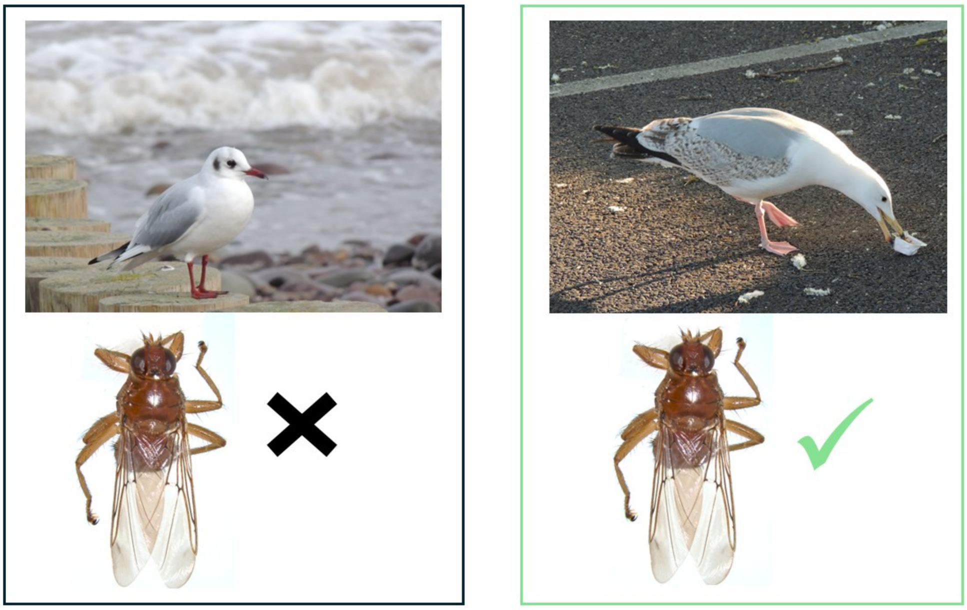
Abstract

The Hippoboscidae are a family of obligate blood-feeding ectoparasites of birds (louse flies) and mammals (keds) that are known to vector diseases. Citizen scientists collected 4365 Hippoboscids of 12 species, from 117 host species, in the UK, Ireland and the Isle of Man, as part of the "Mapping the UK's Flat Flies Project". Of the 212 host-parasite interactions recorded, 70 were previously unreported in the region. Analyses of host characteristics showed evidence of niche separation by host size of the sympatric generalist species *Ornithomya avicularia* (Linnaeus, 1758) and *Ornithomya fringillina* (Curtis, 1836). Comparisons with data from a previous study, published in 1962, showed that all three generalist species in the genus *Ornithomya* increased their host associations, during a period of climate and other anthropogenic changes: for example, the switch by some species of gulls (Laridae) to anthropogenic food sources has occurred over the same period that louse flies have started to parasitise them. These changes may have consequences for animal and human health.

Keywords

Citizen science, vectors, climate change, birds, wildlife disease, host-parasite interactions.

Graphical Abstract



- A study of louse flies in the United Kingdom, Isle of Man and Ireland found 212 different interactions between Hippoboscids and their hosts, of which 70 were previously unrecorded.
- No louse flies were found of aquatic species of birds.
- Host-switching to gulls (Laridae) has occurred during a period in which these species have started relying on anthropogenic food sources and less on marine food sources.

Introduction

It has been predicted that, with climate change, parasites are more likely to switch to novel host species, in association with range shifts and changes in host availability (Brooks and Hoberg, 2007). Migrant birds are known to transport parasites between their summer breeding grounds, stop-over sites and over-wintering areas (Burnus *et al.*, 2024) further increasing the potential for avian parasites to establish on new hosts in new regions. Specialisation by parasites may limit possible host interactions and parasite fitness if they are not on their preferred host, due to the host's defence mechanisms, whether these are behavioural, mechanical or immunological (Møller, Christe and Garamszegi, 2005). However, some species of parasites may be able to survive for several generations on sub-optimal hosts (Araujo *et al.*, 2015).

The Hippoboscidae are a family of obligate ectoparasites of birds (louse flies or flat flies) and mammals (keds) that feed on their hosts' blood. There are over 200 species described worldwide (Dick, 2018), of which 15 have occurred naturally, and two species have been accidentally imported but not become established, in the United Kingdom (UK), Ireland and the Isle of Man (collectively referred to hereafter as "the region") (Chandler, 2024). Of the naturally occurring species, 11 are known to breed on hosts in the region: three species of keds are found on mammals (*Hippobosca equina* (Linnaeus, 1758) , *Lipoptena cervi* (Linnaeus, 1758) and *Melophagus ovinus* (Linnaeus, 1758)) and eight species of louse flies on birds (*Crataerina pallida* (Latreille, 1812), *Ornithomya avicularia* (Linnaeus, 1758) , *O. biloba* (Dufour, 1827), *O. chloropus* (Bergroth, 1901) , *O. fringillina* (Curtis, 1836), *Pseudolynchia canariensis* (Macquart, 1839), *P. garzettae* (Rondani, 1879) and *Stenepteryx hirundinis* (Linnaeus, 1758)) (Hutson, 1984; Wawman, 2024).

Some species of Hippoboscid are generalists, able to feed and breed successfully on a range of hosts, but others are monoxenous or stenoxenous, restricted to either a single host or a few host species (Hutson, 1984). *Ornithomya avicularia*, *O. chloropus* and *O. fringillina* are generalists (Corbet, 1956; Hill, 1962a) and individual *O. chloropus* are known to move between host species (Corbet, 1956), whereas the other species in the region have more restricted host ranges (Hutson, 1984; Wawman, 2024).

Host-switching has occurred on multiple occasions throughout the evolutionary history of the Hippoboscidae, including switches between birds and mammals (Petersen *et al.*, 2007; de Moya, 2019) and the occurrence of mammalian *Babesia* spp. in *Ornithomya,* which normally parasitise birds, is likely to be due to host-switching (Čisovská Bazsalovicsová *et al.*, 2023). Substantial range shifts have occurred in the generalist *Ornithomya* species (Wawman, 2025) and new species have colonised the region (Wawman, 2024), increasing the potential for host switching.

The Hippoboscidae are known to vector a range of diseases and a large range of pathogens have been identified from them (Bezerra-Santos and Otranto, 2020) thus host-switching may have implications for both human and animal health. Some of these pathogens are known to be zoonotic, for example, *Icosta americana* (Leach, 1905) has been shown to harbour West Nile Virus (WNV) (Farajollahi *et al.*, 2005). *Bartonella schoenbuchensis*, which causes deer ked dermatitis in humans, has been shown to be vertically transmitted in *L. cervi* (de Bruin *et al.*, 2015).

While a range of hosts have been reported for some species of Hippoboscids, there have been few large scale studies of their host species distributions, covering a wide range of hosts and ectoparasites. In the UK the only in depth study from the region was published in 1962, using records from museums and published literature, when analytical techniques and data visualisation were limited by a lack of computing power, and it only covers three species in the genus *Ornithomya* (Hill, 1962a). More recent systematic studies of host distribution restricted themselves to either louse flies (Lehikoinen *et al.*, 2021; Levesque-Beaudin and Sinclair, 2021; Lee *et al.*, 2022; Nartshuk, Matyukhin and Shokhrin, 2022; Keve *et al.*, 2024) or keds (Salvetti *et al.*, 2020), the exception being a study of the common Hippoboscidae of Slovakia (Mlynárová *et al.*, 2024).

This study uses data obtained from a large citizen science project, the Mapping the UK's Flat Flies Project, to explore the host-parasite relationships of both keds and louse flies in the UK, Ireland and Isle of Man. It aims to determine the current host-parasite relationships, and to compare the new data for the generalist *Ornithomya* species with that collected for the 1962 study (Hill, 1962a), to look for evidence of host switching, which has been predicted to occur with climate change, and to produce an up-to-date list of Hippobosid-host interactions for the region.

Methods

The methods of collection and identification of flies have been previously described (Wawman, 2024) and are only described briefly here for completeness. From 2020 onwards, British Trust for Ornithology (BTO) bird ringers were recruited to collect flat flies that left birds during normal bird ringing activities. Ringers known to be catching less frequently ringed, groups of birds were approached directly to look for louse flies on wildfowl, seabirds, waders, herons and egrets, gulls and terns, birds of prey, Nightjars, etc. All UK bird observatories were also invited to take part. Ringers were sent a collection kit and asked to return any flies that they had collected at the end of the season with their associated metadata, including date, location and host species.

They were each sent a collection kit and asked to return any flies that they had collected at the end of the season with their associated metadata, including date, location and host species. Additional flies were sent by entomologists and members of the public who made contact via social media and the Hippoboscidae and Nycteribiidae Recording Scheme https://dipterists.org.uk/hippoboscidae-scheme/home, last accessed 12th February 2025).

The Hippoboscids were identified using a binocular microscope with reference to keys and species descriptions (Hill, 1964; Maa, 1964, 1966, 1969b; Hutson, 1981, 1984; Maa and Petersen, 1987; Oboňa *et al.*, 2022). Three records of *Pseudolynchia canariensis* and one of *Ornithomya fringillina,* clearly identifiable from photographs, were also included in the analyses despite the specimens being lost.

Data for historical comparisons were obtained from a previous study of the *Ornithomya* species in the UK and Ireland (Hill, 1962a), that used records that the author considered reliable together with his identification of flies in his own and other collections including those from museums. The dates of collection of the specimens is not stated, but all must be earlier than 1963, thus they are prior to the period of rapid global warming that began around 1980 (Hansen et al, 2006).

These data, together with that from a range of other publications, including many that would be classed as “grey literature”, such as bird observatory and bird ringing group reports, were used to produce a comprehensive list of previously reported host interactions for the region since the first UK record of a Hippoboscid in record in 1773 (White, 1789). A list of all the references consulted can be found in the Supporting Information S1. Where possible the original publications were reviewed and, if considered reliable, were given priority over more recent decisions. For example, Thompson refuted Theobald’s claim that *Lipoptena cervi* was found on “fowls” (domestic chickens), but the original report is accompanied by an illustration of an alate *L. cervi* (under the synonym

Ornithobia pallida (Meigen, 1930)), and therefore the record is retained in the historic dataset used for comparisons (Theobald, 1896; Thompson, 1954). The taxonomy of all species was updated, for example, the misspelling of *Ornithomya* as "*Ornithomyia*" was corrected (Maa, 1965); records of *Ornithomya lagopodis* (Sharp,1907) were updated to *O. chloropus* (Bergroth, 1901*)* (Hill, 1964). Corrections were made to records where necessary: for example, the only UK record of *Olfersia spinifera* (Leach, 1917), was initially reported as being from a Magnificent Frigatebird *Fregata magnificens* (Mathews, 1914) (Graham *et al.*, 1954), but later examination of the skin concluded that the host was an Ascension Frigatebird *Fregata aquila* (Linnaeus, 1758) (Chalmers, 2013).

The following groups of flies were excluded from the analyses of current host-parasite associations: flies originating from outside the study region or before 2020; any flies that were free flying or where the host species was uncertain; flies that were too damaged to be identified to species.

A total list of 282 potential host species was compiled to produce a standard matrix for the analyses (see table S2). The potential avian host species were based on the British Trust for Ornithology's "Alphabetical list of regularly occurring UK bird species" (https://www.bto.org/understanding-birds/birdfacts/about-birdfacts/alphabetical-list-regularly-occurring-uk-bird-species, last accessed 4th November 2024) with the addition of domestic chicken *Gallus gallus domesticus* (Linnaeus, 1758) (Theobald, 1896) and rare and vagrant bird species on which louse flies have been found in the region: Great Snipe *Gallinago media* (Latham, 1787) (this study), Ascension Frigatebird *Fregata aquila* (Graham *et al.*, 1954; Chalmers, 2013)*,* Little Bittern *Ixobrychus minutus* (Linnaeus, 1766) (Thompson, 1955), Red-footed Falcon *Falco vespertinus* (Linnaeus, 1766) (Hill, 1962a)*,* Paddyfield Warbler *Acrocephalus agricola* (Jerdon, 1845), (Wawman, 2024)*,* White's Thrush *Zoothera aurea* (Holandre, 1825) (Hill, 1962a), and Citrine Wagtail *Motacilla citreola* (Pallas, 1776) (Corbet, 1955). Redpolls, whether recorded as Common Redpoll *Acanthis flammea* (Linnaeus, 1758)*,* Lesser Redpoll *A. cabaret* (Statius Müller, 1776) *or as "redpoll*", were merged to form a single species, Redpoll *Acanthis flammea* for the analyses in line with current understanding of their taxonomy (Mason and Taylor, 2015; Funk *et al.*, 2021) and historic recording of this host in the publications related to Hippoboscid host species in the region. Mammal species were added only if Hippoboscids have been collected from them in the region.

In the plots avian species are listed according to the British Ornithological Union's List (British Ornithologists' Union, 2024), which places the species in taxonomic order, apart from the merger of Redpolls. Mammal species were added to the end of the list, and at right-hand side of the Bipartite plots.

The data were analysed in R version 4.2.1 (R Development Core Team, 2022). The packages dplyr, version 1.1.4 (Wickham *et al.*, 2023), lubridate, version 1.9.3 (Grolemund and Wickham, 2011), and tidyr, version 1.3.0 (Wickham, Vaughan and Girlich, 2023) were used to process the data prior to the analyses.

It had been hoped to explore the louse fly host associations in terms of both host ecology and phylogenetic relationships to look for evidence of niche separation. Initial exploration of the data, showed that due a due to a range of issues standard modelling techniques would not produce reliable outputs. The issues included, the large number categorical variables (for example, various measures of habitat and ecology, e.g. woodland, coastal or moorland habitats and type of nest, colony nesting, feeding habitats), highly correlated variables (e.g. host family and host mass (Kruskal-Wallis chi-squared = 201.28, degrees of freedom = 34, p-value < 2.2e-16), non-normally distributed variables (binomial and categorical), and, when modelling was attempted using binomial and multinominal glms, various non-normally distributed and over-dispersed residuals, even when appropriate distributions and link functions were chosen.

It was, however, possible to explore the relationship between the two sympatric fly species and their hosts masses, using boxplots to visualise the data. Bird host species weights (see table S2) were obtained from the BTO's Bird Ringers' App (BTO IS and Demography Team, 2016). The sympatric fly species' (*O. fringillina* and *O. avicularia*) hosts' masses, were analysed using a binomial generalised linear model (glm), fly species ~ host mass, with a cloglog link function using the package arm version 1.13-1 (Gelman and Su, 2022).

A co-phylogeny for host and louse flies could not be produced to explore host switching because DNA sequences were not available for two of the louse fly species (*Pseudolynchia garzettae* and *Icosta minor*).

The bipartite plots and network analyses were performed using the package bipartite version 2.18 (Dormann *et al.*, 2022). As the main metrics of network structure are strongly affected by the size of the interaction matrix (Blüthgen *et al.*, 2007; Morris *et al.*, 2014) the comparison of the networks was limited to the three generalist *Ornithomya* species, with reliable data available from the earlier study (Hill, 1962a), and the same list of host species was used for both, when plotting the bipartite diagrams. The number of interactions was equalised by waiting until the Mapping Project had received exactly the same number of flies (3533) of the same three *Ornithomya* species as in the 1962 study before starting the analysis. In all calculations of network metrics the full web was used, by using the code “emptylist=FALSE” during the production of the matrix, and “empty.web=FALSE” in the calculations. However, as bipartite does not support the retention of empty rows and columns in the species level metrics the default “empty.web”=TRUE was used.

Producing bipartite plots to clearly show all of the interactions in the networks proved challenging because of the large dataset. Various methods were attempted, including plotting all species interactions on a 1:1 basis and/or reducing the number of host species by using family or order, and grouping families together, but none proved satisfactory. The plots included in this publication are therefore a compromise in which, for the comparison of the current dataset with the data from the 1962 paper on the Ornithomyae (Hill, 1962a), in order to decrease the size of the plots, the host species are plotted by family with some related families, with similar ecologies grouped, and all of the Passeriformes placed in one group, as listed in Table S2. The group “waders” contains the families Haematopodidae, Recurvirostridae, Charadriidae and Scolopacidae. The Seabird group combines the (Alcidae (auks), Phaethontidae (divers), Hydrobatidae (petrels), Procellariidae (shearwaters and Fulmar), Sulidae (Gannet) and Phalacrocoracidae (shags and cormorants). These related groups of species have similar ecology and would be expected to have similar chances of coming into contact with louse fly species.

Results

Current data host-parasite associations

A total of 4365 flies and puparia of 12 species were received, of which 4085 could be linked to 117 host species (Table 1). Of the 212 host-parasite interactions , 70 were previously unreported in the region. A table of references showing all previously reliably reported host-Hippoboscid associations, and those from this study, is shown in Table S3.

The newly recorded interactions included the first record of the Pigeon Louse fly *Pseudolynchia canariensis* in association with its host the feral pigeon *Columba livia domestica* (Gmelin, 1789), it having only previously been reported as free-flying individuals. Significant globally previously unreported interactions included (i) eight flies of two *Ornithomya* species were found on seven individual gulls (Laridae), of three species, at six different sites, and (ii) alate Deer Ked *Lipoptena cervi* on three species of Passerine.

Table 1. Host species associations recorded in the study, showing the total number of louse flies of each species taken from each host species. The three generalist *Ornithomya* species totals are shown in the left-hand columns, the keds in the right-hand columns, with the most host specific species found on birds in the centre.

New host-parasite interactions are highlighted in red in bold typeface.

Rock Dove *Columbia livia* and feral pigeon *Columbia livia domestica* are listed separately because of their differing habitats, although they are only counted as a single species. Redpoll *Acanthis flammea* is treated as a single species.

The underlined totals of previously published associations and overall total (underlined) also include the following seven interactions that are not included within the table, as the louse fly species were not caught during the study: *Icosta ardae* with Bittern *Botaurus stellaris*, Little Bittern *Ixobrychus minutus*, and Purple Heron *Ardea purpurea; Olfersia spinifera* with Ascension Frigatebird *Fregata aquila; Ornithophila metallica* with Whitethroat *Curruca communis;* the two accidental imports of *Ornithophila gestroi* with Red-billed Leiothrix *Leiothrix lutea* and Ring-necked Parakeet *Psittiacula krameri. One damaged fly and one puparium were not identifiable to species level are included as* Ornithomya sp. and these are excluded from the totals indicated by an asterisk.

Family	**Binomial**	**Common name**	Generalist louse flies				Stenoxenous louse flies					Rare	Keds			
			Ornithomya avicularia	***Ornithomya chloropus***	***Ornithomya fringillina***	***Ornithomya sp.***	***Ornithomya biloba***	***Crataerina pallida***	***Stenepteryx hirundinis***	***Pseudolynchia canariensis***	***Pseudolynchia garzettae***	***Icosta minor***	***Hippobosca equina***	***Lipotena cervi***	***Melophagus ovinus***	**TOTAL**
Phasianidae	*Lagopus lagopus*	Red Grouse		2												2
Phasianidae	*Alectoris rufa*	Red-legged Partridge	1													1
Phasianidae	*Gallus gallus*	Chicken	1													1
Caprimulgida	*Caprimulgus*	Nightjar	**2**								3					5
Apodidae	*Apus apus*	Swift						81	1							82
Cuculidae	*Cuculus canorus*	Cuckoo	2													2
Columbidae	*Columba livia*	Rock Dove			**1**											1
Columbidae	*Columba livia*	feral pigeon	1							**6**						7
Columbidae	*Columba oenas*	Stock Dove	**20**	**2**												22
Columbidae	*Columba palumbus*	Woodpigeon	49													49
Columbidae	*Streptopelia*	Collared Dove	3													3
Haematopodi	*Haematopus*	Oystercatcher		6	**1**											7
Charadriidae	*Vanellus vanellus*	Lapwing		30												30
Charadriidae	*Pluvialis apricaria*	Golden Plover		14												14
Charadriidae	*Charadrius*	Ringed Plover		1												1
Scolopacidae	*Numenius arquata*	Curlew		11												11
Scolopacidae	*Limosa limosa*	Black-tailed Godwit		**1**												1
Scolopacidae	*Arenaria interpres*	Turnstone		**2**												2
Scolopacidae	*Calidris alpina*	Dunlin		19												19
Scolopacidae	*Lymnocryptes*	Jack Snipe		**2**												2
Scolopacidae	*Gallinago media*	Great Snipe		**2**												2
Scolopacidae	*Actitis hypoleucos*	Common Sandpiper	**1**	1												2
Scolopacidae	*Tringa totanus*	Redshank		1												1
Laridae	*Larus marinus*	Great Black-backed		**1**												1
Laridae	*Larus argentatus*	Herring Gull	**2**													2
Laridae	*Larus fuscus*	Lesser Black-backed	**5**													5
Laridae	*Sterna paradisaea*	Arctic Tern		**1**												1
Stercorariida	*Stercorarius skua*	Great Skua		**1**												1
Pandionidae	*Pandion haliaetus*	Osprey	**2**													2
Accipitridae	*Aquila chrysaetos*	Golden Eagle		**1**												1
Accipitridae	*Accipiter nisus*	Sparrowhawk	24	1	**1**			**1**								27
Accipitridae	*Accipiter gentilis*	Goshawk	**9**													9
Accipitridae	*Circus cyaneus*	Hen Harrier		**24**												24
Accipitridae	*Milvus milvus*	Red Kite	**2**													2
Accipitridae	*Buteo buteo*	Buzzard	11													11
Tytonidae	*Tyto alba*	Barn Owl	75	**11**				**2**								88
Strigidae	*Athene noctua*	Little Owl	7													7
Strigidae	*Asio otus*	Long-eared Owl	29	4												33
Strigidae	*Asio flammeus*	Short-eared Owl	1	6												7
Strigidae	*Strix aluco*	Tawny Owl	22													22
Picidae	*Jynx torquilla*	Wryneck		**1**												1
Picidae	*Dendrocopos major*	Great Spotted	80						**1**							81
Picidae	*Picus viridis*	Green Woodpecker	21													21

Family	**Binomial**	**Common name**	Generalist louse flies				Stenoxenous louse flies					Rare	Keds			
			Ornithomya avicularia	***Ornithomya chloropus***	***Ornithomya fringillina***	***Ornithomya sp.***	***Ornithomya biloba***	***Crataerina pallida***	***Stenepteryx hirundinis***	***Pseudolynchia canariensis***	***Pseudolynchia garzettae***	***Icosta minor***	***Hippobosca equina***	***Lipotena cervi***	***Melophagus ovinus***	**TOTAL**
Falconidae	*Falco tinnunculus*	Kestrel	12	9												21
Falconidae	*Falco columbarius*	Merlin	2	224												226
Falconidae	*Falco subbuteo*	Hobby	**5**					**1**								6
Falconidae	*Falco peregrinus*	Peregrine	2													2
Corvidae	*Garrulus glandarius*	Jay	5													5
Corvidae	*Pica pica*	Magpie	29													29
Corvidae	*Pyrrhocorax pyrrhocorax*	Chough	**26**													26
Corvidae	*Coloeus monedula*	Jackdaw	74													74
Corvidae	*Corvus frugilegus*	Rook	38													38
Corvidae	*Corvus corone*	Carrion Crow	51													51
Corvidae	*Corvus cornix*	Hooded Crow	**7**	**1**												8
Paridae	*Periparus ater*	Coal Tit			**6**									**1**		7
Paridae	*Poecile montanus*	Willow Tit			**1**											1
Paridae	*Cyanistes caeruleus*	Blue Tit	9	**2**	47											58
Paridae	*Parus major*	Great Tit	22	16	37											75
Panuridae	*Panurus biarmicus*	Bearded Tit				**1**										1
Alaudidae	*Alauda arvensis*	Skylark		4	1											5
Hirundinidae	*Riparia riparia*	Sand Martin		3			2		37							42
Hirundinidae	*Hirundo rustica*	Swallow	4	3	2		45		3							57
Hirundinidae	*Delichon urbicum*	House Martin						3	211							214
Cettiidae	*Cettia cetti*	Cetti's Warbler			**4**											4
Aegithalidae	*Aegithalos caudatus*	Long-tailed Tit	1		6											7
Phylloscopidae	*Phylloscopus trochilus*	Willow Warbler	1	4	91											96
Phylloscopidae	*Phylloscopus collybita*	Chiffchaff			33											33
Acrocephalidae	*Acrocephalus schoenobaenus*	Sedge Warbler	**5**	1	5							**1**				12
Acrocephalidae	*Acrocephalus scirpaceus*	Reed Warbler	23		44											67
Locustellidae	*Locustella naevia*	Grasshopper Warbler	**1**	**9**												10
Sylviidae	*Sylvia atricapilla*	Blackcap	**7**	**1**	46											54
Sylviidae	*Sylvia borin*	Garden Warbler	**2**		2											4
Sylviidae	*Curruca curruca*	Lesser Whitethroat	1													1
Sylviidae	*Curruca communis*	Whitethroat	1	2	36											39
Sylviidae	*Curruca undata*	Dartford Warbler			1											1
Regulidae	*Regulus ignicapilla*	Firecrest			**2**											2
Regulidae	*Regulus regulus*	Goldcrest			49									**1**		50
Troglodytidae	*Troglodytes troglodytes*	Wren	1	3	10											14
Sittidae	*Sitta europaea*	Nuthatch	1		2											3
Certhiidae	*Certhia familiaris*	Treecreeper			10											10
Sturnidae	*Sturnus vulgaris*	Starling	146	21												167
Turdidae	*Turdus merula*	Blackbird	331	41	**7**	1										380
Turdidae	*Turdus iliacus*	Redwing	2	1										**1**		4
Turdidae	*Turdus philomelos*	Song Thrush	35	4	**4**											43

Family	**Binomial**	**Common name**	Generalist louse flies				Stenoxenous louse flies					Rare	Keds			
			Ornithomya avicularia	***Ornithomya chloropus***	***Ornithomya fringillina***	***Ornithomya sp.***	***Ornithomya biloba***	***Crataerina pallida***	***Stenepteryx hirundinis***	***Pseudolynchia canariensis***	***Pseudolynchia garzettae***	***Icosta minor***	***Hippobosca equina***	***Lipotena cervi***	***Melophagus ovinus***	**TOTAL**
Muscicapidae	*Muscicapa striata*	Spotted Flycatcher	1	1	1											3
Muscicapidae	*Erithacus rubecula*	Robin	23	17	132											172
Muscicapidae	*Ficedula hypoleuca*	Pied Flycatcher	**1**	1												2
Muscicapidae	*Phoenicurus phoenicurus*	Redstart	**1**		**1**											2
Muscicapidae	*Saxicola rubetra*	Whinchat		3												3
Muscicapidae	*Saxicola rubicola*	Stonechat		**4**	2											6
Muscicapidae	*Oenanthe oenanthe*	Wheatear		39	1											40
Passeridae	*Passer domesticus*	House Sparrow	146	65	44											255
Passeridae	*Passer montanus*	Tree Sparrow	3		4											7
Prunellidae	*Prunella modularis*	Dunnock	70	9	73											152
Motacillidae	*Motacilla flava*	Yellow Wagtail		1												1
Motacillidae	*Motacilla cinerea*	Grey Wagtail	1	2												3
Motacillidae	*Motacilla alba*	Pied Wagtail	4	20	1											25
Motacillidae	*Anthus pratensis*	Meadow Pipit	**3**	151	4											158
Motacillidae	*Anthus trivialis*	Tree Pipit	**2**	11	2											15
Motacillidae	*Anthus petrosus*	Rock Pipit		5	1											6
Fringillidae	*Fringilla coelebs*	Chaffinch	69	**45**	70											184
Fringillidae	*Pyrrhula pyrrhula*	Bullfinch	8	1	**5**											14
Fringillidae	*Chloris chloris*	Greenfinch	36	**2**	**20**											58
Fringillidae	*Linaria cannabina*	Linnet	6	5	5											16
Fringillidae	*Acanthis flammea*	Redpoll		2	**5**											7
Fringillidae	*Loxia curvirostra*	Crossbill	**1**													1
Fringillidae	*Carduelis carduelis*	Goldfinch	**19**	**35**	62											116
Fringillidae	*Spinus spinus*	Siskin	**13**	**60**	**31**											104
Calcariidae	*Emberiza calandra*	Corn Bunting	2													2
Calcariidae	*Emberiza citrinella*	Yellowhammer	**4**		7											11
Calcariidae	*Emberiza schoeniclus*	Reed Bunting	**8**		3											11
Cervidae	*Dama dama*	Fallow Deer												13		13
Cervidae	*Capreolus capreolus*	Roe Deer												36		36
Cervidae	*Cervus elaphus*	Red Deer												15		15
Bovidae	*Ovis aries*	Sheep													55	55
Equidae	*Equus ferus caballus*	Horse											4	**2**		6
Hominidae	*Homo sapiens*	Human	1	**1**										20		22
	Total number of flies		1636	974	923	2	47	88	253	6	3	1	4	89	55	4081
	Total number of interactions		74	64	47	2	2	5	5	1	1	1	1	8	1	212
	New host species interactions		**24**	**22**	**13**	**1***	**0**	**3**	**1**	**1**	**0**	**1**	**0**	**4**	**0**	**69***
	Previously published associations		68	71	45		3	4	4	0	1	2	4	9	1	219
	Total known host associations		**92**	**93**	**58**		**3**	**7**	**5**	**1**	**1**	**3**	**4**	**13**	**1**	**288***

Bipartite (Figure 3) plots showed a complex web of interactions between species, including *Homo sapiens* (Linnaeus, 1758), who were reported as being bitten by *Lipoptena cervi*.

Louse flies were recorded from all of the commoner families of passerines, with the exception of the Cinclidae, of which the only species in the region is its only aquatic songbird, the Dipper (White-throated Dipper) *Cinclus cinclus* (Linnaeus, 1758). The other two passerine families with no flies recorded were the Bombycillidae represented by the irruptive winter migrant, Waxwing (Bohemian Waxwing) *Bombycilla garrulus* (Linnaeus, 1758), which is almost always caught outside the louse fly season, and Oriolidae, a family containing only the Golden Oriole *Oriolus oriolus* (Linnaeus, 1758), which no longer breeds in the region. A puparium of one of the *Ornithomya* spp. was received from a Bearded Tit *Panurus biarmicus* (Linnaeus, 1758) (family Panuridae) but a fly failed to emerge, and could not be identified to species, either morphologically or with DNA sequencing.

Amongst the other avian families, louse flies were absent from the aquatic families, Anatidae (geese, swans and ducks), Rallidae (rails), Podicipedidae (grebes), Alcidae (auks), Phaethontidae (divers/loons), Hydrobatidae (petrels), Procellariidae (shearwaters), Sulidae (gannets), Phalacrocoradae (cormorants) and Ardeidae (herons, bitterns and egrets). This was despite many of the bird ringers ringing these species, with the exception of the Podicipedidae, at a range of sites and being encouraged to compete to find the first louse fly on these species in the region.

After removal of flies that were free flying or where the host was uncertain (n=276), a puparium from a Bearded Tit and a damaged fly that could only be identified to genus, 4079 Hippoboscidae of 12 species, from 116 host species, were included in the analysis of current host-parasite distributions.

Selected network metrics for all the species of Hippoboscidae collected for this study are shown in Table 2, with the full results in Table S4. The degree is the number of host associations for the ectoparasite species, and the Species Specificity Index (SSI) is a coefficient of variation of interactions, normalised between 0 and 1, which does not take the species relationships such as taxonomy or ecology into account. A high SSI indicates a high level of specificity, but is unreliable if only one interaction is present in the matrix as seen here in the case of *Icosta minor* (Bigot, 1858).

Table 2. Selected Network metrics for all the species of Hippoboscidae collected for this study, calculated in the R package bipartite (Dormann *et al.*, 2022). The degree is the number of host associations for the ectoparasite species, and the Species Specificity Index (SSI) is a coefficient of variation of interactions, normalised between 0 and 1, which does not take the species relationships such as taxonomy or ecology into account. A high SSI indicates a high level of specificity, but is unreliable if only one interaction in present in the matrix as seen here in the case of *Icosta minor*. The results show that *Ornithomya avicularia*, *O. chloropus* and *O. fringillina* are generalists and suggest that *Lipoptena cervi* may also be less host specific than the remaining species, but give no indication of whether Hippoboscids are able to survive on a given host. The full network metrics are available in Table S4.

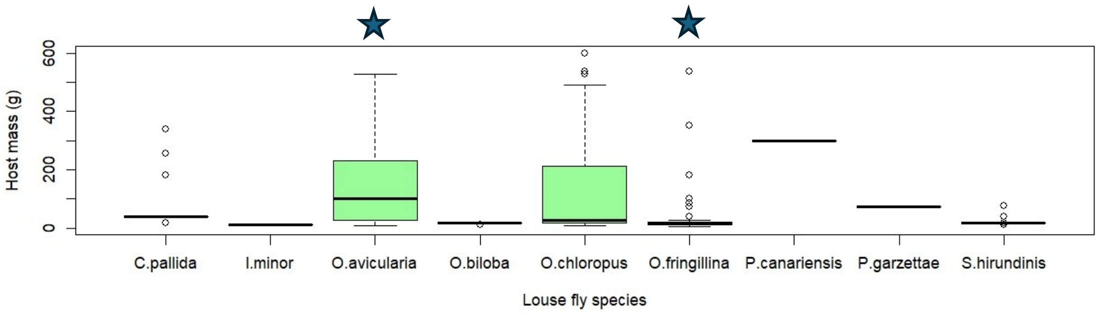
Hippoboscid species	Degree	Species Specificity Index
Ornithomya avicularia	74	0.255
Ornithomya chloropus	64	0.298
Ornithomya fringillina	47	0.240
Ornithomya biloba	2	0.958
Crataerina pallida	5	0.921
Stenepteryx hirundinis	5	0.845
Pseudolynchia canariensis	1	1
Pseudolynchia garzettae	1	1
Icosta minor	1	1
Hippobosca equina	1	1
Lipoptena cervi	8	0.508
Melophagus ovinus	1	1

For species of Hippoboscid the host masses fell within a narrow range, with this being especially narrow for most monoxenous and stenoxenous species (having only one or two related hosts), but wider for the generalist species (Figure 1).

The niches of the two sympatric generalist species, *O. avicularia* and *O. fringillina,* were largely separated by the weight of their hosts. A binomial glm (glm(formula = fly species ~ bird mass, family = binomial(link = cloglog), data =data) (Figure 2) showed a low probability ($p<0.05$) of finding *Ornithomya fringillina* on birds with a mass of over 80g, and a very low probability ($p<0.01$) of finding it on birds with a mass of 100g or more (model prediction probability $p<0.001$).

Figure 1. Boxplots showing the relationship between mean host mass and louse fly species: a) with host mass capped at 600g; b) with host mass expressed as a natural logarithm. Both show that only the three generalist species, *Ornithomya avicularia, O. chloropus* and *O. fringillina* are frequently found on a range species of different masses, with *O. fringillina* parasitising smaller host species. The blue stars indicate the two sympatric species which have a statistically significant difference in host species mass ((p<2e^{-16}).

a)



b)

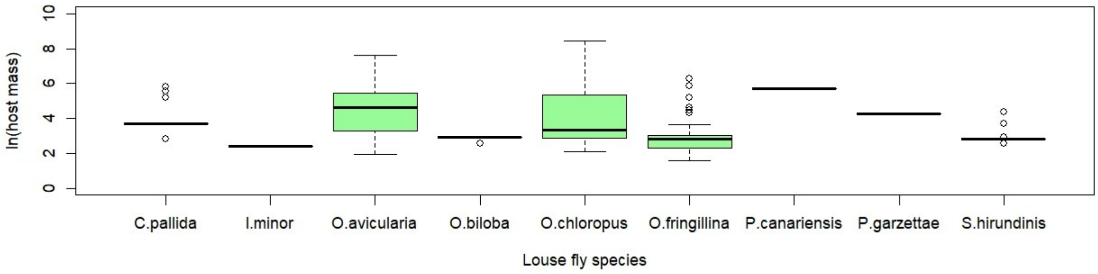
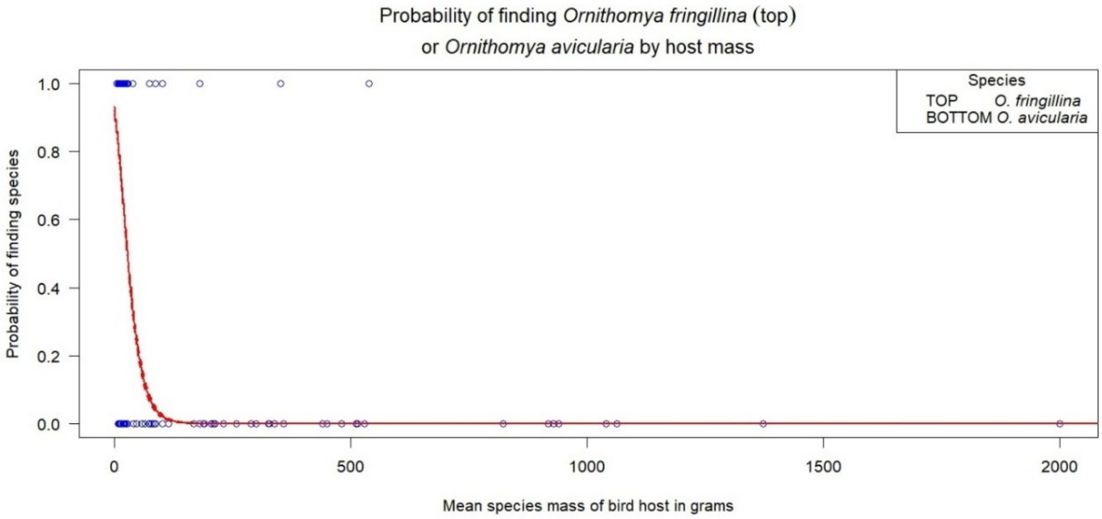


Figure 2: Probability of finding the sympatric species *Ornithomya fringillina* (top) or *Ornithomya avicularia* (bottom) by bird host mass in grams (solid red line), with upper and lower standard error lines (dotted lines) predicted from a binomial glm: glm(formula = fly species ~ bird mass, family = binomial(link = cloglog) (p<2e^{-16}).



Comparison with data from Hill, 1962

3533 flies in the genus *Ornithomya* (*O. avicularia* n=1636, *O. chloropus* n=974, and *O. fringillina* n=923) were used to compare the data with the same number of flies in the earlier dataset (*O. avicularia* n=1030, *O. chloropus* n=2083 after correcting the total, and *O. fringillina* n=420) (Hill, 1962a).

A comparison of the two sets of data, current and pre-1962, (Hill, 1962a) for the *Ornithomya* species (Table 3) showed that the total number of interactions for all three generalist species had increased during the 60 years since the previous study, with the connectance, or proportion of possible interactions realised, increasing from 0.147 to 0.219 of possible interactions detected. All three species increased their number of interactions (network degree): *O. avicularia* from 43 to 74, *O. chloropus* from 56 to 64 and *O. fringillina* from 25 to 47. The SSI for all three species decreased indicating a decrease in host specificity. A full table of all the network metrics calculated by the bipartite package for both networks of species can be found in Table S5.

Table 3. Selected network metrics comparing the data from the earlier study (Hill, 1962a) and the current study for the three generalist species in the genus *Ornithomya*. The figures show an increase in the degree (number of host species for each louse fly species), and the connectance, (the number of potential interactions that are realised), together with a decrease in the Species Specificity Index (SSI) of all three species. The full network metrics are available in Table S5.

	Hill, 1962			**This study**		
	n	**Degree**	**SSI**	**n**	**Degree**	**SSI**
Species						
Ornithomya avicularia	1030	43	0.438	1636	74	0.254
Ornithomya chloropus	2083	56	0.416	974	64	0.297
Ornithomya fringillina	420	25	0.620	923	47	0.239
Total	3533			3533		
Network metrics						
Total interactions	124			185		
Connectance	0.147			0.219		

Bipartite plots made from both sets of data, for the *Ornithomya* species, show a complex web of interactions even when plotted at the level of grouped families (Figure 3). The 1960s web is dominated by the presence of *O. chloropus*, whereas in the current web, most of the interactions are with *O. avicularia*. Very few modern interactions are with birds in the family Phasianidae, which suggests that a lot of Hill's specimens came from gamebirds that had been shot. He had no records of louse flies from mammals. Notable recent additions to the list of species interactions include those between gulls (Laridae) and *O. avicularia* and *O. chloropus*.

Figure 3. Bipartite plots showing the host parasite relations of the three commonest *Ornithomya* species, plotted against hosts. The ectoparasites are shown at the top with the hosts along the bottom. a) records from Hill, (1962), b) the current study.

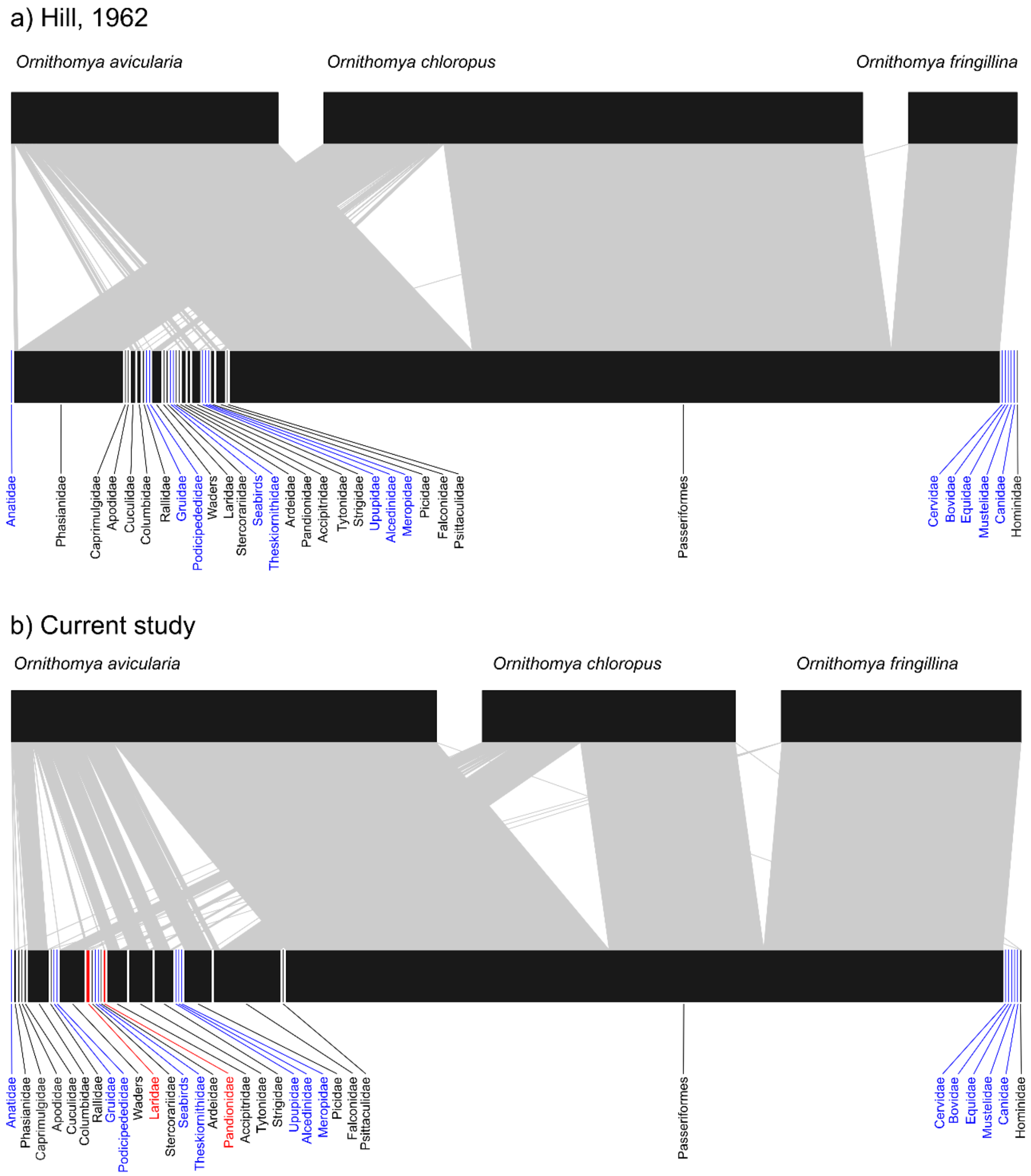
In order to decrease the size of the plots, the host species are plotted by family, and three groups of families with similar ecology have been merged: all Passeriformes; Waders (families Haematopodidae, Recurvirostridae, Charadriidae and Scolopacidae); and Seabirds (Alcidae (auks), Phaethontidae (divers), Hydrobatidae (petrels), Procellariidae (shearwaters and Fulmar), Sulidae (Gannet) and Phalacrocoracidae (shags and cormorants).

The two avian families highlighted in red (Laridae and Pandionidae) in Figure 3b are those with first records of louse flies for the UK in this study. The significance of the flies on Osprey is uncertain as the host was a sick juvenile taken to a rescue centre.

Seabirds and the bird families Anatidae, Gruidae, Podicipedidae, Seabirds, Threskiornithidae, Upupidae, Alcedinidae, and Meropidae, that have never been recorded as having louse flies in the region are labelled in blue. Note the aquatic nature of most of the avian families (Anatidae, Gruidae, Podicipedidae, Seabirds, Threskiornithidae and Alcedinidae) that do not have louse flies. Note also that although they are highlighted in blue, all of the mammalian species have been recorded as hosts of keds, the group of Hippoboscidae that parasitise mammals.

Families labelled in black are those with published host associations of any species of louse fly in the region. This includes records of these three species of *Ornithomya* from other studies, as well as those of other species of louse fly.

Bird hosts' "families" are listed according to the British Ornithological Union's List (British Ornithologists' Union, 2024) which places the species in taxonomic order and the relevant mammalian host families have been added on the right hand side.



Discussion

A total of 4365 flies and puparia of 12 species were received from 117 host species. Of these host-parasite interactions, 70 were previously unreported in the region, including the first globally reported detections of louse flies on three species of gulls, and of the Deer Ked *L. cervi* on three species of birds. Comparisons with data from the 1962 paper (Hill, 1962a) showed that all three generalist species in the genus *Ornithomya* had increased the number of host species with which they were associated. However, even for the genus *Ornithomya* these analyses underestimate the true increase in complexity as they do not include the new colonist, *Ornithomya biloba*, or take into account interactions of their hosts with other Hippoboscids.

A low SSI, indicating a high level of specificity, confirms that *Ornithomya avicularia*, *O. chloropus* and *O. fringillina* are generalists. *Lipoptena cervi* (SSI 0.508) appeared to be less host specific than the remaining species. Importantly, since they are based on occurrence only, these metrics give no indication of the level of fitness of a species on a given host species or whether it is even able to survive on it. The host species totals of the species with a high SSI that is less than one, are useful in suggesting possible mechanisms for the presence of other ectoparasite species. For example, *C. pallida*, was found on Hobby *Falco subbuteo* (Linnaeus, 1758) and Sparrowhawk *Accipiter nisus* (Linnaeus, 1758), both of which are bird predators, and it is likely that the flies transferred to them from their prey.

Whereas the monoxenous and stenoxenous species are separated by their host species the niche separation of the generalist species is more complex. A mark-recapture study of *O. chloropus* on Fair Isle - originally identified as *O. fringillina* - before the species were revised in 1962 (Hill, 1962b) – concluded that flies that were released without a host attached themselves to the first bird that they could regardless of species, and did not attempt to return to the original host species, although flies did move between hosts (Corbet, 1956). *Ornithomya chloropus* is largely separated from the other two species by its preference for higher latitudes and northern altitudes but *O. avicularia* and *O. fringillina* are sympatric across most of their range (Wawman, 2025). However, the smaller species, *Ornithomya fringillina*, has a preference for smaller birds and *O. avicularia* for larger bird species, but despite there being a high degree of correlation between the masses of members of each bird family, host family was not significant.

In this region, the Laridae (gulls) are the only aquatic species which have louse flies, despite the bird ringers in the study being encouraged to search for them on all species, and especially seabirds. This study found eight louse flies on gulls: five *O. avicularia* on Lesser Black-backed Gull *Larus fuscus* (Linnaeus, 1758), and two on Herring Gull *L. argentatus* (Pontoppidan, 1763), and one *O. chloropus* on Greater Black-backed Gull *L. marinus* (Linnaeus, 1758). All of these hosts were caught within 5km of the sea and most on islands around the coast. Worldwide, there are only two previous records of louse flies on gulls. The first was of "*Ornithomya fringillina*" on a "gull *Larus* sp." in Denmark (Johnsen, 1948), but, unfortunately, only two species of *Ornithomyae* are recorded in his study, and it is probable that Johnsen did not recognise *O. chloropus,* as the two species were not often separated until the genus *Ornithomya* was revised in 1962 (Hill, 1962b). The second record is of *O. avicularia* on a Black-headed Gull *Chroicocephalus ridibundus* (Linnaeus, 1766) in the Netherlands (Van Eck and Van Den Broek, 1969). Louse flies should be obvious on the pale plumage of gulls and the total number of gulls of these three species ringed annually in the UK is now only around a third of that in the 1960s (Robinson, Leech and Clark, 2024) so it is unlikely that they would have gone unrecorded if they were present in the 1950s and early 1960s. Gulls have only colonised urban areas in the last 60 years (Rock and Vaughan, 2013) and this, with the associated change in diet to anthropogenic sources, such as food waste from landfill sites, has led to gulls mixing with other avian species. Carrion Crows *Corvus corone (Linnaeus, 1758)*, and Starlings *Sturnus vulgaris* (Linnaeus, 1758) are frequently infested with louse flies, that could move to new hosts such as gulls. Some of the species of louse fly such as those in the genus *Olfersia*, for example *Olf. spinifera* found on frigatebirds (Fregata spp.), pelicans (Pelecanidae), cormorants (Phalacrocoracidae) and boobies (Sulidae), and *Olfersia fumipennis* (Sahlberg, 1886) found on Osprey *Pandlion haliaetus* (Linnaeus, 1758), must be able to tolerate submersion but it is possible that United Kingdom louse flies cannot, as they were not found on aquatic species.

In addition to various mammalian hosts, the Deer Ked, *L. cervi* was found on Goldcrest *Regulus regulus* (Linnaeus, 1758), Coal Tit *Periparus ater* (Linnaeus, 1758), and Redwing *Turdus iliacus* (Linnaeus, 1758). It has previously been recorded on birds, including, Peregrine *Falco peregrinus* (Tunstall, 1771) in Denmark (Johnsen, 1948), Song Thrush *Turdus philomelos* (Brehm, 1831) in Slovakia (Krišovský *et al.*, 2024), Rufous-tiled Robin *Larvivora sibilans* (Swinhoe, 1863), Oriental Turtle Dove *Streptopelia orientalis* (Latham, 1790), Marsh Tit *Poecile palustris* (Linnaeus, 1758) and Radde's Warbler *Phylloscopus schwarzi* (Radde, 1863) in Eastern Russia (Nartshuk, Matyukhin and Shokhrin, 2022). The presence of a parasite on a host, does not prove that it is able to successfully parasitise it. All three of the specimens caught were still alate – *L. cervi* shed their wings upon finding a suitable host – which could be consistent with incidental findings rather than true examples of parasitism. However, the low number of reported interactions between *L. cervi* and birds may be a result of the historical tendency to study louse flies and keds separately, or because bird ringers collecting louse flies may not realise the significance of delate Deer Keds.

Species such as *L. cervi*, which is known to bite humans, and parasites present on urban host species such as feral pigeons and gulls, bring with them an increased risk of spreading diseases to humans, particularly in the presence of other vectors that bite humans, and they may act together to maintain enzootic cycles of disease, including potential zoonoses.

Clearly there can be issues with comparing current data to that published 60 years ago. Some of the species from which ectoparasites were obtained recently have undergone marked population changes since the 1960s, for example, Red Kites *Milvus milvus* (Linnaeus, 1758) increased their breeding distribution – measured as their presence in 10km squares - by 2035%, and Goshawk *Accipiter gentilis* (Linnaeus, 1758) by 1446%, whereas other species numbers and ranges have declined (Balmer *et al.*, 2013). Many of Hill's specimens were from museums and of unstated age, but this should not be a problem as the significant increase in regional temperatures only occurred after this period (Dentener *et al.*, 2013). Amongst Hill's totals, although there were some louse flies from bird observatories and other bird ringers, some of the host species totals, for example, those of corvids and game birds are almost certainly from birds which had been shot such as Red Grouse *Lagopus lagopus* subsp. *scotica* (Latham, 1787). In the current study, the records are more widely distributed across the region, and very few were from hosts that had been shot. Bird ringers' capture methods have changed over the period, with mist nets, introduced in the late 1950s, replacing various traps as the main capture method for most ringers. Until at least the mid-1970s, bird ringers in the region could use chloroform in a Fair Isle Apparatus (Williamson, 1954) or insecticidal powders to remove ectoparasites from wild birds (Spencer, 1976). All of these changes could easily cause a change in the proportions of host species and ectoparasites caught.

Some species of louse fly that might be expected in the region were not detected, although they may have been missed as only small numbers of their hosts are ringed. These species may have "missed the boat" - not arrived with the hosts that colonised the region - or "drowned on arrival" – arrived but failed to establish viable populations (MacLeod *et al.*, 2010). The enemy release hypothesis suggests that the absence of these parasites on their hosts, may have enabled these bird species to colonise the region more easily: however, the processes are complex (Colautti *et al*,, 2004). A combination of other parasites, diseases, and ecological factors such as food availability and competition from native species in the new range are likely to have more influence than louse flies which have been shown to have little impact on their hosts.

Olfersia fumipennis is commonly found on Osprey around the world, including other parts of Europe (Maa, 1969b; Hutson, 1984; Beuk, 2010; Reeves and Lloyd, 2019; Lehikoinen *et al.*, 2021). Only *O. avicularia* was found parasitising Osprey in this study, and the two flies were on a diseased juvenile taken to a rescue centre. Although there are currently around 300 pairs of Osprey breeding in the region, they became extinct in the UK in 1847, and slowly recolonised after a pair arrived naturally in Scotland in 1954. Birds were reintroduced into England in 2001 (https://www.roydennis.org/animals/raptors/osprey/species-recovery/scotland, last accessed 9th November 2024). The introduced Osprey were not treated for parasites and none were observed (Roy Dennis pers. comm.), and when hosts arrived naturally, it is likely either no *Olf. fumipennis* were present, or that their population was too small for the parasites to establish.

Similarly, *Icosta_ardeae* (Macquart, 1835) is found on Ardeidae (herons, bitterns and egrets) over large parts of the Palearctic, Nearctic and Africa (Maa, 1969a) but has only previously been recorded in the region as a vagrant on three occasions (Hutson, 1984; Chandler, 2024). The number of potential host species and the size of their populations breeding in the region has increased markedly since the 1960s, especially for Little Egret *Egretta garzettae* (Linnaeus, 1766) and Bittern *Botaurus stellaris* (Linnaeus, 1758), with more recent colonisations by Great White Egret *Ardea alba* (Linnaeus, 1758), and Cattle Egret *Bubulcus ibis* (Linnaeus, 1758), but no *I. ardeae* were found in this study. This may be in part because most of these species are ringed as nestlings before they are fully feathered.

The stochastic nature of the records used in this study means that it is impossible to determine reliable infestation rates for any given species. The number of flies caught are likely to be influenced not only by the random sampling of birds and factors which cause flies to choose to leave their avian hosts, but by the visual acuity, agility and determination of the bird ringers involved, whether they are ringing indoors or outside, and the time pressure under which they find themselves. Targeted sampling, using a knockdown method to trap louse flies in a controlled environment would produce data that could be used to more accurately compare infestation rates.

Future research could include additional analyses of how the host ecology effects the likelihood of infestation by louse flies, for example, ticks have been found to be more common on ground feeding birds (Burnus et al., 2024). Continued monitoring to look for future host switches and range shifts may be important especially as some of these species are known to vector disease. Continued specimen collection, followed by the use of molecular methods, such as a metagenomics approach or targeted PCR to search for pathogenic microorganisms, and researching these species vectorial capacity will be important in determining the risk of possible disease transmission both within and between species.

Supplementary Information

S1. Sources of information checked for host species records.

S2. Table of host species and their masses used in the models.

S3. Table of known host-Hippoboscid interactions from the United Kingdom, Republic of Ireland and Isle of Man.

S4. A table of the network metrics calculated by the bipartite package for all species of Hippoboscids in the current study: a) species metrics, b) network metrics.

S5. A table comparing the network metrics calculated by the bipartite package for the three generalist species in the genus *Ornithomya* (*O. avicularia, O. chloropus* and *O. fringillina*) from the 1960s study (Hill, 1962a) and the current study: a) species metrics, b) network metrics.

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Author Contributions

Denise C. Wawman: Conceptualization; project administration; investigation; data curation; methodology; visualization; formal analysis; validation; writing – original draft; resources; writing – review and editing.

Adrian L. Smith: Supervision; resources; writing – review and editing.

Ben C. Sheldon: Supervision; writing – review and editing.

Ethical statement

All wild birds were handled by bird ringers licensed by the British Trust for Ornithology.

Data availability

On publication the data will be made available either on the Dryad website or on the University of Oxford ORA website.

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CHAPTER 4

An ornithological approach to a longitudinal study of the epidemiology of avian pox in a small passerine, the Dunnock *Prunella modularis*

Introduction

In this chapter I explore the epidemiology of avian pox infection in the Dunnock *Prunella modularis* using a 15.5 year dataset from birds ringed and recaptured in my garden on Exmoor.

I use these data in a mark recapture analysis, compare the survival rates of affected and unaffected Dunnocks, and look for evidence of density dependent infection rates.

I present the information from three of the pieces of the Supporting Information from this paper as additional sections within this chapter as some of the information contained in them is an important part of this thesis.

In section 4 S1, I discuss the diagnosis of avian pox in a wild population of Dunnocks.

Chapter 4 S2 presents a methodology for estimating the incubation period of a disease in a population of wild birds using feather growth, using avian pox in Dunnocks as a model system.

Chapter 4 S3 contains estimates of the duration of avian pox infection in Dunnocks.

Further supporting information from this chapter can be found in the Appendix Supporting Information Chapter 4 at the end of this thesis

4.1

An ornithological approach to a longitudinal study of the epidemiology of avian pox in a small passerine, the Dunnock *Prunella modularis*

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ABSTRACT

Long-term, longitudinal studies of disease in wild bird populations are rare. Diseases are important determinants of bird survival and may spill-over into other species including livestock and, in some cases, humans. Avian pox is a globally distributed disease, resulting from infection by viruses in the genus Avipoxvirus. Despite its broad distribution there are few long-duration longitudinal studies of its epidemiology, and hence limited understanding of basic processes such as seasonality, the incubation period, time course of infections and mortality rates of affected birds. Here we report the results of a 15.5 year study involving 1471 captures of a wild population of 588 Dunnocks *Prunella modularis*, a species recorded as affected by avian pox since the 1940s. Longitudinal data from one site in the United Kingdom estimated the mean annual prevalence of avian pox to be 8.3% (annual range 0 to 12.4%) but found no evidence of increased mortality in affected birds (apparent survival 0.37 (SE 0.12, CI 0.18 - 0.61, n=36) for the group with avian pox, and 0.32 (SE 0.03, CI 0.26 - 0.38, n=437 for birds in which it was not detected). The likely disease incubation period of avian pox in Dunnocks was 13-48 days, from an estimate of age based on the growth of the primary feathers of juvenile birds post-fledging. In most years, the disease followed a seasonal pattern with a peak in late summer. The majority of birds that developed lesions did so in their first calendar year and there was no evidence of disease recurrence, suggesting that a single infection may produce life-long immunity. The results of this study are consistent with Avipoxvirus circulating in Dunnocks with relatively minor systemic effects on individuals.

KEY WORDS

Wildlife disease; Incubation period; Survival; Feather growth; avipoxvirus

INTRODUCTION

Infectious diseases are important determinants of avian survival and fitness but longitudinal field studies are relatively rare in the literature. Such studies provide important insights into host-pathogen interactions in wildlife species and can be used to identify trends in disease dynamics and outcomes (Dunn *et al.*, 2021). Moreover, some infections can threaten other wildlife, humans and their livestock with devastating consequences (Mackenzie and Jeggo, 2019) and emerging infectious diseases, such as trichomonosis in Greenfinch *Chloris chloris* and Chaffinch *Fringilla coelebs*, have led to marked decreases in populations of wild birds (Robinson *et al.*, 2010; Hanmer *et al.*, 2022). Many studies of avian disease are biased towards the detection of novel microbial pathogens, especially those which may be zoonotic, without determining their effects on their host (Plaza, Blanco and Lambertucci, 2020).

Avian pox is caused by one of seven double-stranded DNA viruses in the genus Avipoxvirus (APV) in the family Poxviridae (ICTV, 2024). Most of these seven species naturally infect only one or a small group of related bird species (Gyuranecz *et al.*, 2013), although some have been shown to switch host species (Buenestado *et al.*, 2004; Fukui *et al.*, 2016). Some species of APV can infect a wide range of avian hosts, although different host species vary in their susceptibility to infection (Bolte, Meurer and Kaleta, 1999). The most widely studied is fowlpox virus because it primarily infects chickens and other domestic poultry (Van Riper and Forrester, 2007).

Pox viruses in wild bird species have been less frequently studied, and there have been few long-duration (multiple year) longitudinal studies of endemic avian pox in wild bird populations and none in the United Kingdom (UK). Most long-term studies have taken place on the Hawaiian Islands, where non-native mosquitos carrying avian pox have been introduced, affecting the Oahu Elepaio *Chasiempis sandwichensis ibidis,* a monarch flycatcher found on the island of Oahu (Vanderwerf, 2009; VanderWerf *et al.*, 2023), three honeycreepers, ʻIʻiwi *Drepanis coccinea*, the Hawaiʻi ʻAmakihi *Chlorodrepanis virens* and the ʻApapane *Himatione sanguinea,* and the introduced Japanese White-eye *Zosterops japonicus* (Samuel et al., 2018). The lack of long-term studies may be because most reported outbreaks are short-lived or because avian pox occurs as sporadic cases, for example, in the United States an outbreak in Bobwhite Quail *Colinus virginianus* that began in July 1978 subsided in nine months (Davidson, Kellogg and Doster, 1980) and on Marion Island in the Indian Ocean, where seabirds have been studied since the 1980's, a single case was detected in each of two years, with seven more cases in two species in 2015 (Schoombie *et al.*, 2018). Considerable between year variation in the prevalence of avian pox has also been found in some populations, for example, in the Laysan Albatross *Phoebastria immutabilis* the prevalence ranged from 3% in years with low rainfall to 88% in years with high rainfall over a five year period (Young and VanderWerf, 2008). Short duration studies may miss important patterns of seasonal and between year variation in the incidence and prevalence of diseases, which may only become apparent with a longer-term study.

APV may be transmitted by direct bird to bird contact, via aerosols or biting vectors or by indirect contact with surfaces or dust, but not from mother to offspring via the egg (Van Riper and Forrester, 2007). Avian pox is often a seasonal disease in cooler regions where vectors are not active during the winter (Van Riper and Forrester, 2007; Lachish, Lawson, *et al.*, 2012). The incubation period of avian pox, from the initial infection challenge to the onset of clinical signs, is variable, depending on both the host species and species of APV, ranging from a few days in some species of domestic poultry (Kirmse, 1967a; Van Riper and Forrester, 2007) to one month in wild birds (Kirmse, 1967b). In UK Great Tits *Parus major*, the incubation period can be only a few days as nestlings were found with skin lesions (Lachish, Bonsall, *et al.*, 2012). The duration of observable disease is also variable but is around a month for domestic chickens (Van Riper and Forrester, 2007) while lesions were reported to have persisted on the foot of a Northern Flicker *Colaptes auratus* for 13 months until surgical removal (Kirmse, 1967b).

Avian pox has two presentations a diphtheric or 'wet' form affecting the respiratory and upper gastrointestinal tracts which can cause respiratory problems and difficulty swallowing, and a cutaneous nodular or 'dry' form which causes proliferative skin lesions around the featherless areas typically on the legs and head (Tripathy, 2022). Given the characteristic appearance of skin lesions seen in avian pox, and the high correlation with diagnosis by DNA sequencing, biopsy of lesions and virus isolation (van Riper, van Riper and Hansen, 2002; Lawson *et al.*, 2012), most studies use a syndromic surveillance approach to define cases of avian pox in epidemiological studies of free-living wild passerine species (Senar and Conroy, 2004; Vanderwerf, 2009; Lawson *et al.*, 2012), which may miss all but the most severe case of the diphtheric form of the disease.

Mortality rates vary between species, from estimates of 0.6 - 1.2% in Northern Bobwhite (Bobwhite Quail) (Davidson, Kellogg and Doster, 1980) to possibly as much as 100% in Galapagos Mockingbirds *Mimus parvulus* (Vargas, 1987). In the UK, Great Tit survival was decreased by 26.5% per month for juveniles and 13.1% for non-juveniles (Lachish, Bonsall, *et al.*, 2012). Avian pox may have long-term sequelae for survivors such as loss of digits and bill deformity (Van Riper and Forrester, 2007; Sheppard *et al.*, 2022). It has also been suggested that avian pox may have been the cause of a change in the colouration of House Finch *Carpodacus mexicanus* plumage in California from red to yellow (Zahn and Rothstein, 1999). Birds that have recovered from avian pox are generally considered immune to further infection with the same species of APV (Van Riper and Forrester, 2007). In Great Tits, avian pox led to a decrease in the number of offspring fledged and their subsequent juvenile survival if adults were infected during the breeding season (Lachish, Bonsall, *et al.*, 2012), but the long-term survival and fitness effects of infection for individuals in wild populations are poorly documented.

The Dunnock is a small, brown, non-migratory passerine with a mean body weight of 21g which, although common throughout Europe, is on the United Kingdom Amber List of Birds of Conservation Concern (British Trust for Ornithology, 2023a). The sexes are similar in appearance and it is only possible to sex them in the hand during the breeding season when full brood patches or cloacal protuberances are present (Svensson, 1992). Dunnocks are a sedentary species: post-juvenile dispersal is rarely more than 2km and adults show a high degree of breeding philopatry (Davies, 1992). The first putative report of avian pox in Dunnocks in the UK was in August 1949, from a site in Yorkshire: the lesions were described as “large swellings on the feet, ankle joints and over the eyes” (Edwards, 1955). In the UK, the Dunnock is known to be a species affected sporadically by avian pox in which the disease is considered endemic (Lawson *et al.*, 2012).

This study aims to improve the current understanding of avian pox in wild passerines, using data from a 15.5 year study at a single site to compare survival rates of Dunnocks with and without detectable avian pox, and to compare these to the survival rate of the whole population, to estimate the incidence and prevalence of the disease, and to look at the interactions between annual rates of avian pox, survival and population size (a proxy for population density). It also aims to explore the duration of clinically detectable infection and the seasonality of avian pox, with reference to the age structure of the population, breeding and moult cycles as avian immunity may vary with age, reproductive status and other stresses. Additionally, this study introduces a method of estimating the incubation period of a disease from the age of birds determined using the timing of growth of the primary feathers in fledglings. The authors also discuss how the methods used and the results obtained can be generalised to other diseases in populations of wild birds.

MATERIALS AND METHODS

Data collection

Dunnocks were captured in mist nets and ringed in a single garden in a rural location on the north-east edge of Exmoor, in Somerset, England (51.2° N, 3.51°W), during a 15.5 year period from February 2008 to August 2023 as part of a British Trust for Ornithology (BTO) Retrapping Adults for Survival (RAS) Study (https://www.bto.org/our-science/projects/bird-ringing-scheme/ringing-surveys/retrapping-adults-survival-ras, last accessed 12th April 2023). RAS studies aim to capture all adult birds of the study species in the study area each year and try to keep the trapping effort constant across breeding seasons. All birds were ringed with uniquely numbered BTO rings following the rules of the BTO Ringing Scheme (Redfern and Clark, 2001). From 30th September 2010 until 21st April 2017, Dunnocks ringed from the end of their post-juvenile moult onwards were also given a unique set of colour rings which allowed individual birds to be identified in the field. No Dunnocks needed to be excluded from ringing due to the presence of avian pox lesions.

At each capture the age, sex of adults in the breeding season (together with codes for the presence or absence of cloacal protuberances and blood patches), moult status and whether or not the longest primary was growing were recorded, using the BTO codes (Redfern and Clark, 2001), and notes were made of any injury, external signs of disease, or ectoparasite infestation seen, including the sites of avian pox lesions.

To decrease the risk of disease transmission associated with capture and handling, previously ringed birds with open/ulcerated or scabbed skin lesions consistent with avian pox were released at the net without further processing and biometrics were not collected: age codes, moult and sites of skin lesions from these birds were only recorded if these were obvious to the ringer while extracting birds from the net. However, for most birds it was possible to determine their age when the data were missing by using age codes from other captures of the same individual.

Avian pox was diagnosed from the presence of typical lesions and confirmed by DNA sequencing of a lesion from the leg of an affected Dunnock. The methods of diagnosis used in this study are discussed more fully in the Supporting Information 4.S1.

A case of avian pox was defined as an observation of skin lesions with a macroscopic appearance and distribution characteristic of the disease - typically featherless, proliferative, lesions on the legs, feet and/or head of a Dunnock - on one or more occasions, without an intervening capture where no avian pox was observed, and is hereafter referred to as ‘avian pox’.

Analysis

The data were analysed in R version 4.2.1 (R Development Core Team, 2022). The packages dplyr (Wickham, Francois, *et al.*, 2023) and lubridate (Grolemund and Wickham,

2011) were used to process the data prior to analysis (to reformat the date to produce separate columns for year, month, and Julian day, and to produce a matrix for the models) and plots were made in base R with the packages *scales* (Wickham and Seidel, 2022) and *ggplot2* (Wickham, Chang, *et al.*, 2023). Bayesian model was used to generate an estimate the 95% credible intervals for plot of the proportion of Dunnocks with avian pox which was run using the R packages jagsUI (Kellner and Meredith, 2021).

From the information in the BTO age codes, birds' ages were classed as "first calendar year" (1cy), "second calendar year"(2cy), "adult" and "unknown". Birds were classed as unknown age if their age was not recorded and could not be determined, either due to lack of data due to the a priori decision to release diseased birds at the net, or because of conflicts in the data which had no clear resolution after reviewing previous capture data, active moult patterns, etc.

Records of birds with suspected non-pox disease (cnemidokoptosis, n=1), and birds for which the avian pox status was uncertain, due to single observations of birds with slightly swollen toes (n=2) or missing or ischaemic toes in the absence of prior observations of disease (n=2) were excluded. Although other studies have included birds with missing or ischaemic toes in their analyses (van Riper, van Riper and Hansen, 2002; Vanderwerf, 2009), and ischaemia of the digit, with eventual loss of the toe, is often seen as a consequence of avian pox (van Riper, van Riper and Hansen, 2002), it may also be due to injury and gives no information about the timing of the episode of disease. Birds ringed in the final year of the study were also excluded as they had no chance of being recaptured during the following year.

Two separate subsets of data were produced, for birds which had pox at some point and those which were not detected as having avian pox (pox and no pox), for use in subsequent analyses. The mean number of captures per bird in each group was calculated, together with confidence intervals and standard errors, in base R.

Analyses of disease rates and seasonality

The lifetime prevalence (proportion of birds affected in the population over the duration of the study expressed as a percentage) of APV in Dunnocks across the study period was calculated by dividing the number of birds with avian pox by the total number of birds remaining in the study after exclusions.

The incidence avian pox was calculated, by dividing the number of newly detected cases in a month by the total number of individual birds caught.

Monthly prevalence estimates were produced by dividing the number of captures with avian pox per month by the total number of captures per month, as some birds were captured both with and without observable pox lesions in the same month. As for some months the number of birds caught with avian pox lesions was zero, which also gives a standard error of zero, a Bayesian model was used to generate an estimate the 95% credible intervals for the plot of the proportion of Dunnocks with avian pox. This was done in R, using the package jagsUI (Kellner and Meredith, 2021), using a Poisson distribution (dpois) and the uninformative priors in a uniform distribution (dunif) of 1-10,000 for population (Nt) size, and 0-1 for the proportion of birds with avian pox (disease_frac). The model being specified as follows:

```
model{
 # Likelihood
 captures_total ~ dpois(Nt)
 captures_diseased ~ dpois(Nt*disease_frac)
 # Priors
 Nt ~ dunif(0.0, 1e4)
 disease_frac ~ dunif(0.0, 1.0)
}
```

The model was run with 3 Markov chains, for 10000 iterations with iterations “burn-in” 500. Convergence was judged to have been achieved when the Rhat values were 1.000 or 1.001, and the output for the for the total population, and known percentage of birds with avian pox were used to check that the values produced by the model were correct.

Individual age class categories were produced by subsetting the data by age class, as were the numbers of birds in moult or with signs that they were actively breeding as indicated by the presence of brood patches and cloacal protuberances).

Analyses of survival and detection rates

Two set of analyses were conducted. The first to compare the survival and detection rates of the group with avian pox and the group in which avian pox was not detected. The second to generate survival and detection rates for the population as a whole, that could be used to look at the relationship between the annual incidence of avian pox, and the survival rate, and size of the whole study population (as a proxy for population density).

After an exploration of the seasonality of cases of avian pox, the survival analysis was run in years from 1st June to May 31st, to avoid splitting avian pox seasons across two years, using Julian Day 152, generated by the R package lubridate (Grolemund and Wickham, 2011), as the start of the year in R to split the years.

The data were analysed in Program MARK version 10.0 (White and Burnham, 1999) using Cormack-Jolly-Seiber (CJS) models to calculate the apparent annual survival and annual detection probabilities. CJS models use mark-recapture data to calculate estimates based on the following assumptions:

That every marked individual in the population has the same probability (P) of being captured or resighted.

That every individual has the same probability of survival (ϕ *or* phi) until the next sampling period.

That sampling periods are instantaneous.

That no marks (rings) are lost and they are recorded accurately.

All emigration from the sampled area is permanent. However, CJS models, such as that in Program MARK are unable to distinguish between emigration and death (White and Burnham, 1999) and thus are only able to calculate apparent survival, with permanent emigrants assumed to be dead.

In all of the mark-recapture analyses birds found dead were treated as birds alive in that year with no further captures. The final models were chosen on the basis of the lowest Akaike Information Criterion (AIC). Two sets of CJS models were run.

For the first set of analyses birds were divided into two groups, those in which avian pox was detected (pox) and those in which it was not (no pox). Two sets of survival analyses were performed. The first set compared the survival of these two groups of Dunnocks, pox and no pox. Resightings of colour ringed birds were excluded from these analyses as their disease status was unknown. This first group of analyses used only birds ringed or detected with avian pox during their first year of life (1cy and 2cy birds), to remove the possibility of bias due to age-related differences in survival and recapture probability affecting the results. The pox and no pox groups were analysed both separately and within the same model to check reproducibility. Models were run in which annual survival and detection probabilities were allowed to vary with time, and in which they were not, although the former failed to converge for the pox group so were quickly rejected.

To compare the survival rates, the death rate ratio, a method for comparing the mortality rates in two groups where the true population size is unknown, was calculated using the following formula:

Death Rate Ratio = Death rate group of interest (Avian pox)/ Death rate comparison group (No avian pox)

Where, *death rate = (1 – the mean survival rate for the group)*.

In order to look at the effects of population size, number of cases of pox per year, and annual infection rates on the annual survival rate, and the effect of infection rate on total population size, a second set of CJS analyses was run in Program MARK. These models used the data from the from all capture records, for all age classes, including colour ring resightings, to obtain survival and detection rates for the whole population. The apparent survival rate P, and the detection probability phi, were allowed to vary with time, to estimate separate survival rates for each year, to allow for differences in detection rate (due to varying ringing effort, changes in habitat, etc.) and changes in survival between years.

These data (annual survival data from the whole population analysis in which the survival and detection probabilities were allowed to vary with time) were used to look at the relationship between the annual incidence of avian pox, and the survival rate, and size of the whole study population in a given year. These analyses that were performed using standard frequentist linear models (lms), in base R, assuming the data were normally distributed (that is using the default for a linear model in R, family=Gaussian):

model1<-lm(survival estimate ~ annual pox cases)

model2<-lm(survival estimate ~ annual pox cases/total population) ,that is, survival against avian pox annual prevalence model3<-lm(survival estimate ~total population)

model4<-lm((pox cases/total population)~total population), that, is the infection rate against total population.

The methods for estimating disease incubation period from the timing of feather growth in fledglings is discussed in the Supporting Information, 4.S2, and the estimation of the duration of infection from the interval between captures of affected birds in 4.S3.

RESULTS

A total of 588 Dunnocks were ringed in the study area, in all months of the year, during the 15.5 year study period. No birds were excluded from ringing because of avian pox: of the three birds with lesions present at first capture, two caught in 2017 had lesions in the late stages of healing, and a third with active lesions, caught during the period when colour ringing was taking place, was ringed on the other leg and not colour ringed. Avipoxvirus infection was confirmed by PCR with the sequence identified as APV clade B1 (see Supporting Information 4.S1).

Across all age categories, after removal of captures of birds of uncertain avian pox status or other disease (n=5) and birds that were ringed in the final partial year of the study (n=29), 46 cases of avian pox were recorded, 8.3% (46/554) of the total study population after exclusions, (annual range of 0 to 12.4%). No bird was observed to have more than one episode of avian pox.

The most common site for lesions was on the feet (45.6% of cases). 15.1% (7/46) of diseased Dunnocks had lesions on the head, at the base of the bill (Table 4.S1.1). None of the lesions on the head were considered large enough to impair the birds' vision and although some on the feet were up to 13 mm in diameter (Figure 4.S1.1f) the Dunnocks continued to feed. While the case definition in this study focused on the dry form of avian pox, it is noteworthy that no birds with skin lesions had concurrent indications of diphtheric (wet) form of the disease: however, these would not be detected by an external examination unless severe enough to cause problems with swallowing or respiration.

The results of the estimates of disease incubation period and the results of the duration of infection are available in the Supporting Information S2 and S3 respectively, but in summary, the maximum incubation period of avian pox in Dunnocks was estimated to be 13 - 48 days based on the timing of disease onset of most accurately aged, recently fledged, birds (4.S2). It was not possible to determine the duration of disease with confidence due to the low frequency of observations, but maximum bounds observed were 36 - 669 days (4.S3).

Disease Rates and Seasonality

82.6% (38/46) of avian pox cases occurred in Dunnocks in their first year (Table 1).

Avian pox was observed in 5.6% (52/927) of captures of birds in their first calendar year, and 2.2% (6/270) captures of birds in their second calendar year, that is, the previous year's juveniles, before their first post-nuptial moult, and 3.6% (10/280) of adult captures (Table 2).

Table 1: Ages of Dunnocks at first detection of avian pox, after correcting for missing values using data from other captures, showing the number of cases and percentage of cases with avian pox in each age class.

Age Class	**Number of cases**	**Percentage of total cases**
First calendar year	38	82.6%
Second calendar year	4	8.7%
Adult	3	6.5%
Unknown age	1	2.2%
Total	46	100.0%

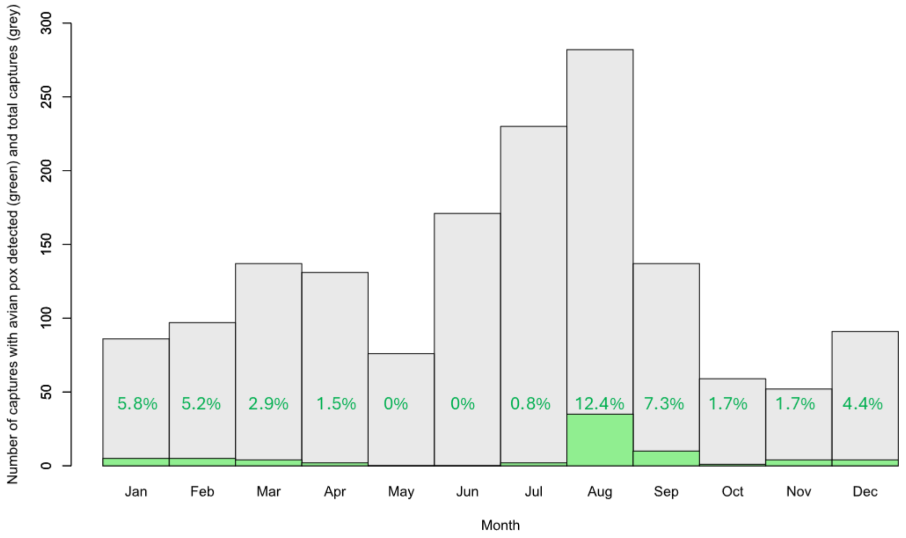
Table 2. Total captures with avian pox and total number of captures in each age class, and percentage of captures with avian pox as a percentage all captures in that age class.

Age Class	**Number of captures with avian pox**	**Total number of captures**	**Percentage of captures with avian pox**
First calendar year	52	927	**5.6%**
Second calendar year	6	270	**2.2%**
Adult	10	280	**3.6%**
Unknown age	4	72	**5.6%**
Total	72	1549	**4.6%**

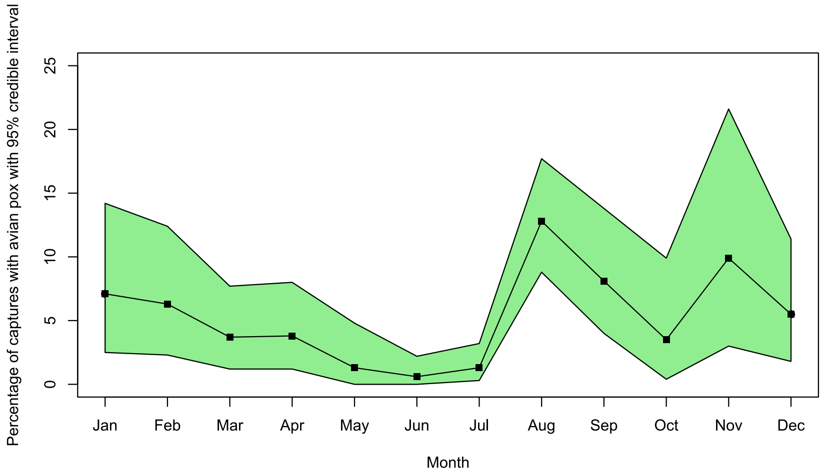
Cases of avian pox were detected in each calendar year except 2014, with a seasonal pattern, occurring during 10 months of the year with no cases detected in the population in May and June despite 247 captures occurring in those months (Figures 1a, b). 45.6% (21/46) of newly detected cases occurred in August, when 12.4% (35/282) of captures had avian pox (Table S4.1 in the appendix for this chapter).

Figure 1. Seasonality of avian pox in Dunnocks: a) the number of captures with avian pox (green) and total number of captures (grey) with the percentage of captures of Dunnocks with avian pox shown in each month in green; b) Percentage of captures with avian pox show with a credible interval derived from the Bayesian model described in the methods.

a)



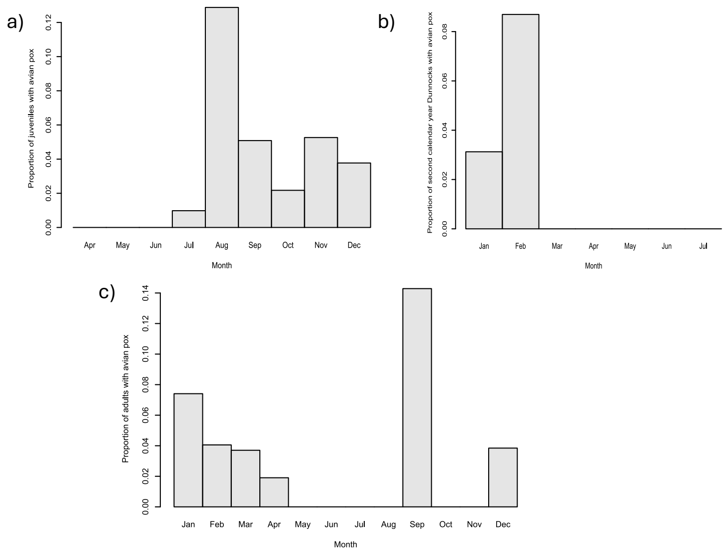
b)



Whilst juvenile cases peaked in August (Figure 2a) those of adult birds showed a bimodal distribution with peaks in February and September (Figure 2c), consistent with an association with the early part of their reproductive cycle and main period of moult

(Figures S4.1a and b). A table showing the number of cases and prevalence of avian pox is available in table S4.1

Figure 2. a-c). Proportions of Dunnocks detected with avian pox each month in each age class for all years combined. a) First calendar year birds, b) second calendar year years, c) adults



Survival and Detection Rates

The estimates of mean annual survival rates and mean annual detection rates for both the whole study population of Dunnocks, and separately for first year birds with and without avian pox are shown in Table 3. The annual survival rate was estimated to be 0.32 (SE 0.03, CI 0.27 - 0.37) for the population as a whole with no exclusions.

Table 3. Results of a Cormack-Jolly-Sieber model showing survival and detection rates of Dunnocks, for the first calendar year ages (1cy) groups with avian pox (pox) and birds that were not detected as having avian pox (no pox) and for the whole study population (all birds), given to three decimal places, with standard errors (SE), lower confidence intervals (LCI) and upper confidence intervals (UCI).

Group	Statistic	Estimate	SE	LCI	UCI	Number
Pox 1cy	**Survival (Phi)**	**0.365**	0.116	0.177	0.606	36
Pox 1cy	Detection probability (p)	0.448	0.207	0.136	0.807	36
No Pox 1cy	**Survival (Phi)**	**0.319**	0.031	0.261	0.385	437
No Pox 1cy	Detection probability (p)	0.519	0.069	0.385	0.651	437
All birds	**Survival (Phi)**	**0.315**	0.026	0.265	0.368	588
All birds	Detection probability (p)	0.579	0.061	0.456	0.692	588

The estimated mean annual survival rates, of birds that were ringed in their first year of life, were 0.37 (SE 0.12, CI 0.18 - 0.61, n=36) for the group with avian pox, and 0.32 (SE 0.03, CI 0.26 - 0.38, n=437) for the group without avian pox, using individual models for the two groups, with constant survival and detection rates. The results of the analyses comparing the two groups were identical whether the two groups were analysed separately or in the same model. The death rate ratio of 0.93 and overlapping confidence intervals of the CJS models indicate that there was no difference in death rates between the two groups.

The mean number of total captures per bird over the whole study period was significantly greater in Dunnocks with avian pox (4.50 (162/36, SD 3.40, n=36) than for those without skin lesions (2.70 (1180/437, SD 2.45, n=437) (p<0.01, Welch two sample t-test).

Models in which the two groups (pox and non pox) were considered, and the annual survival and detection probabilities were allowed to vary by year, failed to produce meaningful results. Annual estimates of survival for the whole study population, with no exclusions are shown in the appendix of Supporting Information for Chapter 4, Table S4.2, together with the number of cases of avian pox and the estimated population sizes.

Analyses did not detect any correlations between the study population size (an indication of population density), survival rates and incidence of avian pox in the population (Appendix Figure S4.2 a-d). All model outputs had a negative adjusted R-squared, high p-value and F-statistic all strongly indicating that the null hypotheses, that there is no correlation between the variables, should be accepted for all of the models (Appendix Table S 4.3).

Only 10 Dunnocks were found dead during the course of the study, none of which had skin lesions consistent with avian pox.

DISCUSSION

This 15.5 year study found no significant difference between the survival rates of the 36 first year Dunnocks that suffered from avian pox and the 437 first year birds where no skin lesions were observed, with estimated mean annual survival rates of 0.37 (CI 0.18 - 0.61) and 0.32 (CI 0.26 - 0.38), respectively. Avipoxvirus infection was confirmed by PCR with the sequence identified as APV clade B1. Overall, avian pox lesions were detected in 8.3% of Dunnocks (lifetime prevalence). Most affected birds were juveniles, and there was no evidence of disease recurrence. The peak prevalence of avian pox was in August, with fewer cases in all other months of the year, with the exception of May and June when no cases were detected in the 247 individual captures of Dunnocks. The maximum incubation period of avian pox in Dunnocks was estimated to be 13 - 48 days.

The apparent similarity in survival rates between birds found to have avian pox and those which did not suggests that avian pox in Dunnocks has a low case mortality rate. The observation that none of the lesions appeared to impair vision or feeding would also support the hypothesis that endemic avian pox is a milder disease, with a lower case fatality rate, in UK Dunnocks than in some other species. Studies in other wild bird populations have found higher mortality rates, for example, in 1996 a single outbreak of avian pox in Serins *Serinus serinus* in north-eastern Spain found a survival rate of 0.46 in birds with avian pox compared to 0.87 in healthy birds (Senar and Conroy, 2004), i.e. a death rate ratio of 4.15, compared with 0.93 estimated by this study.

It is possible that the CJS model failed to detect a difference in the survival rates of the two groups. Studies on simulated data have shown that in some cases CJS models have low power and may fail to detect trends in survival (Ross and Weegman, 2022). Confounding variables such as transience and differences in dispersal patterns, may cause additional problems (Conroy *et al.*, 1999), and a higher recapture rate for the avian pox cohort in comparison to the group with no observed skin lesions may mask differences in survival: in an outbreak of avian pox in Spain there was a 0.81 recapture rate for diseased Serins, compared to a 0.21 recapture rate of healthy birds (Senar and Conroy, 2004).

In this study the annual detection probability calculated by the CJS model was slightly lower in the avian pox group (0.49 compared to 0.52 for birds without avian pox) but the confidence interval was very wide. However, the total number of captures per bird in the avian pox group was significantly higher (4.5 compared to 2.7 in the group in which avian pox was not detected) and the increased frequency of capture may have increased the probability that the disease would be observed. If the duration of infection could be as short as 36 days, it is entirely possible that it may not have been detected in the majority of Dunnocks, especially in those caught less frequently in the group in which it was not detected.

The prevalence of avian pox of 8.3% in this study is similar to the prevalence of lesions of 7.2% observed in House Finches *Haemorhous mexicanus* over a single season (McGraw *et al.*, 2022). Other studies, using different laboratory methods have shown that a high proportion of some species of wild birds are infected with APV: 69.2% of a mixture of introduced species in New Zealand were seropositive (Ha *et al.*, 2013) and PCR detected APV in the spleens of 43% of wild birds, mostly waterfowl and other larger species, in Italy (Bertelloni *et al.*, 2022). The apparently low rates of disease in adults in this study could be due to the observational approach or a lack of detection but might suggest that many infections are subclinical. No evidence of recurrent disease was seen in this study, suggesting that APV infections in Dunnocks may induce long-term immunity to further infection as has been reported in other birds (van Riper and Forrester, 2007). Mechanistically, immunity has been suggested to be largely T cell mediated with a smaller role for antibodies (Van Riper and Forrester, 2007).

The estimate of the period of feather growth from hatching (S1), in Dunnocks, of 13 to 48 days is in the same range, although with a lower minimum, as that of other small passerines. In the Australian Zebra Finch *Poephila guttata castanotis* this has been shown to be 27-29 days from hatching (Sossinka, 1980). The wings are fully grown at approximately 40 days in the Cactus Wren *Campylorhynchus brunneicapillus* (Ricklefs, 1975), and 30 - 35 days in European Starling *Sturnus vulgaris* (Starck and Ricklefs, 1998). The feather growth analysis was important in estimating the incubation period, from infection to the onset of lesions, in Dunnocks, based on the two birds caught with avian pox and a growing wing, of 13 - 48 days and one caught as a very recent fledgling (within an overall estimation of 13-146 days). This result should be regarded as an estimate because of the multiple potential sources of uncertainty, including the precise age of the birds and the exact date of the onset of clinical signs, but the method shown in the process chart (Figure 4.S2.2) could be applied to other species, and refined with further data on the rate of progress of the disease. Avian pox was detected in the nestlings of Great Tits suggesting a shorter incubation period (Lachish, Bonsall, *et al.*, 2012) because Great Tits fledge at 18 - 21 days (British Trust for Ornithology, 2023b) whereas Dunnocks fledge at 12 - 14.5 days (British Trust for Ornithology, 2023a). No Dunnock nestlings were included in this study but if Dunnock nestlings can be infected and fail to survive, it would lead to an over-estimation of the disease incubation period and survival rates of affected birds, and an underestimate of the incidence of avian pox in Dunnocks.

As in a previous study looking at the incidence of non-Paridae pox, in which 49.5% of cases were in Dunnocks, (Lawson *et al.*, 2012), the peak in observed cases in this study occurred from late July to mid-September. The peak of cases in autumn might partially be due to the stress of moult as birds were actively moulting at this time. However, at this time of year, a peak in the number of cases is likely to be affected by a combination of a higher population density and a large number of immunologically naïve juveniles in the population. This is supported by the observation that 82.6% of cases occurred in juveniles, although comparisons of annual population density and the annual incidence of disease did not show a correlation. Adults with persistent, possibly subclinical, infections may be transmitting APV to their offspring, but infection rates are driven by other mechanisms, such as the presence of vectors in which viral infections may overwinter (Folly *et al.*, 2022). Mosquitoes in the genera *Aedes* and *Culex* have been proven to be mechanical vectors of APV with the virus remaining viable on the proboscis for up to 28 days (Kligler, Muckenfuss and Rivers, 1929; DaMassa, 1966). A seasonal peak of abundance of ornithophilic mosquito species is observed in the UK in summer and early autumn months (Cull *et al.*, 2024), similar to that observed with avian pox. There is also evidence that APV can be vectored by mites, *Dermanyssus gallinae* (Shirinov, Ibragimova and Misirov, 1972; Huong *al.*, 2014), stable flies *Stomoxys calcitrans* (Alehegn, Chanie and Mengesha, 2014), fleas (Smits *et al.*, 2005) and midges (Lee *et al.*, 2017) and the louse flies *Ornithomya avicularia* and *O. fringillina* (Wawman *et al*, 2025).

Avian pox in adults has a bimodal distribution, with peaks in February and September. While it is possible the infections early in the year were continuing undetected from the previous year – as the maximum duration of infection was estimated to be 36 - 669 days - these peaks correlate with increased periods of stress and hormonal changes which can result in poorer immune responses, for example, birds being in poorer condition after the winter, the trade-offs between maintaining the immune system, pathological processes and the increased energetic demands of the breeding season (Sheldon and Verhulst, 1996) or moult (Hamilton and Zuk, 1982). Seasonal variation is evident in the immune systems of wild birds (Valdebenito *et al.*, 2021). In male vertebrates, testosterone, which peaks during the breeding season, is known to lower the immune response to infection (Folstad and Karter, 1992) and changes are necessary in the female reproductive tract to prevent destruction of both spermatozoa and the fertilised ovum (Wigby *et al.*, 2019). In domestic hens, a decrease in immunity as hens come into lay increases the risk of *Salmonella enterica* Serovars Enteritidis and Pullorum infection in the reproductive tract (Wigley *et al.*, 2005; Johnston *et al.*, 2012) and leads to an increase in the numbers of *Salmonella* bacteria present in non-reproductive tissues. Dunnocks are usually double-brooded with the earlier period of their reproductive cycle in February coinciding with the first observed seasonal peak of disease in birds of breeding age. A brood patch score of two – complete defeathering (Redfern and Clark, 2001) – roughly corresponds to the start of egg laying (Hinde, 1961; Jones, 1971), and in this population these were present from February to May.

The uncertainty around the possibility of subclinical infections, carrier state and the incubation period of avian pox in Dunnocks and other small passerines in this region makes it difficult to disentangle the causes of seasonality without further studies using invasive sampling methods to determine the immunological status of birds and the role of vectors in disease transmission. Repeated blood sampling of a wild population of Dunnocks to look for both APV and antibodies to APV might yield more information about the incubation period, duration of active infection and the presence of subclinical infection. It would also allow exploration of the immunological response to infection and how this varies between birds and throughout the year. Regular sampling of mosquitoes, midges, ticks, and biting flies throughout the year would enhance knowledge about how APV is circulating in potential vector populations. While the gold standard would be challenge studies on captive birds, combining regular observations and sampling, these would be challenging and might not be generalisable to wild populations exposed to a wide range of climatic conditions, predators, other infectious diseases and parasites.

Future longitudinal studies of disease in wild small passerines could be improved by more frequent captures, across a larger area, so that fewer birds are lost to follow-up, and a larger population is available, to give more robust estimates of demographics. Although colour ringing of individuals may boost survival estimates, it is not helpful if birds need to be categorised as either clinically sick or healthy at each capture. It could however be useful if there is a short period, at a specific time of year when infection is transmitted - perhaps in the case of a vector borne disease - at which time individuals can be categorised, but care would need to be taken to avoid transmitting the infection to other birds and possibly humans. With novel infections emerging due to anthropogenic changes, it may be helpful to produce estimates of the growth of wing feathers in fledglings of multiple species, which could be used to estimate disease incubation periods, especially as immunological naïve juveniles are most likely to be affected, although it would be better to calculate these from birds whose age is known from the date of hatching.

This manuscript provides key foundations for future studies by demonstrating the prevalence of avian pox in Dunnocks and its seasonality and demography that could be generalised to other species. The use of ornithological knowledge of the timing of feather growth and moult could be useful in exploring the incubation periods of other infectious diseases in various species of birds.

SUPPORTING INFORMATION

S1 Diagnosis of avian pox in Dunnocks *Prunella modularis* (FOLLOWS as Chapter 4.S1)

S2 Estimating the incubation period of avian pox in Dunnocks *Prunella modularis* (FOLLOWS as Chapter 4.S2)

S3 Avian pox in Dunnocks *Prunella modularis:* disease progression and duration (FOLLOWS as Chapter 4.S3)

S4 Additional tables and figures (APPENDIX Supporting Information Chapter 4)

Table S4.1. Monthly incidence, prevalence and number of captures – all years combined

Figure S4.1 plots of monthly proportions of adult Dunnocks with brood patches, and all birds in moult

Table S4.2. Annual population, proportion of Dunnocks with Avian Pox, survival and detection rates from CJS model

Figures S4.2 Plots comparing annual incidence, survival and study population size.

Table S4.3 Results, given to three decimal places, of fit for models comparing survival r ates, avian pox rates and population size.

Data Availability

The dataset will be published in the Oxford University Research Archive, ORA, https://ora.ox.ac.uk on completion of the study.

The avipoxvirus sequence is available at GenBank (https://www.ncbi.nlm.nih.gov/genbank. Last accessed 25th July 2024) with accession number PP756527.

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Author Contributions

Denise C. Wawman: conceptualisation; resources; data collection; methodology; data analyses; validation; data visualisation; writing – original draft; review and editing (equal).

Steven Fiddaman: laboratory testing for APV; molecular analyses, plotting phylogeny showing pox clades; review and editing.

Becki Lawson: veterinary and diagnostic advice; review and editing (equal).

Ben C. Sheldon: review and editing; supervision (equal).

Adrian L. Smith: resources, review and editing (equal); supervision (equal).

Conflict of Interest

The authors declare that they have no conflicts of interest.

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Ethical Statement

All birds were captured under licence (BTO ringing permit number S5420) held by DCW. DCW processed or supervised the processing of all birds.

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4.S1 – Diagnosing avian pox in Dunnocks

Garden bird disease surveillance conducted across Great Britain since the early 1990s has regularly received disease incident reports consistent with avian pox in Dunnocks, which typically manifests as sporadic morbidity and associated mortality, consistent with an endemic disease pattern (Lawson et al, 2012; GWH *unpublished data*). Post-mortem examinations of multiple Dunnocks have confirmed the diagnosis through histological examination combined with Sanger sequencing of APV which clustered in the Canarypox virus subclade B1 (Lawson et al., 2012). Post-mortem examination of approximately 90 Dunnocks conducted over the period 2005 - June 2024 inclusive, identified skin lesions suspected or confirmed as avian pox in 19 cases and diagnosed only two birds with proliferative skin lesions caused by another aetiology, the parasitic infestation cnemidokoptosis (Seilern-Moy et al., 2021): the scaley appearance and distribution of skin lesions in these cases was distinct from those of avian pox.

Given the characteristic appearance of skin lesions with avian pox, and the high correlation with diagnosis by DNA sequencing, biopsy of lesions and virus isolation (Lawson et al., 2012; van Riper, et al., 2002), most studies use syndromic surveillance approach to define cases of avian pox in epidemiological studies of free-living wild passerine species (Lawson et al., 2012; Senar & Conroy, 2004; Vanderwerf, 2009).

Figure 1. Avian pox skin lesions in Dunnocks. a-c) early lesions at the base of the bill: a) and b) are the same Dunnock fledgling on 4 August 2021 and 12 August 2021. c) early lesion at the base of a Dunnock's bill. d) Lesions at the base of the bill, in a known third calendar year adult Dunnock. e) typical lesion on the distal phalanx, as seen on the first study case in 2008. f) an unusually large lesion covering the distal tarsus and proximal part of the foot.

Study methods and results

Birds were identified by the bird ringer, DCW, as having avian pox lesions. These lesions were photographed when the condition of the birds allowed this to be done without compromising bird welfare.

All available images from Dunnocks with skin lesions suggestive of avian pox (10 of the 46 birds) (see Figure S1.1 and Figure S1.2 for examples) were retrospectively reviewed by BL, a veterinary surgeon specialising in wild bird disease investigation, who considered that the characteristic macroscopic appearance of proliferative skin lesions and their distribution on the head and feet of affected Dunnocks was consistent with a presumptive diagnosis of avian pox in this species. None of the images were suggestive of cnemidokoptosis which has been previously reported in Dunnocks in Southern England (Seilern-Moy et al., 2021). The locations of the lesions seen in the study can be seen in Table S1.1.

Table S1.1. Sites of avian pox skin lesions observed on Dunnocks in the study population

Location of lesion	**Number of cases**	**Percentage of total cases**
Feet only	19	41.3
Feet and legs	2	4.3
Feet and head	5	10.8
Feet and breast	1	2.2
Leg(s) only	4	8.7
Head only	2	4.3
Site not recorded	13	28.3
Total	46	

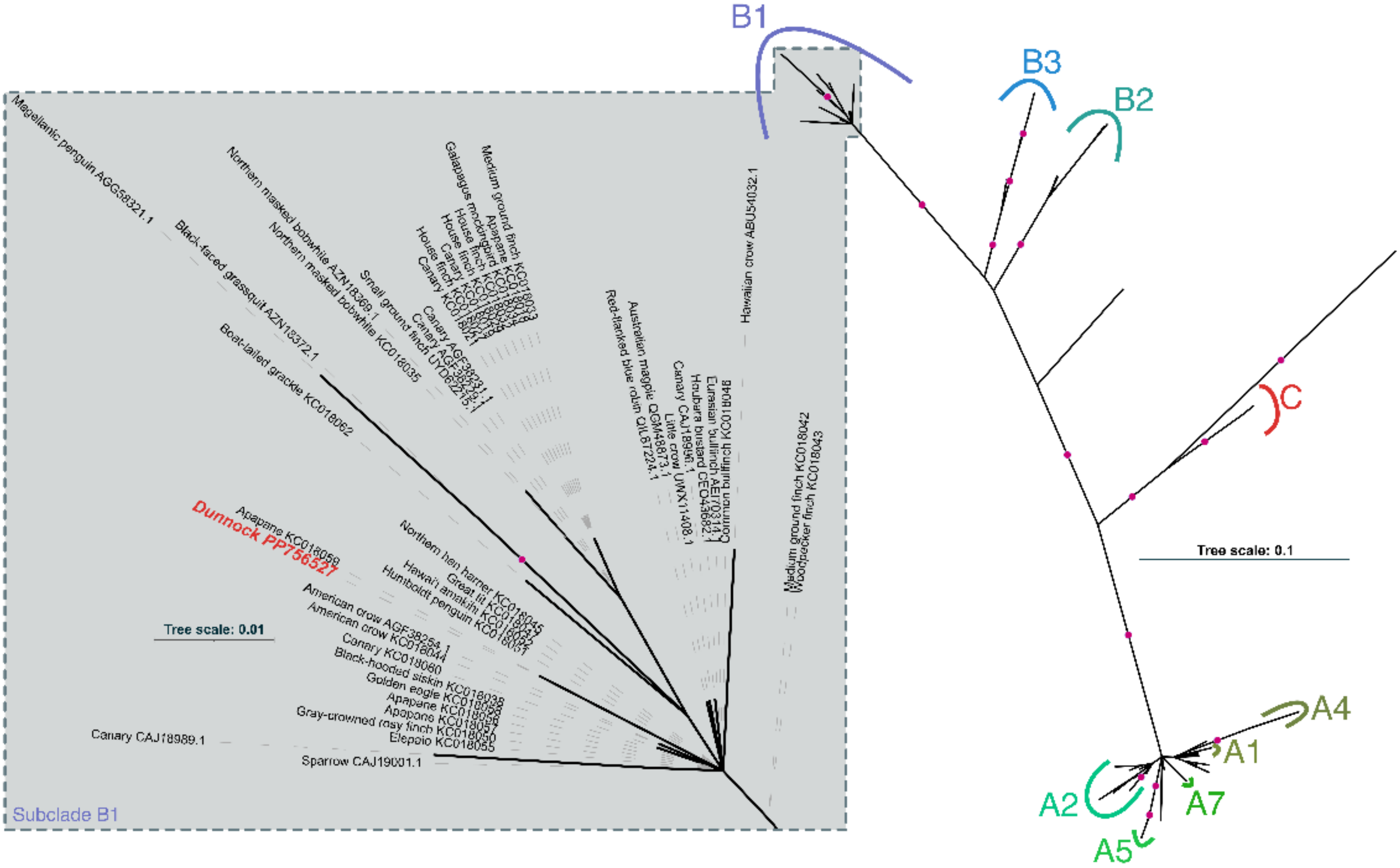
In addition, a molecular diagnosis was obtained from a single skin lesion shed by a Dunnock (Figure S1.2). Using the DNeasy Blood and Tissue kit (QIAGEN) according to the manufacturer’s instructions, high molecular weight DNA was extracted from the skin lesion. Screening for APV was carried out through amplification of a 578-bp PCR product of the Avipoxvirus 4b core protein gene (*fpv*167) as previously described, using primer sequences 5`-CAGCAGGTGCTAAACAACAA-3` and 5`-CGGTAGCTTAACGCCGAATA-3` (Lawson et al., 2012). Amplification was achieved using the high-fidelity Q5 polymerase (NEB) under the following cycling conditions: 98 °C (5 min); 40×[98 °C (1 min); 64 °C (20 sec); 72 °C (20 sec)]; 72 °C (7 min). Following confirmation of a product of the correct size on an agarose gel, APV was confirmed through bidirectional Sanger sequencing (Source BioScience) using the same primers as for amplification.

Initial exploration of the DNA sequences used the R packages *seqinr* (Charif & Lobry, 2007) and *ape* (Paradis & et al, 2023) to align the sequences and produce a basic phylogeny, in R version 4.2.1 (R Development Core Team, 2022). The final phylogeny was based on a maximum likelihood tree of 1000 bootstraps in RAxML (Stamatakis, 2014) using the nomenclature used by Gyuranecz et al. (Gyuranecz et al., 2013)

Figure S1.2. Avian pox skin lesions on the Dunnock from which avipoxvirus was sequenced. It was a fledgling, ringed with no signs of avian pox on 25 July 2023. a) first detection of disease on 11 August 2023, b) same lesion on 20 August 2023. c) and d) after the same lesion sloughed off on 25 August 2023.

The 537 base pair DNA, 4b core protein gene sequence obtained from the avian pox lesion is available in GenBank with accession number PP756527. Phylogenetic analysis showed that the sequence was identical to that in the Canarypox virus B1 subclade previously found in Dunnock in the UK (Lawson et al., 2012) (Figure S1.3).

Figure S1.3. Maximum likelihood phylogeny showing how the sequence of Avipoxvirus from the current study (in red) fits into the various clades of avipoxvirus. It was based on a maximum likelihood tree of 1000 bootstraps in RAxML (Stamatakis, 2014) using the nomenclature used by Gyuranecz et al. (Gyuranecz et al., 2013). The right hand side of the plot shows the whole avian pox phylogeny, with the Canary Pox subclade B in the grey box on the left hand side. The position of the sequence obtained from the Dunnock lesion in this study is shown in red.



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S2 – Estimating the incubation period of avian pox in Dunnocks *Prunella modularis*

Abstract

Estimating the incubation period of a disease in a wild population is difficult, as it requires an accurate determination of both the date of exposure to the pathogen and the onset of clinical signs, but the exact date of exposure to a disease cannot be known and most populations are not sampled on a daily basis to determine the onset of signs of disease. However, if a disease affects a study population of young birds, of varying ages, each of which is known exactly from the date of hatching, the dates of captures of diseased birds can provide an estimate of the maximum possible disease incubation period. In many cases the exact age of a bird is not known, as they were not ringed as nestlings, but other estimates of age can be used, such as the timing of juvenile primary feather growth.

The Dunnock, *Prunella modularis* is a small passerine that is known to be affected by avian pox. Using data from a longitudinal study of avian pox in Dunnocks, the duration of primary feather growth in fledgling Dunnocks was estimated to be 13 – 48 days. Three methods, using this and other estimates of the age of juvenile Dunnocks, concluded that the maximum incubation period of avian pox in Dunnocks lies between 13 and 146 days, with the most likely maximum being 13 - 48 days as the estimates were derived from the most recently hatched birds, which a shorter time in which they could exposed to the disease.

Introduction

Most studies to calculate the incubation periods of diseases are laboratory based challenge studies that have known dates of exposure to the pathogen, from which it is possible to calculate an incubation period from the date of this exposure to the onset of clinical signs. However, in wild populations the dates of exposure and exact timing of the onset of clinical signs are not known, so it is not possible to obtain accurate figures.

As avian pox is not vertically transmitted from the female via the egg, infection with avipoxvirus (APV) must occur after hatching (Van Riper & Forrester, 2007). The maximum possible disease incubation period of avian pox, from first infection to the onset of disease, could be estimated from known age birds captured with avian pox. If it can be assumed that the incubation period is constant for all individuals, data from the youngest birds will give the best estimates, as they have had less time in which exposure to the pathogen could have occurred, when combined with a high frequency of recaptures.

Ideally, age would be known from the date of hatching, from birds ringed as nestlings in monitored nests, and avian pox would be detected as soon as skin lesions develop, however in most cases the birds will have only been ringed after fledging, so it may be necessary to use the known duration of their developmental stages (Figure S2.1). For example, the nestling stage of Dunnocks *Prunella modularis* lasts 12-14.5 days (British Trust for Ornithology, 2023) so birds seen fledging can be assumed to be 12-14.5 days old.

Once birds that were not ringed in the nest have been fledged for an unknown amount of time the estimates need to rely on other information. As most passerines fledge with wings that are not fully grown, the presence of growing primaries (seen as the partial remains of the feather sheath at the base of the feather, in a juvenile bird not in wing moult) indicate that a bird is recently fledged. If the duration of feather growth is known, this can be used to provide an estimate of age, which can be used to calculate disease incubation periods, assuming that the disease does not delay primary feather growth. Estimates of the period of wing growth in newly fledged birds are only available for a few species of Passerine. In the Australian Zebra Finch *Poephila guttata castanotis* this has been shown to be 27-29 days from hatching (Sossinka, 1980). The wings are fully grown at approximately 40 days in the Cactus Wren *Campylorhynchus brunneicapillus* (Ricklefs, 1975), and 30 - 35 days in European Starling *Sturnus vulgaris* (Starck & Ricklefs, 1998). This time period has not previously been estimated for Dunnocks.

As well as basic age codes (Table S2.1), the British Trust for Ornithology (BTO) ringing scheme codes other categories that can be used to help age birds more accurately. These include codes for moult, including general moult codes, feather scoring systems, and a separate code for the active growth in the primary feather that forms the wing point (Redfern & Clark, 2001). Age codes include, for example, 1J, for birds that have recently fledged are and flying weakly, 3J for juvenile birds that have completed less than 90% of their post-juvenile moult, and 3 for juvenile birds that are further through their moult or have finished moulting. Expert opinion (a discussion amongst bird ringing trainers) suggested that for Dunnocks the initial fledgling period usually lasted from one to five days, but occasionally up to 11 days, with five days being the most likely duration of the 1J period.

Figure S2.1. Duration of Dunnock developmental stages, used for estimating the incubation period of avian pox.

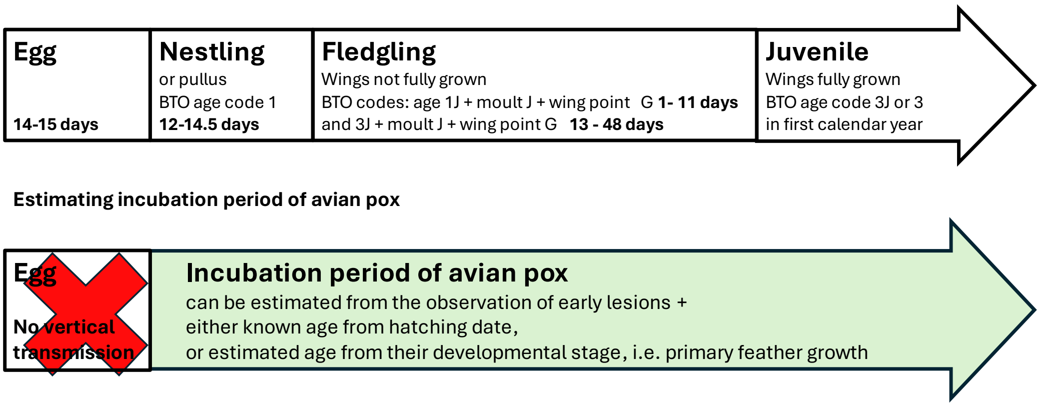


Table S2.1. Description of age categories used in the study

Age category	Description	BTO ringing scheme age codes
First calendar year (1cy)	birds in the first calendar year of life: juveniles	1J, 3J and 3
Second calendar year (2cy)	birds in the second calendar year of life up until the first post-nuptial moult in late summer/autumn when they become indistinguishable from adults	5
Adult	all birds after their first post-nuptial moult, although this technically includes some birds in their second calendar year, they are indistinguishable from older adults	4 in autumn and early winter, and 6 in from the New Year until the post-nuptial moult
Unknown	age could not be determined either due to lack of data due to the a priori decision to release diseased birds at the net or to conflicts in the data which had no clear resolution after using previous capture dates, active moult patterns, etc	4 from the New Year, in winter, spring and summer, and age code 2 at any time

The other important information needed to estimate a disease incubation period in a wild population is some knowledge of the progress and duration of clinical signs (see S3). Clearly, if a bird is caught with very early clinical signs it will be closer to the date of exposure than one caught as the disease is healing. Thus any estimates are best made from the earliest signs of infection, some of which may not be specific to the disease in question and may require further captures to verify the diagnoses.

In summary, if a disease is not vertically transmitted via the egg, it should be possible to estimate the incubation period from a combination of the duration of the nestling stage and estimates of a juvenile bird's time since fledging from feather growth, with some knowledge of the disease progression. The method described here proposes the use of birds whose age has been estimated to estimate the maximum incubation period, that is from the earliest possible date of exposure to the disease causing agent until the onset of infection.

This study aims to present methods that provide a framework for estimating, firstly, the duration of feather growth, and secondly, the maximum disease incubation period, using the example of avian pox in Dunnocks. It utilises data from a small number of birds in the study population to provide these estimates. These estimates should be verified from a larger number of records.

Methods

Estimating the duration of feather growth

Ideally, the duration of feather growth would be calculated from frequent observations of fledged birds ringed as nestlings whose age is known exactly from the date of hatching. In the absence of these data it can be estimated from the duration of the nestling period, the estimated age of a bird ringed as a fledgling (1J), and the interval between that capture and the following captures:

Minimum duration of feather growth = Duration of nestling period (12 – 14.5 days rounded to 15 days for Dunnocks) + estimate of age of a recently fledged bird at ringing (0 - 11 days) + time from ringing until last capture with wings growing.

Maximum duration of feather growth = Duration of nestling period (12 - 15 days for Dunnocks) + estimate of age of a recently fledged bird at ringing (0 - 11 days) + time from ringing until first capture with wings fully grown.

These calculations of the period of primary wing growth, data from 10 Dunnocks ringed at age 1J, with no signs of avian pox, gave estimates of the period of active primary feather growth from hatching of a minimum of 13 - 42 days (mean 23.5 days, n=7, from birds caught at least twice with the wings growing but not subsequently) and maximum of 25 - 48 days (mean 35.4 days, n=5, from birds recaptured after the wings had stopped growing). Thus the duration of primary feather growth in fledgling Dunnocks is estimated to be 13 – 48 days from hatching.

Estimating the disease incubation period

Ideally the disease incubation period would be calculated from the date of onset of infection from birds of known age, ringed as nestlings whose date of hatching is known, that are later retrapped with the disease.

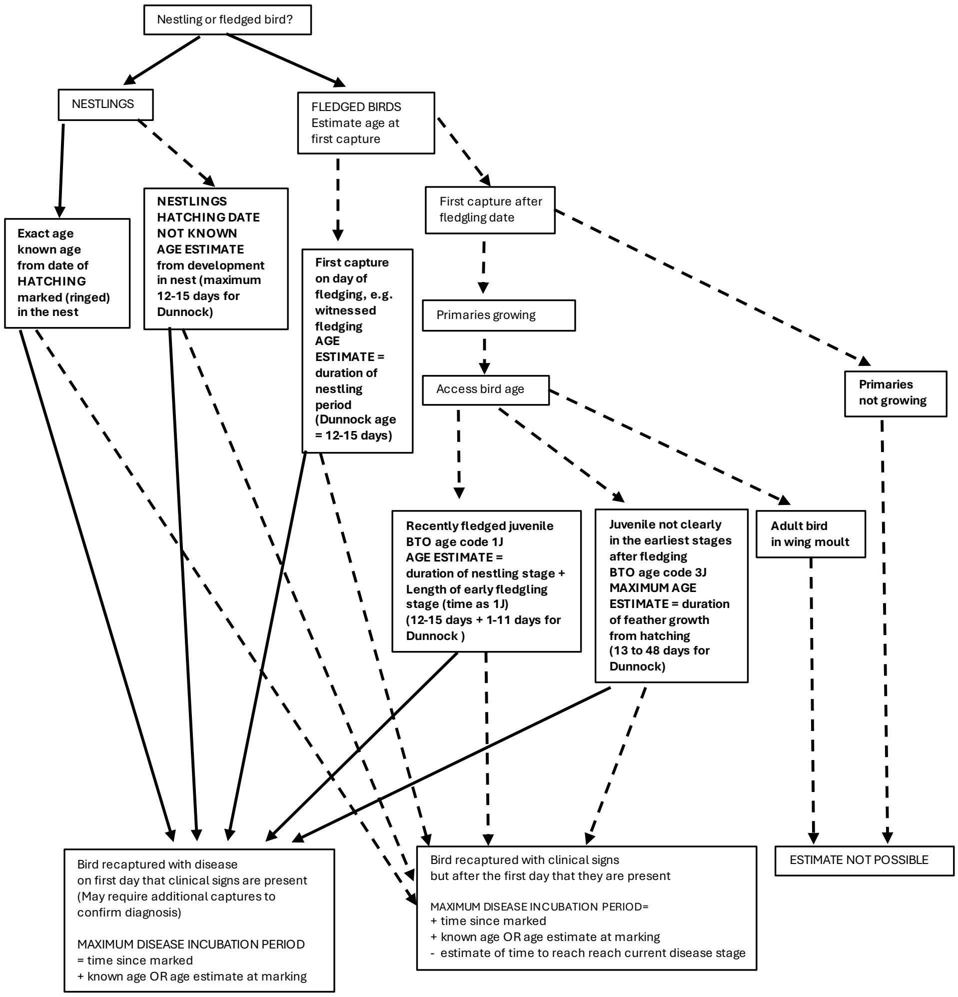
In the methods described below, bird's ages can be estimated by summing the relevant estimates of the duration of various stages (the duration of the nestling stage (12 - 14.5 days, rounded to 12 - 15 days), duration of the newly fledged (1J) period, assumed to be 5 days, and the duration of primary feather growth of 13 - 48 days) and adding the interval between the capture at which the bird's age was estimated and the observed onset of signs of disease.

The process chart in Figure S2.2 allows for a range of scenarios, for birds of different ages. Solid lines indicate known time periods, e.g. from ringing to recapture and dotted lines estimates. The numbers given are for Dunnocks. It can be seen that estimates towards the left of the plot (using younger birds) will be more accurate than those for older birds, with it not being possible to estimate the age and hence the incubation period of disease in birds shown on the far right, ringed after the completion of their initial feather development as fledglings.

These calculations will all be overestimates as they assume that the birds were caught on the first day that signs of infection were apparent and measure the time from hatching, rather than the time from exposure to the disease. They also assume that the disease does not delay wing growth.

The examples given below use data from birds caught as part of the study that later developed avian pox to illustrate the methods. For simplicity, the estimates that follow assume that the bird was caught on the first day that clinical signs of infection were visible and use 5 days for the duration of the 1J (newly fledged and flying weakly stage).

Figure S2.2. Process chart for estimation of the maximum incubation period of a disease from first possible exposure to the development of clinical signs, from the growth of juvenile primary feathers, using avian pox in Dunnocks as an example. The solid lines indicate known time periods and the dotted lines estimates.



Method 1a

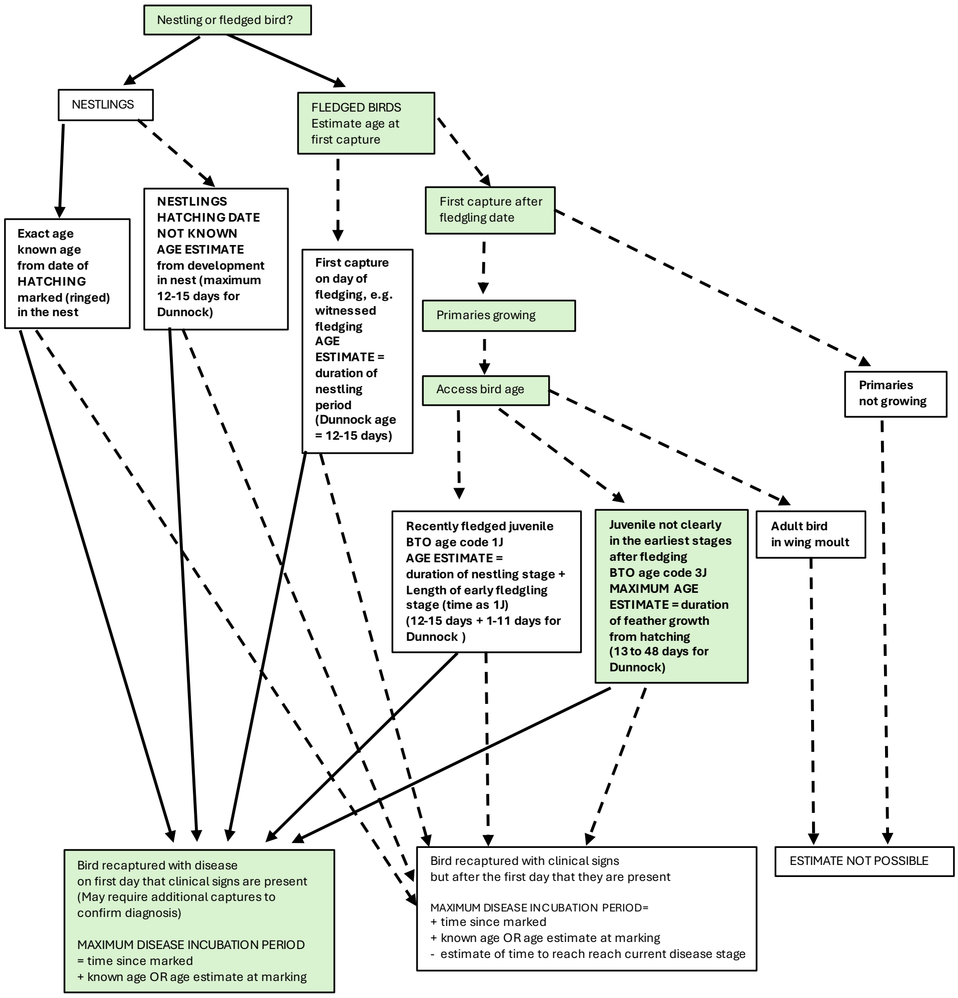
If a bird is caught with avian pox while its wings are still growing, assuming that the disease has not delayed development, the bird's age must lie within the known duration of wing growth in juveniles of that species. The maximum age of juvenile Dunnocks with a wing that is still growing, is 13 - 48 days.

This figure can be used to produce an estimate of the maximum incubation period of avian pox in a bird caught with avian pox, that has previously been seen growing primary feathers (Figure S2.3, highlighted in green).

15 birds that were initially ringed with a growing wing, after the immediate fledging period (BTO code 3J) developed avian pox, after a mean of 37 days (range 0 – 98 days) from the

point at which their primary wing feathers were last recorded as being in active growth. These birds would have been estimated to be 13-48 days old at that capture, giving a minimum incubation period of avian pox somewhere between 13 and 146 days.

Figure S2.3. Process chart for estimation of the maximum incubation period of a disease from first possible exposure to the development of clinical signs, from the growth of juvenile primary feathers, using avian pox in Dunnocks as an example. The solid lines indicate known time periods and the dotted lines estimates. The boxes highlighted in green show the process for estimating the age and hence the incubation period of a avian pox in a juvenile Dunnock, first caught when its primary feathers are still growing, but not within the initial fledgling period, and later recaptured with avian pox on the first day that clinical signs were apparent (Methods 1b and b).

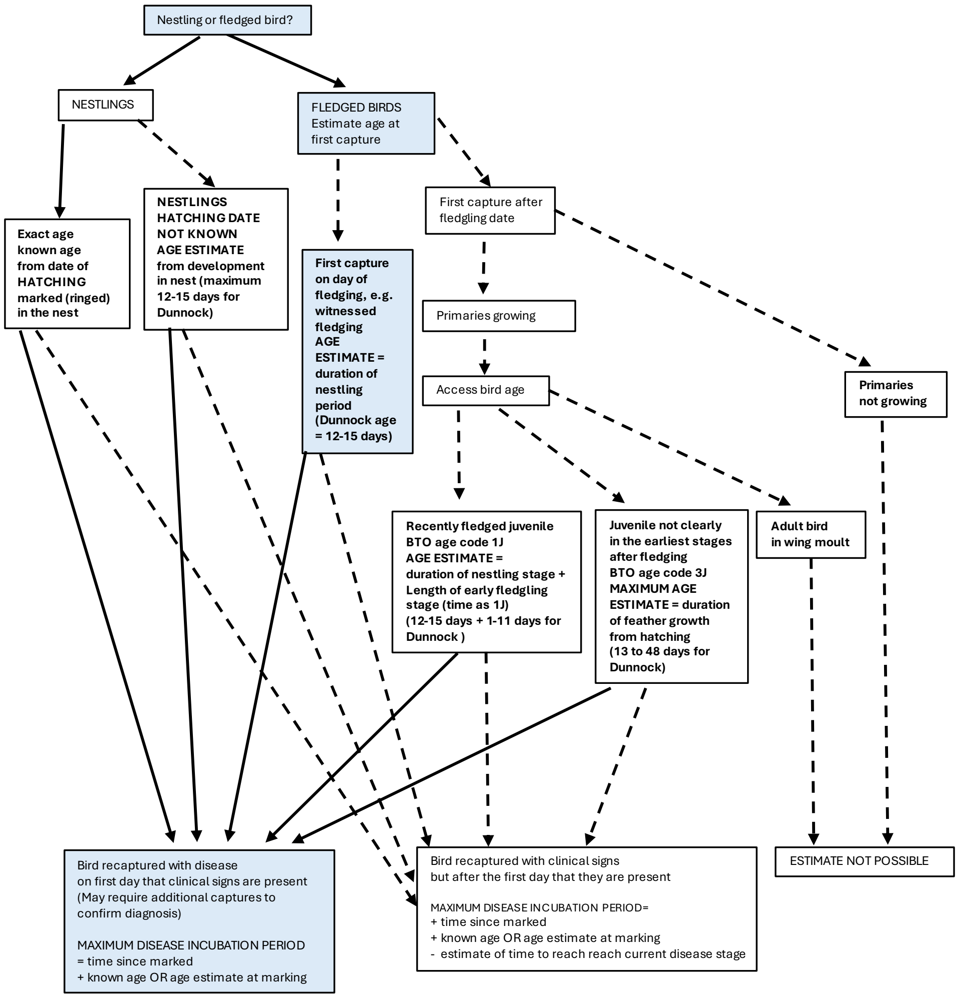


Method 1b

This is a special case of applying to two of the birds, included in Method 1 (Figure S2.3). Two juvenile Dunnocks had signs of avian pox while their wings were still growing, which would suggest that for them maximum possible the incubation period had to lie between 13 and 48 days, the estimate of the time from hatching until the wings are fully grown.

Method 2

Figure S2.4. Process chart for estimation of the maximum incubation period of a disease from first possible exposure to the development of clinical signs, from the growth of juvenile primary feathers, using avian pox in Dunnocks as an example. The solid lines indicate known time periods and the dotted lines estimates. The boxes highlighted in pale blue show the process for estimating the age and hence the incubation period of avian pox in a juvenile Dunnock, first caught, within a few days of fledging, when its primary feathers are still growing, and later recaptured with avian pox on the first day that clinical signs were apparent (Method 2).



The maximum possible incubation period of avian pox in Dunnocks initially caught and coded as age 1J (fledglings) was calculated as follows:

Minimum (assumes the bird was first caught on day it fledged) as shown in Figure S2.4 highlighted in pale blue:

Nestling period minimum (12 days) + time from first 1J capture to first detection of clinical APV infection

Maximum (assumes bird is a 1J for 5 days):

Nestling period maximum (rounded to 15 days) + 5 days + time from first 1J capture to first detection of clinical APV infection

For example, one apparently healthy Dunnock fledgling ringed at age code 1J (just fledged) was trapped 11 days later with detectable avian pox infection. Assuming that its primary growth and early development (used to determine that it had just fledged) had not been delayed as a prodromal effect of the infection, and that the bird was caught in the earliest stages of detectable disease, this would suggest that, in this case of avian pox, the maximum incubation period must lie between 23 and 31 days (12 + 0 + 11 days and 15 + 5 + 11 days) (Figure S2.4).

Conclusion

The duration of primary feather growth in fledgling Dunnocks is estimated to be 13 – 48 days.

A combination of methods for estimating the incubation period of avian pox suggested that the maximum incubation period of avian pox in Dunnocks lies between 13 and 146 days, with an estimate of 13 - 48 days derived from birds closer to hatching and of more accurately known age. If the incubation period is constant across all birds, the true incubation period is likely be obtained from the birds with the shortest interval in which they could be exposed to APV, however, it should be remembered that these methods, relying on wing growth, assume that the early stages of the disease do not delay primary feather growth.

As these estimates are from a wild population, the date of exposure to the pathogen is not known, and in some, if not all cases, this will have greatly overestimated the disease incubation period, as will the assumption that, when captured with avian pox, the birds had just developed signs of the disease.

Studies on the duration and course of infection in Dunnocks may, given a sufficient sample size and a high frequency of recaptures, allow an estimate of the time from the start of infection to a bird's current condition, as the lesions follow a pattern gradually increasing in size, often developing a crust on the surface and then resolving. This could allow the start date of signs to be estimated later in the course of the disease, although it is likely that the progression through these stages will not be the same in all individuals. Challenge studies in a laboratory would be needed to produce more exact figures but the results may not be applicable to a wild population, exposed to other pathogens and different stresses to birds in a laboratory.

These estimates are generated from a small sample sizes, further work will be required to collect more data to refine these calculations, but the process could be generalised to other species and other diseases, including, diseases that are known to be transmitted transovarially, by adding the incubation period of the egg (from the date it was laid to the date the nestling hatches) to the calculations.

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4.S3 Avian pox in Dunnocks *Prunella modularis:* disease progression and duration

These observations relate to 46 Dunnocks *Prunella modularis* captured with avian pox as part of the main longitudinal study.

Twelve Dunnocks were captured more than once while affected by avian pox. Their lesions were seen to progress from healthy, to slight swelling, to raised areas or lesions with unbroken skin. Six birds developed pustules and open lesions, possibly due to secondary infections following an injury before these scabbed over. One lesion was seen to separate from the leg, without blood loss, leaving normal scales where it had been (see S1, Figure S1.2). This lesion was used for molecular confirmation of the diagnosis.

Most birds healed without scarring but two of the 46 birds with avian pox suffered from ischaemia of the tissues around the lower tarsometatarsus, resulting in necrosis of the foot and tissue of the distal tarsometatarsus. A further two birds were seen with missing toes, probably due to ischaemia caused by previous avian pox, but were excluded from the study because their loss of toes could have been due to other causes.

Calculating the duration of disease was complicated by the sparse data, which in most cases was right or left censored or both, with most birds (34/46) only seen with signs of avian pox on one occasion during the course of the study. Consequently, the duration of disease can only be described with a few summary statistics as seen in Table S3.1 and the plots in Figures S3.1 and S3.2.

It is apparent from Table S3.1 that attempts to calculate the duration of clinical signs of avian pox were hampered by large periods of uncertainty around the date of both the onset of clinical signs and recovery, and the large number of birds only seen with avian pox on one occasion. The minimum possible duration of clinical signs, the period in which pox was observed assuming that the bird did not recover in the intervening period, was in the range of 1-101 days (mean 7.15, median 1, SD 17.42, n=46) and was mainly influenced by a single outlier. The maximum possible duration, from healthy capture to healthy capture with a period of disease in between, was 36-336 days (mean 175.23 days, median 125 days, SD 128.18, n=12). This estimate was also influenced by outliers that were not seen from a long period between captures, as indicated by the large difference between the mean and median values.

Table S3.1 Summary statistics describing the duration of avian pox (values expressed to 2 decimal places). The sample sizes given are the number of birds in each group. The observed duration is the interval from the first to last capture of a bird with avian pox, (34 birds were only seen once with signs of disease).
The maximum possible duration is the interval from healthy capture to healthy capture with a period of disease in between estimated from birds caught on more than one occasion with avian pox. Birds caught with uncertain intervals between appearing healthy and having signs of avian pox and between having signs of avian pox and appearing healthy are seen in the bottom two rows describing the uncertainty.

Time period	**Sample size**	**Mean (days)**	**Median (days)**	**Range (days)**	**Standard deviation**
Observed duration	46	7.15	1	1 - 101	17.42
Maximum possible duration	12	175.23	125	36 - 669	128.18
Uncertain period before pox first observed	36	67.14	28	3 - 624	122.09
Uncertain period after pox last observed	16	60.06	46	3 - 165	50.26

A plot of the duration of disease for individual birds, aligned by date (Julian Day), can be seen in the timeline in Figure S3.1. The dark green represents the known duration of infection, the interval from the first to last capture of a bird with avian pox, which in the case of a single capture is only one day. The light green represents the period of uncertainty around these dates, being the intervals from the last healthy capture to the first capture at which signs of avian pox were observed, and that from the last capture of the bird with avian pox to the first healthy recapture. It should be noted that the bars for two of the birds have been cropped to make them fit on the plot.

The boxplots in Figure S3.2 were produced after the exclusion of three outliers in which long periods elapsed between captures with and without clinical signs of avian pox. They suggest that for most birds the duration of observable disease lies between 1 and 100 days . However, as the maximum duration would be seen if a bird developed avian pox immediately after a previous capture when it was healthy, was detected with the disease, and then recovered immediately prior to the next capture, it is likely to be a large overestimate when recaptures are infrequent. Similarly the minimum duration is likely to be an underestimate.

Figure S3.1. Timeline showing the duration of avian pox skin lesions in individual Dunnocks. The dark bars are the known duration. Uncertainty around the duration is shown as pale bars – this being the time periods from the last capture without avian pox until the first observation of avian pox and that from the last capture with avian pox until the first capture without. Two birds, NF80852 and V840352 have the start of their timelines cropped at 1 May to ensure that the plot fits: the correct dates are 2 June in the previous year for NF80852 and 10 May in the previous year for V840352.

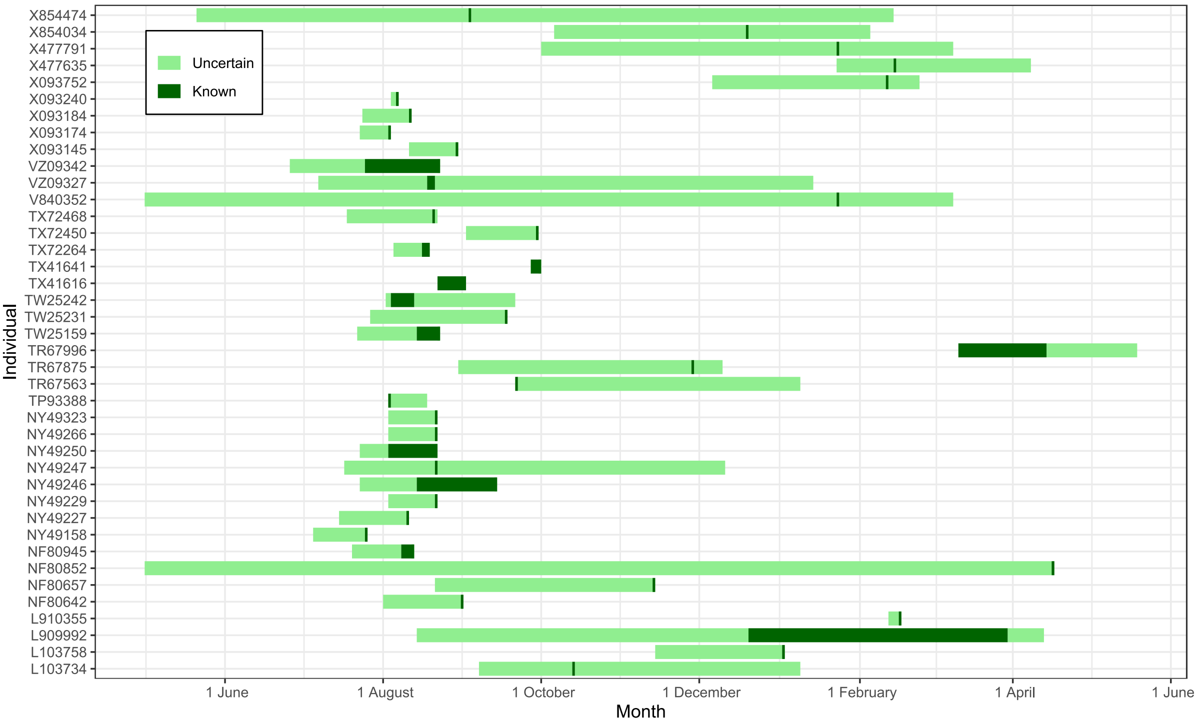
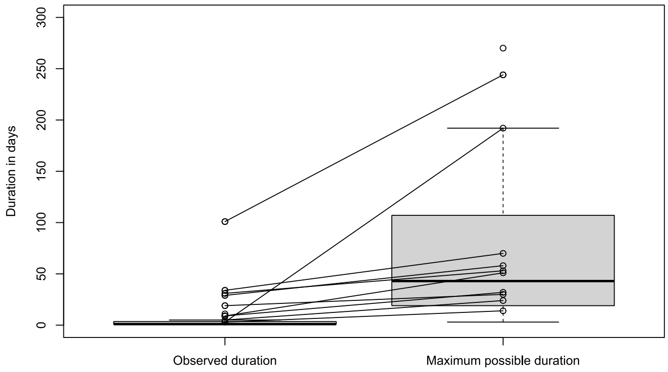


Figure S3.2. Boxplots showing the duration of avian pox in Dunnocks, after exclusion of outliers. The grey area is the inter-quartile range, that is, the range which includes 50% of the sample, with the median shown as a black line. The upper and lower whiskers represent 1.5 times the interquartile ranges and the dots are outliers.

The first column is the known duration of disease and the second the maximum possible duration, if each Dunnock developed avian pox immediately after a capture, was detected with the disease and then recovered immediately prior to the next capture. The y-axis is cropped at 300, and three outliers for which 433 days, 623 days and 164 days elapsed between their last capture without and first capture with pox, have been excluded.

The paired values plots are the estimated durations of avian pox in the 10 birds with captures both before and after clinical signs of avian pox had been observed (one outlier having been excluded).



Conclusion

There was insufficient data to produce a reliable estimate of the duration of avian pox in Dunnocks, although the limited data available would suggest that the duration of observable external signs of infection is probably usually in the order of 1-100 days.

More frequent observations of a larger number of birds are needed to determine the duration of clinical signs of avian pox in Dunnocks with any degree of accuracy.

CHAPTER 5

A first report of the detection of Avipoxvirus genomic sequences in louse flies (Diptera: Hippoboscidae)

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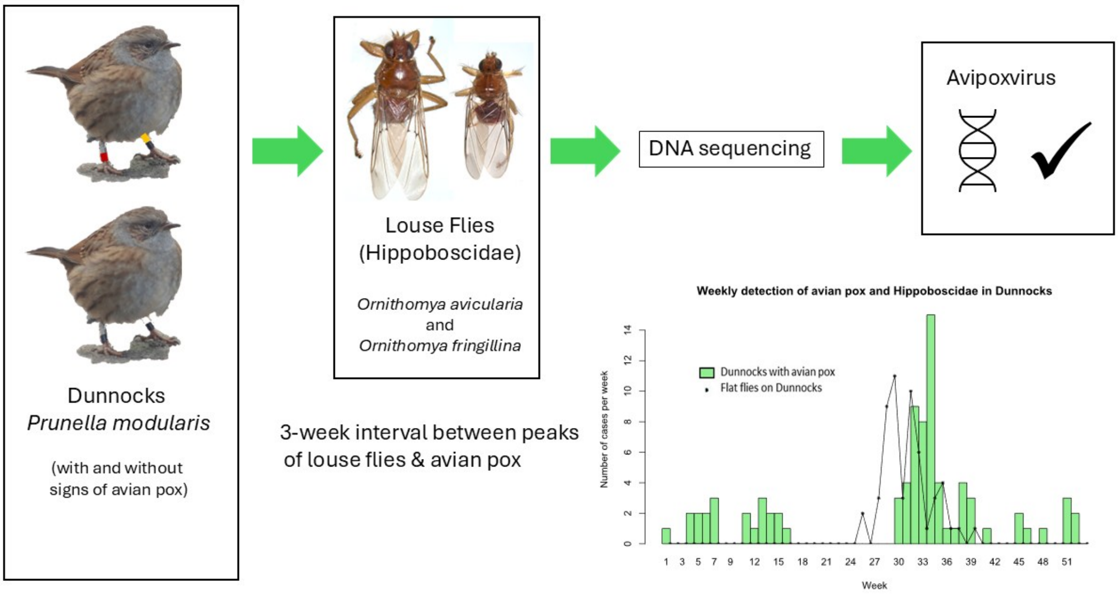
GRAPHICAL ABSTRACT



Key Findings

- Louse flies on Dunnocks were seen to peak seasonally three weeks prior to the peak of avian pox lesions, an interval consistent with the previously estimated incubation period of APV in Dunnocks.
- APV DNA was detected in two species of louse flies, *Ornithomya avicularia* and *Ornithomya fringillina,* taken from Dunnocks, both with and without lesions consistent with avian pox, at multiple sites in England.
- No APV RNA was detected.
- Collectively these data support the premise that louse flies may mechanically vector APV.
- The detection of APV in louse flies, from apparently healthy birds, and from sites where disease has not been observed in any host species, suggests that the Hippoboscidae could provide a non-invasive and relatively cheap method of monitoring avian diseases.

Abstract

The Hippoboscidae are ectoparasites of birds and mammals, which, as a group, are known to vector multiple diseases. Avipoxvirus (APV) is mechanically vectored by various arthropods and causes seasonal disease in wild birds in the United Kingdom.

Signs of avian pox and the presence of louse flies (Hippoboscidae) on Dunnocks *Prunella modularis* were recorded over a 16.5 year period in a rural garden in Somerset, United Kingdom. Louse flies collected from this site and other sites in England were tested for the presence of APV DNA and RNA sequences.

Louse flies on Dunnocks were seen to peak seasonally three weeks prior to the peak of avian pox lesions, an interval consistent with the previously estimated incubation period of APV in Dunnocks. APV DNA was detected on 13/25 louse flies, *Ornithomya avicularia* and *Ornithomya fringillina,* taken from Dunnocks, both with and without lesions consistent with avian pox, at multiple sites in England. No APV RNA was detected.

Collectively these data support the premise that louse flies may vector APV. The detection of APV in louse flies, from apparently healthy birds, and from sites where disease has not been observed in any host species, suggests that the Hippoboscidae could provide a non-invasive and relatively cheap method of monitoring avian diseases. This could provide advanced warnings of disease, including zoonoses, before they become clinically apparent.

Keywords: Vector; Parasite; Disease detection; Methods; Avian pox; Wildlife disease

Introduction

The Diptera in the family Hippoboscidae are related to the Tsetse flies, and both sexes are obligate haematophagous ectoparasites. There are over 200 species worldwide (Dick, 2018) of which eleven species breed in the United Kingdom (UK), three on mammals (keds) and eight, louse or flat flies, on birds (Hutson, 1984; Wawman, 2024).

Some species of louse fly are proven vectors of various pathogens and others have been isolated from them without formal proof that these flies are acting as vectors (Bezerra-Santos and Otranto, 2020). *Ornithomya avicularia* and *Pseudolynchia canariensis* are proven biological vectors of *Haemoproteus* sp. (Baker, 1963; Cepeda *et al.*, 2019), and trypanosomes have been shown to develop within the midgut of *O. avicularia*, and to reach the infective stage, but transmission only occurs when birds ingest the flies (Baker, 1967). For most other pathogens, the evidence that louse flies are acting as vectors is weaker: West Nile Virus (WNV) was detected in *Icosta americana* from WNV infected raptors (Farajollahi *et al.*, 2005); *Crataerina melbae* was proposed as a vector of trypanosomes in Alpine Swifts *Tachymarptis melba* (Cigler *et al.*, 2024)*;* an unidentified Hippoboscid was suggested as a potential vector when found in association with Newcastle Disease Virus (NDV) infected Laughing Doves *Streptopelia senegalensis* (Obanda *et al.*, 2016). Pathogens have also been identified in louse flies taken from birds without documented signs of disease, including *Babesia* spp. from *O. avicularia* and *O. biloba* (Čisovská Bazsalovicsová *et al.*, 2023), *Rickettsia* sp. from *Crataerina pallida* (Cerutti *et al.*, 2018), and trypanosomes from *O. biloba*, *O. fringillina* and *Ornithoica turdi* (Santolíková *et al.*, 2022).

Avipoxvirus (APV) is a genus of double-stranded DNA viruses within the Chordopoxvirinae subfamily and Poxviridae family (ICTV, 2024). The most studied member of the genus is fowlpox virus, a cause of disease in domestic poultry (Van Riper and Forrester, 2007; Yeo *et al.*, 2019). Other members of the genus cause disease in wild avian species, which is characterised by proliferative lesions on the skin, feet and legs, head and sometimes on the mucus membranes. APV is mechanically vectored by a range of arthropods, including *Aedes* and *Culex* mosquitoes (Kligler, Muckenfuss and Rivers, 1929), midges (Lee *et al.*, 2017), fleas (Smits *et al.*, 2005), the mite *Dermanyssus gallinae* (Shirinov, Ibragimova and Misirov, 1972; Huong *et al.*, 2014) and stable flies *Stomoxys calcitrans* (Alehegn, Chanie and Mengesha, 2014). APV remains viable on the proboscis of *Culex tarsalis* for up to 28 days (DaMassa, 1966). In temperate regions of the world avian pox is a seasonal disease where vectors are not active during the winter (Wawman *et al.*, unpublished results; Van Riper and Forrester, 2007; Lachish *et al.*, 2012).

The Dunnock *Prunella modularis* is a small passerine that is native across Europe. It was first reported with avian pox lesions in the UK in the 1940's (Edwards, 1955). It is affected by avian pox with a seasonal peak in August following an absence of disease in May and June (Wawman *et al.*, unpublished results) which correlates with the seasonal peaks in vectors such as mosquitoes (Cull *et al.*, 2024). Three species of Hippoboscid have been found on UK Dunnocks, *O. avicularia*, *O. fringillina* and *O. chloropus* (Wawman, Smith and Sheldon, unpublished results; Hill, 1962) and their peaks in populations occur seasonally at the time of year which might potentially allow them to be vectors of APV in Dunnocks (Wawman, 2025). This is particularly true when the estimated incubation period, which varies from 13 to 48 days in Dunnocks (Wawman *et al.*, unpublished results), is taken into consideration.

In this study we combined knowledge of the seasonality of avian pox and Hippoboscids on Dunnocks, with molecular techniques to detect APV in association with *Ornithomya* spp.. We also consider whether louse flies and keds could be used as a non-invasive way to sample for viruses in wild populations.

Materials and methods

Samples

From February 2008 until August 2024, Dunnocks were ringed, in a rural garden, near Minehead, in Somerset, as part of the British Trust for Ornithology (BTO) Retrapping Adults for Survival Scheme (https://www.bto.org/our-science/publications/birdtrends/2020/methods/retrapping-adults-survival-scheme, last accessed 2024-09-09). At each capture, in addition to the usual data collected during bird ringing, records were made of signs of disease or the presence of ectoparasites. Louse flies that left Dunnocks during routine ringing activities were collected, identified according to a key (Hutson, 1984), and preserved in 70% ethanol (with distilled water and no other excipients).

During 2023, both at the main avian pox study site near Minehead in Somerset, and at a second site on the Wirral Peninsula near Liverpool where lesions consistent with avian pox had been observed, flies were preserved in RNAlater for DNA and RNA analyses.

Additional flies were collected from all bird species from 2020 to 2023, as part of the "Mapping the UK's Flat Flies Project" (Wawman, 2025) and stored in 70% ethanol for later analyses.

Next Generation Sequencing (NGS)

One fly, taken from a Dunnock with avian pox at the second site, and preserved in RNAlater was chosen for DNA and RNA extraction, using shotgun Next Generation Illumina Sequencing (NGS). The fly was prepared by washing in phosphate buffered saline (PBS) to remove the RNAlater, then in 5% sodium hypochlorite solution to remove contaminants, and finally twice more in PBS to remove the sodium hypochlorite.

DNA and RNA were isolated separately from the fly using the QIAgen AllPrep DNA/RNA MiniKit (Qiagen, Manchester, United Kingdom). Briefly, the fly was homogenized in 300µl RLT buffer using a single 5mm steel bead in a TissueLyserII (Qiagen) for 5 minutes at 30Hz. After this, manufacturer's instructions were followed and DNA was eluted into 60µl buffer EB and RNA was eluted into 50µl RNase-free water. Sequencing libraries were prepared using Nexetra XT kits (Illumina, Cambridge, UK) and sequencing using a Nextseq sequencer (Illumina, Cambridge, UK). Illumina) to generate 2 x 150 base paired-end reads.

The raw data were filtered to remove adaptors and low quality reads using the programs fastp version 0.23.4 (Chen *et al.*, 2018) and multiqc v 1.19 (Ewels *et al.*, 2016). The sequences were aligned and the Dipteran host genomes removed in the program Bowtie2 (Langmead and Salzberg, 2012). Sequences were assembled using MEGAHIT (D. Li *et al.*, 2015). Taxonomic classification was carried out using the program Kracken2 (Wood, Lu and Langmead, 2019), with the program Bracken (Lu *et al.*, 2017) to estimate species abundance and facilitate removal of poor quality and low abundance sequences. Viral sequence detection was performed using ViralVerify (https://github.com/ablab/viralVerify/tags, last accessed 2024-09-16) and ViralComplete (https://github.com/ablab/viralComplete last accessed 2024-09-16) with sequences obtained from the NCBI viral database (https://www.ncbi.nlm.nih.gov/labs/virus/vssi/#/ last accessed 2024-09-16). Avian Pox Virus sequences identified using these methods were isolated and the identity was confirmed using BLAST+ (Camacho *et al.*, 2009).

PCR screening of samples

Twenty-four of the flies previously preserved in 70% ethanol were selected from a range of sites across England, across an area where avian pox is likely to occur in Dunnocks, from sites where avian pox had not been observed on any bird species by bird ringers, as well as sites from which it had been reported from Dunnocks or other species. Twenty-three flies were from Dunnocks and one from a Great Spotted Woodpecker *Dendrocopos major*.

These flies were not washed, to avoid removing evidence that they might be mechanical vectors. Flies were homogenised in liquid nitrogen prior to DNA extraction, using the DNeasy Blood and Tissue kit (QIAGEN) according to the manufacturer's instructions. Screening for APV was carried out through amplification of a 578-bp PCR product of the Avipoxvirus 4b core protein gene (*fpv*167) as previously described, using primer sequences 5`-CAGCAGGTGCTAAACAACAA-3` and 5`-CGGTAGCTTAACGCCGAATA-3` (Lawson *et al.*, 2012). Amplification was achieved using the high-fidelity Q5 polymerase (NEB) under the following cycling conditions: 98 °C (5 min); 40×[98 °C (1 min); 64 °C (20 sec); 72 °C (20 sec)]; 72 °C (7 min). Following confirmation of a product of the correct size on an agarose gel against a positive control of a DNA sequence from a Dunnock pox lesion at the main site (GenBank Accession number PP756527), APV was confirmed through bidirectional Sanger sequencing (Source BioScience) using the same primers as for amplification.

Computational analysis

Other analyses were performed and the phenology plotted in R version 4.2.1 (R Development Core Team, 2022) using packages dplyr (Wickham *et al.*, 2023) and lubridate (Grolemund and Wickham, 2011) to process the data. The map was plotted using the packages maps (Becker *et al.*, 2022), mapdata (Brownrigg, 2022) and scales (Wickham and Seidel, 2022).

Results

In order to investigate the association between avipoxvirus infection, small Passerine bird species and louse flies, Dunnocks were sampled from sites in England. Two species of louse flies were identified from Dunnocks, *Ornithomya avicularia* and *O. fringillina*.

Figure 1 shows the relationship between Dunnocks with evidence of avian pox infection and presence of flat flies (both species) based on cumulative data over the study period. Avian pox infections were reported during the first 16 weeks of the year and then a later surge in infections during weeks 30 to 36, reaching a peak of 15 cases during week 34, then declining for the remaining weeks of the year. Flat flies were only detected on Dunnocks from week 24 and peaked on week 29 with another peak on week 31. This preceded the peak of avian pox cases by 2-3 weeks as shown when the louse fly frequency plot is moved to three weeks later (Figure 2).

Figure 1. Weekly cases of avian pox in Dunnocks (green bars) and numbers of louse flies (*Ornithomya avicularia* and *O. fringillina* combined) found on Dunnocks (black stars and solid lines) for all years combined, from a 16.5 year study in Somerset, UK.

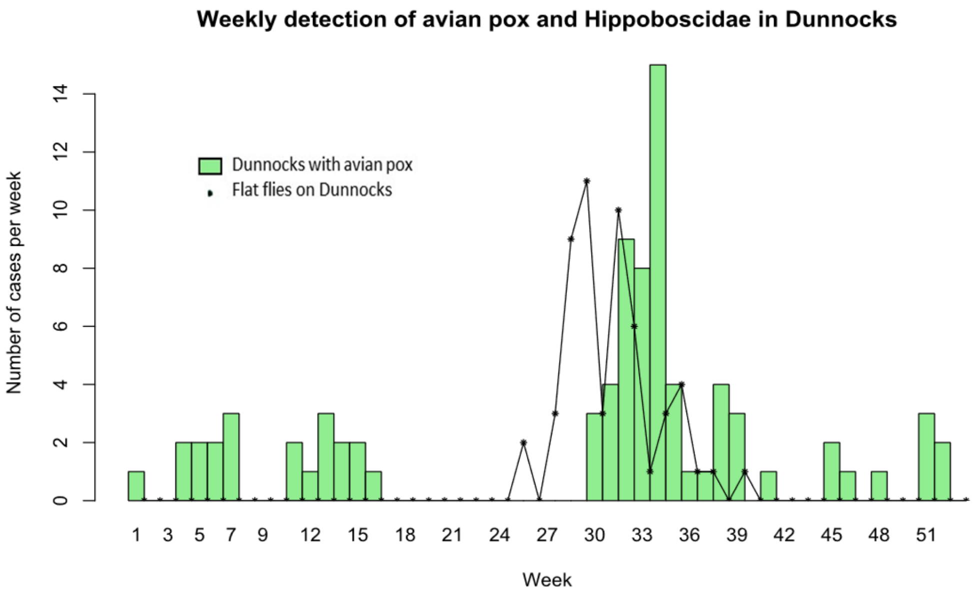


Figure 2. Weekly detection of avian pox in Dunnocks (green dots) and presence of louse flies on Dunnocks (black stars), with the louse flies plotted 3 weeks later than their actual dates, to show the similarity in peaks, otherwise separated by the approximate incubation period of avian pox in Dunnocks.

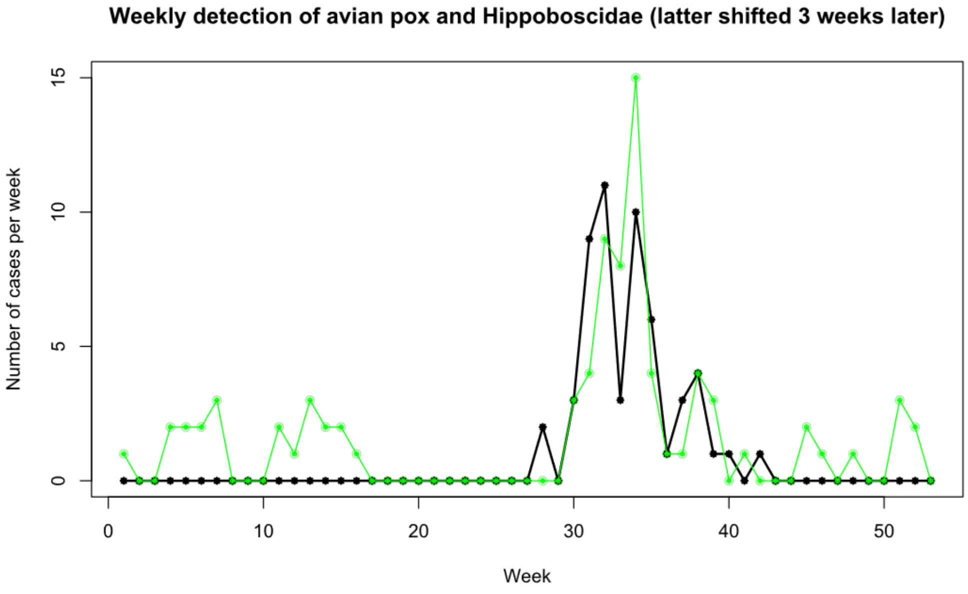


Table 1. Avian pox contig BLAST results from NGS sequencing. This table shows the results for the top blast hit of each of the contigs identified as being avian pox, from the *Ornithomya avicularia* taken from a Dunnock at the second site on the Wirral Peninsula near Liverpool, England.

DNA sequence	Top BLAST hit	Identity (%)	Genbank accession number	E-value	Query coverage (%)	alignment length (bp)
1	Crowpox virus	100	ON408417.1	7.00E-25	100	67
2	Canarypox virus	98.9	AY318871.1	2.00E-36	100	91
3	Canarypox virus	99.21	AY318871.1	4.00E-56	100	127
4	Canarypox virus	93.62	AY318871.1	2.00E-50	100	141
5	Canarypox virus	100	AY318871.1	4.00E-66	100	142

NGS sequencing and classification with Kracken2 identified five non-overlapping sequences of DNA as APV covering a total of 598 base pairs (Table 1) from an *Ornithomya avicularia* taken from a Dunnock with avian pox at the second site (Table 2). However, the length of sequence detected (<600 base pairs) represents less than 0.2% of the Avipoxvirus genome (comparison with Magpiepox virus 2, 298,392bp GenBank Acc. No. MW485973). It is not clear if this represents residual presence of virus on the external surface of the louse fly (e.g. contamination of mouthparts following feeding on the dunnock), despite surface disinfection, or presence within the fly (gut, oral cavity, salivary glands, or other internal organs) but at very low levels. No APV RNA was detected.

To more comprehensively test for the presence of avian pox 24 further samples of louse flies were subjected to PCR-based analysis for avian pox DNA. Eleven of 23 flies tested from Dunnocks and the one from the Great Spotted Woodpecker (Table 2), were PCR positive for APV. These included one *Ornithomya fringillina* from a Dunnock with avian pox at the site on Wirral Peninsula near Liverpool. All PCR-derived sequences were identical across the 512bp where they aligned, and a 100% match to this high-quality central region of the sequence obtained from an avian pox lesion on a Dunnock at the main site. These positive flies were from the main study site (Somerset: n=4), two sites (Corby and Stanford Reservoir in Northamptonshire) where avian pox was occasionally observed in Great Tits *Parus major*, but not in Dunnocks, either during the study or in the previous year (n=3), and three sites (Rutland Water in Rutland, near Sandy in Bedfordshire, and West Down in

Devon) where avian pox had not been observed in any bird species (n=4). The locations of these sites, and those at which no flies tested positive (n=4), are shown in the map (Figure 3).

In total, 13 out of 25 louse flies tested positive for APV, 6/9 *Ornithomya fringillina* and 7/16 *O. avicularia*. Six of the flies were recorded as being female, four male and in three the sex was not recorded (Table 2).

Table 2. Louse flies *Ornithomya* spp. tested for APV. Results of sequencing with details of bird host and site and GenBank accession numbers, for the Avipoxvirus 4b core protein gene sequences.

Sample number	**Date collected**	**Species**	**APV detected method**	**Fly sex**	**Bird age**	**Bird with pox?**	**Species with avian pox at site**	**Site**	**Latitude**	**Longitude**	**GenBank Accession number**
Louse fly host Dunnock *Prunella modularis*											
2402	21 Jul 2021	*O. avicularia*	no		juvenile	no	Dunnocks	Wirral Peninsula, Cheshire	53.31	-3.20	n/a
FF158	15 Jul 2022	*O. fringillina*	no		juvenile	no	Dunnocks	Minehead, Somerset	51.20	-3.51	n/a
FF26	11 Jul 2020	*O. avicularia*	no		juvenile	no	Dunnocks	Minehead, Somerset	52.20	-3.51	n/a
FF64	31 Aug 2020	*O. fringillina*	no		juvenile	no	Dunnocks	Minehead, Somerset	53.20	-3.51	n/a
FF171	01 Aug 2022	*O. avicularia*	no	f	juvenile	no	Dunnocks	Minehead, Somerset	55.20	-3.49	n/a
3197	26 Jul 2021	*O. avicularia*	no		juvenile	no	none seen	West Down, Devon	51.14	-4.29	n/a
FF96	11 Jul 2021	*O. avicularia*	no	f	juvenile	no	none seen	North Hill, Minehead, Somerset	54.21	-3.51	n/a
H003	26 Jun 2022	*O. avicularia*	no	f	juvenile	no	none seen	Brandon, Suffolk	52.39	0.50	n/a
2959	24 Jun 2022	*O. avicularia*	no	f	fledgling	no	none seen	Cameley, North Somerset	51.25	-2.57	n/a
2942	01 Sep 2022	*O. fringillina*	no	m	juvenile	no	none seen	Cameley, North Somerset	51.25	-2.57	n/a
435	12 Jul 2022	*O. avicularia*	no	m	adult	no	none seen	Little Snoring, Norfolk	52.83	0.82	n/a
X366	25 Jul 2023	*O. avicularia*	no	f	juvenile	no	none seen	Bridford, Devon	50.61	-3.70	n/a
JT01	14 Jul 2023	*O. avicularia*	NGS	f	juvenile	yes	Dunnocks	Wirral Peninsula, Cheshire	53.31	-3.20	n/a
2414	10 Nov 2021	*O. fringillina*	PCR		juvenile	yes	Dunnocks	Wirral Peninsula, Cheshire	53.31	-3.20	PQ790037
FF108	02 Aug 2021	*O. fringillina*	PCR	m	juvenile	no	Dunnocks	Minehead, Somerset	51.20	-3.51	PQ790031
FF122	08 Aug 2022	*O. fringillina*	PCR	m	juvenile	no	Dunnocks	Minehead, Somerset	51.20	-3.51	PQ790033
FF167	30 Jul 2022	*O. avicularia*	PCR	f	juvenile	no	Dunnocks	Minehead, Somerset	51.20	-3.51	PQ790032
FF22	07 Aug 2013	*O. fringillina*	PCR		adult	no	Dunnocks	Minehead, Somerset	51.20	-3.51	PQ790030
1566	16 Jul 2022	*O. fringillina*	PCR	f	juvenile	no	Great Tits	Stanford Reservoir, Northamptonshire	52.41	-1.12	PQ790038
1568	31 Jul 2022	*O. avicularia*	PCR	m	juvenile	no	Great Tits	Corby, Northamptonshire	52.41	-0.83	PQ790036
1569	01 Aug 2022	*O. avicularia*	PCR	f	adult	no	Great Tits	Corby, Northamptonshire	52.41	-0.83	PQ790034
3936	10 Jul 2021	*O. avicularia*	PCR	f	adult	no	none seen	Near Sandy, Bedfordshire	52.41	-0.38	PQ790039
4960	12 Jul 2022	*O. avicularia*	PCR		juvenile	no	none seen	Rutland Water, Rutland	52.59	-0.82	PQ790035
X	13 Jul 2022	*O. avicularia*	PCR	m	juvenile	no	none seen	Rutland Water, Rutland	52.59	-0.82	PQ790040
Fly host Great Spotted Woodpecker *Dendrocopos major*											
7589	18 Sep 2023	*O. avicularia*	PCR	m	juvenile	no	none seen	West Down, Devon	51.14	-4.29	PQ790029

None of the Dunnocks without active disease at the time of capture, from which the flies were taken, were later seen to develop avian pox, although most (7/10) were not recaptured. However, most (7/10) were juveniles at the time of capture and would have been expected to leave their natal areas (the ringing sites) during their postnatal dispersal.

Figure 3. Map of the sites from which flies were tested: black squares - no avian pox detected, in either tested louse flies or observed in birds; red squares - avian pox detected but no birds observed with avian pox; red stars – birds observed with avian pox and flies tested positive.

Discussion

APV DNA was detected in 13 of 25 louse flies, of two species, *Ornithomya avicularia* and *O. fringillina*, that were obtained from sites across England. The sequences matched that obtained from an avian pox lesion on a Dunnock at the main site as well as reference sequences from NCBI Genbank. The APV positive flies included one *O. avicularia* and one *O. fringillina* that had been taken from Dunnocks with avian pox lesions, the rest having been taken from Dunnocks with no signs of disease, and a single fly from an apparently healthy Great Spotted Woodpecker. Field studies showed that peaks in the presence of louse flies on Dunnocks were followed three weeks later by peaks in the prevalence of avian pox.

The three week interval falls within the estimate of the incubation period of avian pox in Dunnocks of 13-48 days (Wawman *et al.*, unpulished data). However, phenological comparisons may not be a reliable means of identifying a vector because other vectors' emergence may be triggered by the same climatic conditions as that of the louse flies. Arthropod vectors are known to down-regulate their hosts' immune systems which may promote transmission of avian pox (Wikel, 1999). Moreover, reproduction-associated stress or hormonal induced immunosuppression may also make Dunnocks more susceptible to avian pox at particular times of the year.

Although conclusive evidence that APV is vectored by Hippoboscidae may be challenging to obtain, the detection of avian pox DNA associated with louse flies is strong evidence of the potential for a role in transmission. If, as expected from knowledge of its mode of transmission by other vectors, APV is mechanically vectored, evidence of viral replication in the vector, such as Bollinger Bodies (Bollinger, 1873) or the presence of viral mRNA, would not be expected, and indeed RNA was not detected in this study, although only a single specimen was tested. Using longer sequences to compare viral DNA in avian hosts and parasites might confirm that the same strains are circulating in both (Yeo *et al.*, 2019), but would not prove beyond doubt that Hippoboscids are responsible for transmission.

Isolating APV DNA from a Hippoboscid taken from a Dunnock that later developed avian pox, might more strongly implicate Hippoboscids as vectors. However, finding APV DNA in 52% of the louse flies tested, including flies from sites where no avian pox had been observed in any species of bird, indicates that APV may be circulating in the wild bird population at a far higher rate than expected purely from the observed presence of clinical signs. Lesions were only observed in 8.3% of Dunnocks (Wawman *et al.*, unpublished results) and 7.2% of House Finches *Haemorhous mexicanus* (McGraw *et al.*, 2022), but PCR detected APV in the spleens of 43% of wild birds in Italy (Bertelloni *et al.*, 2022), and 69.2% of a sample of avian species introduced into New Zealand were seropositive (Ha *et al.*, 2013). It would be necessary to use other methods such as invasive sampling techniques to detect the timing of seroconversion in birds in relation to the presence of flies carrying APV, which would be difficult in a wild host population.

Detecting APV in louse flies at sites where no avian pox has been observed, and at sites where avian pox has only been observed in species other than Dunnocks, such as at Stanford Reservoir and Corby, where it was only seen occasionally in Great Tits, might suggest that avian pox is of low virulence in Dunnocks. It is also likely that it exists in an enzootic cycle between different wild bird species and louse flies and other arthropod vectors. The two species of louse flies found to be positive for avian pox in this study, *Ornithomya avicularia* and *O. fringillina* are found on a wide range of bird species (Wawman, Smith and Sheldon, unpublished results) and could be vectoring APV between Dunnocks, Great Tits and other affected species. This hypothesis is supported by the presence of an APV-positive louse fly on a Great Spotted Woodpecker.

Louse flies may have potential as a means of monitoring the potential for vector-transmitted disease in wild bird populations. NGS sequencing could be used to determine which pathogens of potential interest are present in louse flies, potentially by pooling specimens to minimise the cost. Pathogen targeted PCR could be used in cases where focal pathogens have already been identified as a potential cause for concern. Individual based analyses can be used to quantify the numbers of infected individuals, including those in the prodromal phase of disease and those in which infections remain subclinical, and to determine the geographical areas in which diseases are present. Expanding this approach to keds, could also allow diseases to be tracked in the wild deer population, and livestock such as horses, sheep and goats in regions where they are frequently infected.

Other parasites have been used to take samples from wild birds, for example, blood sucking bugs, *Dipetalogaster maximus*, contained within dummy eggs have been used avoid stress when taking blood samples from adult nesting birds including Common Terns *Sterna hirundo* for cortisol assays (Arnold *et al.*, 2008), and Eurasian Kestrel for counting blood parasites, leucocyte profiles and microsatellite analysis for paternity tests and genetic sexing (Sumasgutnet, Rubin and Gamauf, 2014), and have been shown to be a reliable method in Common Swift *Apus apus* (Bauch *et al.*, 2013). Bat flies (Diptera: Nycteribiidae) which are closely related to the louse flies, and sometimes included as part of the Hippoboscidae, have been used to investigate the presence of *Bartonella* spp. *Polychromophilus* spp. and *Trypanosoma* spp. in bats (Szentiványi *et al.*, 2020).

Using louse flies to screen for the presence of disease in a population would have several advantages compared to using serology or other samples from birds. Firstly, serology and other blood tests require invasive sampling techniques, performed by veterinary surgeons or individuals who have undergone additional training and licensing, which limits the sample size and geographical area over which a study can take place, and adds costs to any project: louse flies can be collected by any bird ringer, or wildlife rehabilitator or member of the public who comes across a sick, injured or dead bird hosting louse flies. Citizen science projects, such as the Mapping the UK's Flat Flies Project (Wawman, 2025) could allow widespread coverage across a region. Additionally, serology only indicates that that a bird has produced an immune response at some point during its life, with no way of determining the timing of the infection, whereas because of the short life span of Hippoboscids, assuming that transovarial and transstadial transmission can be ruled out, any infection within them is likely to have been acquired in the same season. Adult louse flies have a life span of around three to six months (Hutson, 1984), so APV virions would have to be acquired in the same year. Using PCR-sequencing approaches to detect viral DNA is specific for the disease under investigation, whereas relying on observations of sick birds in the field, or even in the hand by trained bird ringers, risks both mis-diagnoses and a significant underestimate of prevalence of infection.

A major disadvantage of using wild louse flies is that the sampling is likely to be somewhat random in nature, as only birds with ectoparasites that can be caught can be sampled, and there may be differences in the health of birds with and without parasites, especially if co-infections are present. Quantitative results, such as an estimate of disease prevalence will be difficult to obtain. Sick birds may be easier to catch if flying weakly, or be so sick that they remain hidden and are not caught. Ectoparasites may be affected by the presence of avian endoparasites: the louse fly *Olfersia spinifera*, was found to be less likely to switch hosts when infected with *Haemoproteus iwa* (Levin and Parker, 2014) and ectoparasites may aggregate on certain hosts with co-infection. The prevalence of micro-organisms may not be consistent between vectors and their hosts – a study of bats and bat flies showed twice the prevalence of *Trypanosoma* spp. and *Polychromophilus* spp. in hosts compared to their ectoparasites, but a similar prevalence of *Bartonella* spp. in both groups (Szentiványi *et al.*, 2020).

Vertical transmission leading to infection of louse flies might also be a potential issue for some diseases in which it occurs and might explain the higher rate of detection of APV in the louse flies compared to their hosts. *Bartonella schoenbuchensis* is vertically transmitted in the Deer Ked *Lipoptena cervi* (de Bruin *et al.*, 2015), and *Anaplasma ovis* in the Sheep Ked *Melophagus ovinus* (Zhao *et al.*, 2018), but vertical transmission of viral pathogens has not been reported in louse flies. However, vertical transmission of endosymbionts occurs (Duron *et al.*, 2014) and some arthropod viruses are vertically transmitted via both ova and spermatozoa (Longdon and Jiggins, 2012). Some sigmaviruses, a group of RNA viruses found naturally in Diptera, are known from Hippoboscids, such as the Wuhan Louse Fly sigmaviruses (C.-X. Li *et al.*, 2015), Aksy-Durag Melophagus sigmavirus (Litov *et al.*, 2021), and a sigmavirus from *Lipoptena cervi* in the UK (Jones, Wawman and Johnson, unpublished results). It is possible that compared to the transovarial route, reproduction by adenotrophic viviparity in the Hippoboscidae, could favour vertical transmission, as there is prolonged maternal contact between the female and her offspring, during which time it is fed from a specialised milk gland.

Despite these issues, useful results might be obtained similar to those used in the surveillance used in monitoring other vector borne diseases such as the European network for medical and veterinary entomology (VectorNet) (https://www.ecdc.europa.eu/en/about-us/partnerships-and-networks/disease-and-laboratory-networks/vector-net, last accessed 22nd November 2024), which monitors the ranges of mosquitos, ticks, biting sandflies, and midges across Europe, or other studies such as VB-RADAR in the United Kingdom, which monitors the flaviviruses, WNV and Usutu Virus in mosquitos (https://www.vb-radar.com, last accessed 22nd November 2024). Using louse flies may have advantages over using other arthropod vectors to monitor disease, because, although louse flies switch hosts (Corbet, 1956), those collected by ringers are taken from a host with a ring bearing a unique identifying code, which allows the bird to be followed throughout its life, potentially giving additional information about the progress of diseases that would not be obtained otherwise.

From the phenological and molecular evidence presented in this paper, it is likely that the *Ornithomya* spp. present in the UK, especially *Ornithomya avicularia* and *Ornithomya fringillina*, are vectors of APV in Dunnocks. Further research will be required to determine the exact role of louse flies in vectoring APV in Dunnocks, and in other avian species, and how this occurs. Although mechanical transmission would be the expected route, the possibility of vertical transmission facilitating autochthonous disease transmission should be considered.

Louse flies may provide a relatively cheap and non-invasive method of monitoring disease outbreaks (or assessing potential at risk populations) in wild birds, when combined with targeted DNA sequencing for specific pathogens.

Data availability

Details of the flies sequenced can be found in Table 1 together with the accession numbers for the APV sequences.

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Authors’ Contributions

DCW: conceptualisation, project management, data collection, specimen collection, specimen identification, analysis (phenology), data visualisation; writing: first draft, writing: review and editing; BPJ: lab work (NGS sequencing), analysis (NGS genomics), writing: review and editing; SRF: lab work

(PCR sequencing), writing: review and editing**;** JET: specimen collection, writing: review and editing**;** NJ: resources (NGS sequencing), writing: review and editing**;** ALS: supervision, writing: review and editing

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Ethical standards

All birds handled in this study were ringed under licence: BTO ringing permits S5420 issued to DCW, and S3144 issued to JET for the two main sites, and the permits of other trained ringers talking part in the Mapping the UK's flat flies project elsewhere. All those mentioned in the acknowledgements have given informed written consent for their names to be published.

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CHAPTER 6

Discussion

Discussion

In this thesis I have combined a range of techniques to explore the biology and vectorial capacity of the Hippoboscidae, in the region formed by the United Kingdom (UK), Republic of Ireland (ROI), and Isle of Man (collectively "the region"). The study began following the observation that the peak of avian pox in Dunnocks, in my garden on Exmoor, followed the peak of Hippoboscidae on these birds. The data for the study came from 15.5 years of mark-recapture records for these Dunnocks, and 5 years of specimen collection by bird ringers and others for the Mapping the UK's Flat Flies project (2020-2024). The analyses used multiple techniques from simple generalised linear models and principal component analysis, through to mark recapture analysis, bipartite network analysis, and maximum entropy species distribution models. It is multidisciplinary, drawing on techniques and ideas from the fields of entomology, ornithology, parasitology, taxonomy, ecology, epidemiology, microbiology, genomics, and medicine.

As highlighted in chapter 2, further work is needed to fully resolve the taxonomy of the louse flies, and to DNA sequence previously described species to allow their capture in projects using environmental DNA. This would require international collaborations, with trained bird ringers and banders to collect louse flies from sites worldwide, including countries in the southern hemisphere, from which Hippoboscids have been described but almost none sequenced. It needs entomologists skilled in taxonomy to carefully examine the anatomy of louse flies, including their genitalia, working with laboratories capable of producing long, high-quality DNA sequences to produce phylogenetic trees, so that the full status of species, subspecies and morphotypes can be accurately determined. This would also enable the development of a comprehensive DNA sequence library, to enable further studies into these flies' roles in vector-borne disease transmission to be carried out by researchers without an in-depth knowledge of Hippoboscid identification.

The ongoing theme throughout Chapter 3 is that of anthropogenic change leading to an increased risk of disease transmission. Climate change has led to range changes in the Hippoboscidae, leading three new species to colonise the UK (Chapter 3.1), and an expansion of the ranges and an increased duration of the flight season of *Ornithomya avicularia* and *O. fringillina* (Chapter 3.2). This work could be extended to other Hippoboscid species where there are sufficient historical data available, possibly for all of the keds in the United Kingdom, but not Ireland as the Irish historic data are very sparse.

Combining Maxent Species Distribution Models (SDMs) with climate predictions would allow the estimation of future ranges of these vectors under a changing climate.

The complexity of the network of host parasite associations has increased (Chapter 3.3), as predicted, with warming temperatures, with a notable shift to one avian family, the gulls (Laridae), occurring as they changed from a diet mostly of fish to one dominated by anthropogenic sources. This change brought them into contact with other louse fly hosts and decreased the amount of time that they spend fishing for food. Further monitoring will be necessary to determine whether the new interactions discovered including, for example, whether the Deer Keds *Lipoptena cervi* found on several species of birds, were chance encounters or more significant. As *Lipoptena cervi* is known to transmit several zoonoses, any changes in its host distribution could have significant impacts.

Further work is required to test and expand the method of establishing disease incubation periods by using feather growth to estimate bird ages sketched out in Chapter 4. Ideally, this would involve bird ringers across multiple sites recording feather growth and disease onset in avian species of interest, at sites where ringing takes place at frequent intervals. In an ideal scenario, the uncertainties around the timing of feather growth would be removed by monitoring birds, ringed as nestlings, whose age is known from hatching. While this may be possible for some cavity nesting birds monitored in large nest box schemes with frequent recapturing of juveniles after fledging, it would prove difficult for species which undergo post-juvenile dispersal away from the monitoring sites and for open nesting species such as the Dunnock.

Further research is needed on the Hippoboscidae, and other neglected groups of potential vectors, to determine which pathogens are present within them and whether these ectoparasites are acting as disease reservoirs or vectors, the mechanisms by which they do so, and the risks to wildlife, humans and livestock, in order to put in place potential mitigations. This research would need to start with regional sampling and a metagenomics approach, possibly using pooled samples, to identify the pathogens present in the Hippoboscid population of an area. Further field sampling, combined with PCR, could be used to explore the distribution of diseases or to screen for pathogens of interest, such as zoonoses, potential emergent diseases, and diseases which have a high probability of expanding into new areas due to climate change, changes in land use, and increased international travel.

It may be possible to use the Hippoboscidae to screen for diseases in wild populations of birds and mammals, as suggested in Chapter 5. However, to provide more than the most basic information, this would require work to quantify the relationship between the presence of a disease causing agent in a fly with that of its host's disease status, as very little is known about this relationship, or the prevalence or epidemiology of avian and other wildlife diseases. Quantifying the likelihood of vertical transmission of disease causing agents within Hippoboscids could be done in a laboratory setting, with captive bred flies. These would need to be maintained either on live hosts (Cepeda et al., 2019) or on avian blood fed to them via membranes like those used to maintain other blood-feeding vectors (Nunn et al., 2020) a method previously used to rear *Pseudolynchia canariensis* (Prouty & Coatney, 1934). However, both of these methods are technically difficult and ethically challenging. Additionally, any research would need to take into account the possibility of non-viraemic disease transmission, as seen in arbovirus transmission by co-feeding ticks (Nuttall et al., 1994), as it may be that the disease can spread via vectors despite undetectable levels of viraemia in their hosts. This type of work needs to be multidisciplinary, including taxonomists, ecologists, ornithologists, veterinary and medical scientists, epidemiologists and statisticians, as well as field workers, using an integrated One Health Approach (Mackenzie & Jeggo, 2019).

Regular monitoring projects, like the Mapping the UK's Flat Flies Project that formed a major part of the work for this thesis, need to be set up for neglected vectors in the UK and other parts of the world, as they have been for other vectors, for example, Vector Borne RADAR (https://www.vb-radar.com last accessed 25th February 2025) for mosquitoes in the UK, AIMsurv for invasive Aedes mosquitoes Europe-wide (Miranda et al., 2022), and VectorNet (Wint et al., 2023) which monitors mosquitoes, ticks, sandflies and biting midges across Europe. Such a project could also secure the future of the Mapping the UK's Flat Flies Project.

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CONCLUSION

Conclusion

This thesis details evidence of anthropogenic changes in biogeography and host associations of a group of avian ectoparasites, the Hippoboscidae, across the region, formed by the UK, Ireland and Isle of Man, that could lead to an increase risk of disease transmission both within and between different host species. The evidence presented in this thesis also strongly suggests that the Hippoboscidae vector Avipoxvirus in the UK. However, it also highlights difficulties with the taxonomy of this group and the lack of available DNA sequences.

There is a large amount of work to be done to fully determine the current role of these species in transmitting disease in the region, and how much risk, if any, their changing ranges, phenology and host distribution could pose to avian health.

Further in depth research into this family of ectoparasitic vectors will require multiple collaborations with experts in a range of fields, on a large geographical, possibly global, scale.

APPENDICES

Supporting Information

SUPPORTING INFORMATION

CHAPTER 1

There is no additional information for this chapter

SUPPORTING INFORMATION

CHAPTER 2.1

Table S1. Specimens of *Ornithomya fringillina* examined

Table S2. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of two morphotypes of *Ornithomya fringillina*

Table S3. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of two morphotypes of *Ornithomya fringillina*

Figure S1. PCA Scree plot for the two morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.

Figure S2. PCA Scree plot for the three morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.

Table S1. Specimens of *Ornithomya fringillina* examined.

No.	Species	Country	Sex	County	Morphotype	Location	Altitude	Date	Host species	Host binomial	Collected by
121	O.fringillina	UNITED KINGDOM	♀	Cumbria	3	Watchtree Wetlands	65	21.vii.2020	Chaffinch	*Fringilla coelebs*	Watchtree RG
122	O.fringillina	UNITED KINGDOM	♂	Cumbria		Watchtree Wetlands	65	21.vii.2020	Reed Warbler	*Acrocephalus scirpaceus*	Watchtree RG
125	O.fringillina	UNITED KINGDOM		Cumbria	2	Watchtree	73	20.ix.2020	Dunnock	*Prunella modularis*	Watchtree RG
129	O.fringillina	UNITED KINGDOM	♀	Cumbria		Watchtree	70	19.viii.2021	redpoll	*Acanthis sp.*	Watchtree RG
174	O.fringillina	UNITED KINGDOM		County Durham	3	Butterknowle	208	24.vii.2020	Chaffinch	*Fringilla coelebs*	John Black
175	O.fringillina	UNITED KINGDOM		County Durham	3	Butterknowle	208	3.viii.2020	Dunnock	*Prunella modularis*	John Black
177	O.fringillina	UNITED KINGDOM	♂	County Durham	3	Butterknowle	208	3.viii.2020	Robin	*Erithacus rubecula*	John Black
192	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	3	Flamborough	45	18.vii.2021	Dunnock	*Prunella modularis*	Andy Hood
201	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	18.viii.2020	Dunnock	*Prunella modularis*	John Black
202	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	18.viii.2020			John Black
204	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	18.viii.2020	Goldfinch	*Carduelis carduelis*	John Black
207	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	24.viii.2020	Willow Tit	*Poecile montanus*	John Black
208	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	24.viii.2020	Great Tit	*Parus major*	John Black
285	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Cranwich	10	12.ix.2020	Long-tailed Tit	*Aegithalos caudatus*	Lee Barber
343	O.fringillina	UNITED KINGDOM	♀	Warwickshire	3	Whiteacre Heath	72	1.ix.2021			Dave Clifton
347	O.fringillina	UNITED KINGDOM	♂	Warwickshire	2	Whiteacre Heath	72	17.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Dave Clifton
355	O.fringillina	UNITED KINGDOM		Staffordshire	damaged	Walsall	139	23.x.2021	Goldfinch	*Carduelis carduelis*	Dave Clifton
421	O.fringillina	UNITED KINGDOM		Berkshire	3	Wraysbury	17	4.viii.2020	Robin	*Erithacus rubecula*	Denise Lamsdell
424	O.fringillina	UNITED KINGDOM	♀	Greater London		South Harefield, Broadwater	36	28.vii.2021	Chiffchaff	*Phylloscopus collybita*	Denise Lamsdell
425	O.fringillina	UNITED KINGDOM	♀	Greater London	3	South Harefield, Broadwater	36	28.vii.2021	Robin	*Erithacus rubecula*	Denise Lamsdell
461	O.fringillina	UNITED KINGDOM	♂	Northamptonshire	2	Harrington	162	2.viii.2020	Yellowhammer	*Emberiza citrinella*	Chris Payne
483	O.fringillina	IRELAND		Wexford	3	Kilpierce	55	11.xii.2020	Coal Tit	*Periparus ater*	Mark Stanley
561	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	3	Maidwell	135	5.ix.2020	Chaffinch	*Fringilla coelebs*	Helen Franklin
637	O.fringillina	UNITED KINGDOM		Gloucestershire	3	Bristol, Brenty	61	18.ix.2021	House Sparrow	*Passer domesticus*	Mark Dadds
638	O.fringillina	UNITED KINGDOM	♂	Gloucestershire	2	Bristol, Brenty	61	16.viii.2021	Goldfinch	*Carduelis carduelis*	Mark Dadds
645	O.fringillina	UNITED KINGDOM		Buckinghamshire	2	Marsworth	125	2.ix.2020	Robin	*Erithacus rubecula*	Lynne Lambert
667	O.fringillina	UNITED KINGDOM		Norfolk	3	Walsey Hill	8	6.viii.2020	Dunnock	*Prunella modularis*	Norfolk Ornithologists Association
670	O.fringillina	UNITED KINGDOM		Norfolk	3	Walsey Hill	8	6.viii.2020	Whitethroat	*Curruca communis*	Norfolk Ornithologists Association

674	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Walsey Hill	8	16.viii.2020	Greenfinch	*Chloris chloris*	Norfolk Ornithologists Association
1068	O.fringillina	UNITED KINGDOM	♀	Essex	3	Rayne	69	17.vii.2021	House Sparrow	*Passer domesticus*	Jenny Dunn
1083	O.fringillina	UNITED KINGDOM	♀	Shropshire	2	Whixall Moss	90	31.x.2021	Lesser Redpoll	*Acanthis cabaret*	Bob Harris
1109	O.fringillina	UNITED KINGDOM	♂	Lincolnshire	3	Nocton Fen, Wasps Nest	8	12.x.2021	Chaffinch	*Fringilla coelebs*	Carl Soulsbury
1118	O.fringillina	UNITED KINGDOM	♂	Nottinghamshire	2	Bevercotes Lagoon	20	25.vii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Carl Soulsbury
1281	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	3	Cumrue	58	5.ix.2021	Reed Bunting	*Emberiza schoeniclus*	Ronnie Graham
1289	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	3	Rangebank	48	12.viii.2021	Treecreeper	*Certhia familiaris*	Ronnie Graham
1305	O.fringillina	ISLE OF MAN	♂		2	Lower Ballabeg	60	19.viii.2021	Goldcrest	*Regulus regulus*	Calf of Man Bird Observatory
1306	O.fringillina	ISLE OF MAN			3	Calf of Man	80	23.x.2021	Chaffinch	*Fringilla coelebs*	Calf of Man Bird Observatory
1307	O.fringillina	ISLE OF MAN			3	Calf of Man	80	25.x.2021	Goldfinch	*Carduelis carduelis*	Calf of Man Bird Observatory
1444	O.fringillina	UNITED KINGDOM	♀	Pembrokeshire	2	Skokholm Island	35	14.ix.2021	Robin	*Erithacus rubecula*	Skokholm Bird Observatory
1532	O.fringillina	UNITED KINGDOM		Isle of Wight	damaged	Bembridge	15	28.x.2021	Goldfinch	*Carduelis carduelis*	Isle of Wight Ringing Group
1533	O.fringillina	UNITED KINGDOM		Isle of Wight	damaged	Bembridge	15	4.xi.2021	Goldfinch	*Carduelis carduelis*	Isle of Wight Ringing Group
1541	O.fringillina	UNITED KINGDOM		Northamptonshire	3	Stanford Reservoir	115	4.ix.2021	Blackcap	*Sylvia atricapilla*	Stanford RG (David Neal)
1561	O.fringillina	UNITED KINGDOM		Northamptonshire		Stanford Reservoir	115	29.viii.2021			Stanford RG
1564	O.fringillina	UNITED KINGDOM	♀	Northamptonshire		Stanford Reservoir	115	21.ix.2021	Blackcap	*Sylvia atricapilla*	Stanford RG
1629	O.fringillina	UNITED KINGDOM	♀	Isle of Arran	3	Corriecravie	1	10.viii.2021	Robin	*Erithacus rubecula*	Clyde RG
1632	O.fringillina	UNITED KINGDOM	♂	Isle of Arran	3	Corriecravie	1	1.viii.2021	Robin	*Erithacus rubecula*	Clyde RG
1640	O.fringillina	UNITED KINGDOM		Isle of Arran	3	Corriecravie	1	29.viii.2021	Stonechat	*Saxicola rubicola*	Clyde RG
1681	O.fringillina	UNITED KINGDOM		Powys	3	Nantmel	215	16.x.2021	Dunnock	*Prunella modularis*	Mid-Wales Ringing Group
1695	O.fringillina	UNITED KINGDOM		Powys	3	Nantmel	215	23.viii.2021	Chaffinch	*Fringilla coelebs*	Mid-Wales Ringing Group
1697	O.fringillina	UNITED KINGDOM	♀	Powys	3	Nantmel	215	20.viii.2021	Great Tit	*Parus major*	Mid-Wales Ringing Group
1698	O.fringillina	UNITED KINGDOM	♀	Ceredigion	3	Aberystwyth, Ynyslas, Borth Bog	2	22.viii.2021	Sedge Warbler	*Acrocephalus schoenobaenus*	Mid-Wales Ringing Group
1700	O.fringillina	UNITED KINGDOM	♂	Ceredigion	2	Aberystwyth, Ynyslas, Borth Bog	2	22.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Mid-Wales Ringing Group
1787	O.fringillina	UNITED KINGDOM	♀	North Yorkshire	2&3	Ripon, Ripon Parks	40	4.ix.2021	Reed Bunting	*Emberiza schoeniclus*	East Dales Ringing Group
1861	O.fringillina	UNITED KINGDOM		Leicestershire	2	Stanford Reservoir	110	17.vii.2021	Swallow	*Hirundo rustica*	Stanford Ringing Group
1863	O.fringillina	UNITED KINGDOM		Kent	2	Dungeness Bird Observatory	6	23.vii.2021	Dunnock	*Prunella modularis*	Stanford Ringing Group
1864	O.fringillina	UNITED KINGDOM	♀	Leicestershire	3	Stanford Reservoir	110	19.viii.2021	Swallow	*Hirundo rustica*	Stanford Ringing Group
1963	O.fringillina	UNITED KINGDOM	♂	Hertfordshire	3	Greys	120	16.vii.2021	Blackcap	*Sylvia atricapilla*	Ken Griffin
1986	O.fringillina	UNITED KINGDOM		Stirlingshire		Falkirk	115	16.viii.2021	House Sparrow	*Passer domesticus*	Liam Reid
2196	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Holme, Holme Bird Observatory	2	16.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists' Association
2221	O.fringillina	UNITED KINGDOM	♀	Wiltshire	3	Warminster, Battle	148	1.viii.2021	Whitethroat	*Curruca communis*	ANON
2222	O.fringillina	UNITED KINGDOM	♂	Wiltshire	2	New Zealand Farm	197	18.viii.2021	Blackbird	*Turdus merula*	ANON
2223	O.fringillina	UNITED KINGDOM	♂	Wiltshire	2	New Zealand Farm	197	18.viii.2021	Yellowhammer	*Emberiza citrinella*	ANON
2224	O.fringillina	UNITED KINGDOM	♂	Wiltshire	2	Warminster, Battle	148	27.viii.2021	Yellowhammer	*Emberiza citrinella*	ANON
2225	O.fringillina	UNITED KINGDOM	♀	Wiltshire	2	Warminster, Battle	148	27.viii.2021	Yellowhammer	*Emberiza citrinella*	ANON

2261	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Holme, Holme Bird Observatory	2	21.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists' Association
2262	O.fringillina	UNITED KINGDOM		Norfolk	2	Holme, Holme Bird Observatory	2	22.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists' Association
2263	O.fringillina	UNITED KINGDOM	♂	Norfolk	2	Holme, Holme Bird Observatory	2	27.viii.2021	Whitethroat	*Curruca communis*	Norfolk Ornithologists' Association
2264	O.fringillina	UNITED KINGDOM	♀	Norfolk	2	Holme, Holme Bird Observatory	2	21.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists' Association
2403	O.fringillina	UNITED KINGDOM	♂	Cheshire	3	Hoylake	6	21.vii.2021	House Sparrow	*Passer domesticus*	Jane Turner
2412	O.fringillina	UNITED KINGDOM		Cheshire	3	Hoylake	6	26.viii.2021	House Sparrow	*Passer domesticus*	Jane Turner
2413	O.fringillina	UNITED KINGDOM		Cheshire	3	Hoylake	6	27.viii.2021	Goldfinch	*Carduelis carduelis*	Jane Turner
2414	O.fringillina	UNITED KINGDOM		Cheshire	3	Hoylake	6	10.xi.2021	Dunnock	*Prunella modularis*	Jane Turner
2495	O.fringillina	UNITED KINGDOM		Dorset	2	Portland Bird Observatory	16	7.viii.2021	Whitethroat	*Curruca communis*	Portland Bird Observatory
2602	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	21.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
2606	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	21.vii.2021	Blackcap	*Sylvia atricapilla*	Hugh Insley
2607	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Inverness, Drummond	34	19.vii.2021	Great Tit	*Parus major*	Hugh Insley
2609	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	21.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
2613	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Inverness, Drummond	34	20.vii.2021	Bullfinch	*Pyrrhula pyrrhula*	Hugh Insley
2614	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Inverness, Drummond	34	19.vii.2021	Dunnock	*Prunella modularis*	Hugh Insley
2619	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Inverness, Drummond	34	16.vii.2021	Siskin	*Spinus spinus*	Hugh Insley
2762	O.fringillina	UNITED KINGDOM	♂	Wiltshire	3	Longbridge Deverill, The Marsh	120	13.vii.2021	Blackcap	*Sylvia atricapilla*	R. H. Creighton
2763	O.fringillina	UNITED KINGDOM	♀	Wiltshire	3	Longbridge Deverill, The Marsh	120	17.viii.2021	Blackcap	*Sylvia atricapilla*	R. H. Creighton
2781	O.fringillina	UNITED KINGDOM	♀	Lincolnshire	3	Wainfleet	0	24.viii.2021	Oystercatcher	*Haematopus ostralegus*	Rachel Taylor
2788	O.fringillina	UNITED KINGDOM	♀	Anglesey	2	Cors Ddyga	4	14.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Rachel Taylor
2809	O.fringillina	UNITED KINGDOM		Hampshire	3	Hayling Island, Hayling Golf Course	2	1.viii.2021	Whitethroat	*Curruca communis*	Trevor Codlin
2813	O.fringillina	UNITED KINGDOM	♂	Hampshire	3	Funtley	16	11.vi.2021	Blue Tit	*Cyanistes caeruleus*	Trevor Codlin
2814	O.fringillina	UNITED KINGDOM	♀	Hampshire	3	Funtley	16	11.vi.2021	Blue Tit	*Cyanistes caeruleus*	Trevor Codlin
2861	O.fringillina	UNITED KINGDOM		Fife	3	Bow of Fife	100	3.x.2021	Dunnock	*Prunella modularis*	Dr C. McGuigan
2884	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	3	Stranraer, Leswalt	35	15.viii.2021	Goldfinch	*Carduelis carduelis*	Geoff & Jean Sheppard
2885	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	3	Stranraer, Leswalt	35	15.viii.2021	Goldfinch	*Carduelis carduelis*	Geoff & Jean Sheppard
2889	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	3	Stranraer, Leswalt	35	20.viii.2021	Chaffinch	*Fringilla coelebs*	Geoff & Jean Sheppard
2890	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	3	Stranraer, Leswalt	35	20.viii.2021			Geoff & Jean Sheppard
2892	O.fringillina	UNITED KINGDOM		Dumfries and Galloway	3	Stranraer, Leswalt	35	23.viii.2021	Chaffinch	*Fringilla coelebs*	Geoff & Jean Sheppard
2895	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	3	Stranraer, Leswalt	35	27.viii.2021	Blue Tit	*Cyanistes caeruleus*	Geoff & Jean Sheppard
2896	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	3	Stranraer, Leswalt	35	3.ix.2021	Robin	*Erithacus rubecula*	Geoff & Jean Sheppard
2898	O.fringillina	UNITED KINGDOM		Dumfries and Galloway	3	Stranraer, Leswalt	35	8.ix.2021	Goldfinch	*Carduelis carduelis*	Geoff & Jean Sheppard
2900	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	3	Stranraer, Leswalt	35	20.ix.2021	House Sparrow	*Passer domesticus*	Geoff & Jean Sheppard
2983	O.fringillina	UNITED KINGDOM		Norfolk	3	Walsey Hill	8	20.viii.2021	Blackcap	*Sylvia atricapilla*	Norfolk Ornithologists Association
2989	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Walsey Hill	8	19.viii.2021	Dunnock	*Prunella modularis*	Norfolk Ornithologists Association

2991	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Hempton Marsh	36	28.ix.2021	Robin	*Erithacus rubecula*	Norfolk Ornithologists Association
2997	O.fringillina	UNITED KINGDOM		Norfolk	3	Walsey Hill	8	2.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists Association
2998	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Walsey Hill	8	20.viii.2021	Blackcap	*Sylvia atricapilla*	Norfolk Ornithologists Association
3101	O.fringillina	UNITED KINGDOM	♀	Somerset	2	Portishead, Gordano Valley	0	20.viii.2021	Robin	*Erithacus rubecula*	Gordano Valley RG
3102	O.fringillina	UNITED KINGDOM		Somerset	2	Portishead, Gordano Valley	0	26.ix.2021	Blackcap	*Sylvia atricapilla*	Gordano Valley RG
3182	O.fringillina	UNITED KINGDOM	♂	Devon	2	Ilfracombe, West Down, Buttercombe Barton	160	19.vi.2021	Bullfinch	*Pyrrhula pyrrhula*	Chris Dee
3192	O.fringillina	UNITED KINGDOM	♂	Devon	2	Ilfracombe, West Down, Buttercombe Barton	160	15.vii.2021	Siskin	*Spinus spinus*	Chris Dee
3200	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	2.viii.2021			Chris Dee
3364	O.fringillina	UNITED KINGDOM		Kent	damaged	Sandwich Bay	3	16.x.2021	Goldfinch	*Carduelis carduelis*	Sandwich Bay Bird Observatory
3406	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	11.vii.2021	House Sparrow	*Passer domesticus*	John Black
3414	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	5.viii.2021	Dunnock	*Prunella modularis*	John Black
3415	O.fringillina	UNITED KINGDOM	♂	County Durham		Butterknowle	208	5.viii.2021	Dunnock	*Prunella modularis*	John Black
3416	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	5.viii.2021	Blue Tit	*Cyanistes caeruleus*	John Black
3417	O.fringillina	UNITED KINGDOM	♂	County Durham	3	Butterknowle	208	5.viii.2021	Robin	*Erithacus rubecula*	John Black
3418	O.fringillina	UNITED KINGDOM	♂	County Durham	3	Butterknowle	208	5.viii.2021	House Sparrow	*Passer domesticus*	John Black
3419	O.fringillina	UNITED KINGDOM	♂	County Durham	3	Butterknowle	208	5.viii.2021	Chaffinch	*Fringilla coelebs*	John Black
3581	O.fringillina	UNITED KINGDOM	♀	County Durham	3	Butterknowle	208	5.viii.2021	House Sparrow	*Passer domesticus*	John Black
3584	O.fringillina	UNITED KINGDOM	♂	County Durham	2	Butterknowle	208	19.viii.2021	House Sparrow	*Passer domesticus*	John Black
3585	O.fringillina	UNITED KINGDOM		County Durham	3	Butterknowle	208	24.viii.2021	Chaffinch	*Fringilla coelebs*	John Black
3587	O.fringillina	UNITED KINGDOM		County Durham	3	Butterknowle	208	24.viii.2021	Blue Tit	*Cyanistes caeruleus*	John Black
3589	O.fringillina	UNITED KINGDOM		County Durham	3	Butterknowle	208	30.viii.2021			John Black
3881	O.fringillina	UNITED KINGDOM	♀	West Sussex	3	Cissbury	97	3.x.2021	Robin	*Erithacus rubecula*	Steyning RG
3929	O.fringillina	UNITED KINGDOM		Bedfordshire	2	Sandy, Waterloo Thorns	21	29.viii.2021	Blackcap	*Sylvia atricapilla*	Sara Miller
4101	O.fringillina	UNITED KINGDOM	♂	Highland	2&3	Fortrose	20	12.ix.2021	Great Tit	*Parus major*	Alister Clunas
4102	O.fringillina	UNITED KINGDOM		Highland	3	Fortrose	20	18.ix.2021	Goldfinch	*Carduelis carduelis*	Alister Clunas
4125	O.fringillina	UNITED KINGDOM	♀	Ceredigion	2	Llechryd, Llys y Wern	60	4.x.2021	Goldcrest	*Regulus regulus*	Wendy James
4145	O.fringillina	UNITED KINGDOM	♂	Skye	2	Portree	40	22.vi.2021	House Sparrow	*Passer domesticus*	Jonathan Jones
4221	O.fringillina	UNITED KINGDOM	♀	Staffordshire	3	Kingswinford, Wall Heath, Holbeache Gardens	82	9.vii.2021	Dunnock	*Prunella modularis*	Samuel Bradley
4241	O.fringillina	UNITED KINGDOM	♂	Moray	3	Orton By Fochabers	60	21.viii.2021	Robin	*Erithacus rubecula*	Alastair Young
4244	O.fringillina	UNITED KINGDOM	♀	Moray		Orton By Fochabers	60	16.viii.2021	Robin	*Erithacus rubecula*	Alastair Young
4246	O.fringillina	UNITED KINGDOM		Moray	3	Orton By Fochabers	60	4.ix.2021	Siskin	*Spinus spinus*	Alistair Young
4247	O.fringillina	UNITED KINGDOM		Moray	3	Orton By Fochabers	60	2.x.2021	Chaffinch	*Fringilla coelebs*	Alistair Young
4250	O.fringillina	UNITED KINGDOM	♀	Moray	2	Orton By Fochabers	60	13.ix.2021	Treecreeper	*Certhia familiaris*	Alistair Young
4251	O.fringillina	UNITED KINGDOM		Moray	3	Orton By Fochabers	60		Goldfinch	*Carduelis carduelis*	Alistair Young
4253	O.fringillina	UNITED KINGDOM	♀	Moray	3	Orton By Fochabers	60	10.viii.2021	Robin	*Erithacus rubecula*	Alastair Young
4260	O.fringillina	UNITED KINGDOM		Moray	3	Orton By Fochabers	60	6.xi.2021	Goldfinch	*Carduelis carduelis*	Alistair Young

4321	O.fringillina	UNITED KINGDOM	♂	Surrey	2	Leith Hill, Duke's Warren	250	11.viii.2021	Goldcrest	*Regulus regulus*	Paul Stevenson
4481	O.fringillina	UNITED KINGDOM		Dorset		Hogchester	64	3.viii.2021	Robin	*Erithacus rubecula*	Susan Murphy
4482	O.fringillina	UNITED KINGDOM		Devon	2	Mutters Moor	183	24.viii.2021	Whitethroat	*Curruca communis*	Susan Murphy
4484	O.fringillina	UNITED KINGDOM	♀	Devon	2	Bicton Common,Pebblebed Heaths	121	23.ix.2021	Dartford Warbler	*Curruca undata*	Susan Murphy
4485	O.fringillina	UNITED KINGDOM	♀	Devon	2	Seaton Wetlands, Black Hole Marsh	5	14.xii.2021	Blue Tit	*Cyanistes caeruleus*	Susan Murphy
4722	O.fringillina	UNITED KINGDOM		Derbyshire	3	Creswell. Elmton WTW	117	11.vii.2021	Blackbird	*Turdus merula*	Eleanor Wilkins
4724	O.fringillina	UNITED KINGDOM	♀	Derbyshire		Worksop, Bondhay	123	26.ix.2021	Blackcap	*Sylvia atricapilla*	Eleanor Wilkins
4781	O.fringillina	UNITED KINGDOM	♀	Argyll	2	Audindarroch	30	2.x.2021	Great Tit	*Parus major*	Kirstie Ross
4842	O.fringillina	UNITED KINGDOM	♀	Powys		Talgarth, Llangssty	160	25.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Llangorse Ringing Group
4844	O.fringillina	UNITED KINGDOM	♂	Powys	3	Talgarth, Llangssty	160	11.ix.2021	Treecreeper	*Certhia familiaris*	Llangorse Ringing Group
4845	O.fringillina	UNITED KINGDOM		Powys	3	Talgarth, Llangssty	160	21.ix.2021	Goldcrest	*Regulus regulus*	Llangorse Ringing Group
4904	O.fringillina	UNITED KINGDOM	♀	East Sussex	2	Icklesham	10	13.viii.2021	Garden Warbler	*Sylvia borin*	Rye Bay Ringing Group
4908	O.fringillina	UNITED KINGDOM		East Sussex	2	Icklesham	10	18.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Rye Bay Ringing Group
4912	O.fringillina	UNITED KINGDOM	♀	East Sussex	2	Icklesham	10	28.viii.2021	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
4913	O.fringillina	UNITED KINGDOM	♀	East Sussex	2	Icklesham	10	1.ix.2021	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
4914	O.fringillina	UNITED KINGDOM	♀	East Sussex	2	Icklesham	10	2.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Rye Bay Ringing Group
4915	O.fringillina	UNITED KINGDOM	♀	East Sussex	2	Icklesham	10	9.ix.2021			Rye Bay Ringing Group
4916	O.fringillina	UNITED KINGDOM	♀	East Sussex	3	Icklesham	10	24.ix.2021	Blackcap	*Sylvia atricapilla*	Rye Bay Ringing Group
4917	O.fringillina	UNITED KINGDOM	♀	East Sussex		Icklesham	10	29.ix.2021	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
4918	O.fringillina	UNITED KINGDOM	♀	East Sussex	3	Icklesham	53	14.x.2021	Goldfinch	*Carduelis carduelis*	Rye Bay Ringing Group
4919	O.fringillina	UNITED KINGDOM	♀	East Sussex	3	Icklesham	53	14.x.2021	Goldfinch	*Carduelis carduelis*	Rye Bay Ringing Group
4920	O.fringillina	UNITED KINGDOM	♂	East Sussex	2	Icklesham	53	15.x.2021			Rye Bay Ringing Group
4950	O.fringillina	UNITED KINGDOM	♀	Rutland	3	Rutland Water Nature Reserve	86	25.viii.2021	Robin	*Erithacus rubecula*	Luke Nelson
4951	O.fringillina	UNITED KINGDOM	♂	Rutland	3	Rutland Water Nature Reserve	86	25.viii.2021			Luke Nelson
5126	O.fringillina	UNITED KINGDOM	♀	Suffolk	3	Brandon	15	20.ix.2021	Robin	*Erithacus rubecula*	Greg Conway
5139	O.fringillina	UNITED KINGDOM	♂	Suffolk	2	Brandon	15	30.viii.2021	Robin	*Erithacus rubecula*	Greg Conway
5261	O.fringillina	UNITED KINGDOM		Essex	3	Leigh-on-Sea, Two Tree Island	0	4.vii.2021	Whitethroat	*Curruca communis*	David Wilkinson
5262	O.fringillina	UNITED KINGDOM	♀	Essex	3	Leigh-on-Sea, Two Tree Island	0	11.vii.2021	Whitethroat	*Curruca communis*	David Wilkinson
5263	O.fringillina	UNITED KINGDOM	♀	Essex	3	Leigh-on-Sea, Two Tree Island	0	26.vii.2021	Blackcap	*Sylvia atricapilla*	David Wilkinson
5264	O.fringillina	UNITED KINGDOM		Essex	3	Leigh-on-Sea, Two Tree Island	0	26.vii.2021	Reed Warbler	*Acrocephalus scirpaceus*	David Wilkinson
5265	O.fringillina	UNITED KINGDOM	♀	Essex	3	Leigh-on-Sea, Two Tree Island	0	26.vii.2021	Reed Warbler	*Acrocephalus scirpaceus*	David Wilkinson
5267	O.fringillina	UNITED KINGDOM	♀	Essex	3	Chelmsford	55	8.viii.2021	Goldfinch	*Carduelis carduelis*	David Wilkinson
5268	O.fringillina	UNITED KINGDOM		Essex	2	Gunners Park and Shoebury Ranges Nature Reserve	0	16.viii.2021	Greenfinch	*Chloris chloris*	David Wilkinson
5269	O.fringillina	UNITED KINGDOM	♀	Essex		Gunners Park and Shoebury Ranges Nature Reserve	0	16.viii.2021	Whitethroat	*Curruca communis*	David Wilkinson
5270	O.fringillina	UNITED KINGDOM	♀	Essex	3	Leigh-on-Sea, Two Tree Island	0	29.viii.2021	Whitethroat	*Curruca communis*	David Wilkinson
5315	O.fringillina	UNITED KINGDOM		Norfolk	3	Thetford	13	26.vii.2021	Goldfinch	*Carduelis carduelis*	Joanne Lashwood

5319	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Thetford	13	1.viii.2021	Robin	*Erithacus rubecula*	Joanne Lashwood
5536	O.fringillina	ISLE OF MAN				Calf of Man	80	31.vii.2021	Goldfinch	*Carduelis carduelis*	Calf of Man Bird Observatory
5590	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	12.vii.2021	Dunnock	*Prunella modularis*	A. Turner
5600	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	2	Bancyffordd	205	24.vii.2021	Robin	*Erithacus rubecula*	A. Turner
5605	O.fringillina	UNITED KINGDOM		Skye	3	Portree	40	3.viii.2021	House Sparrow	*Passer domesticus*	Jonathan Jones
5606	O.fringillina	UNITED KINGDOM	♂	Skye	3	Edinbane	5	7.viii.2021	Robin	*Erithacus rubecula*	Jonathan Jones
5610	O.fringillina	UNITED KINGDOM		Skye	3	Edinbane	5	7.viii.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
5611	O.fringillina	UNITED KINGDOM		Skye		Edinbane	5	7.viii.2021			Jonathan Jones
5612	O.fringillina	UNITED KINGDOM	♂	Skye	3	Edinbane	5	7.viii.2021	Robin	*Erithacus rubecula*	Jonathan Jones
5617	O.fringillina	UNITED KINGDOM		Skye	3	Edinbane	5	7.viii.2021			Jonathan Jones
5618	O.fringillina	UNITED KINGDOM		Skye	3	Edinbane	5	7.viii.2021			Jonathan Jones
5784	O.fringillina	UNITED KINGDOM	♀	Cheshire	3	Woolston Eyes	10	3.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5785	O.fringillina	UNITED KINGDOM		Cheshire	2	Woolston Eyes	10	4.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5787	O.fringillina	UNITED KINGDOM		Cheshire	3	Woolston Eyes	10	24.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5793	O.fringillina	UNITED KINGDOM	♂	Cheshire	3	Woolston Eyes	10	22.viii.2021	Whitethroat	*Curruca communis*	Kieran Foster
5794	O.fringillina	UNITED KINGDOM		Cheshire	3	Woolston Eyes	10	19.viii.2021	Robin	*Erithacus rubecula*	Kieran Foster
5796	O.fringillina	UNITED KINGDOM		Cheshire	3	Woolston Eyes	10	14.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5797	O.fringillina	UNITED KINGDOM		Cheshire	2	Woolston Eyes	10	19.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5800	O.fringillina	UNITED KINGDOM		Cheshire	3	Woolston Eyes	10	19.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kieran Foster
5801	O.fringillina	UNITED KINGDOM	♀	Vale of Glamorgan	2	Kenfig NNR	5	21.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Kenfig RG
5802	O.fringillina	UNITED KINGDOM	♀	Vale of Glamorgan	2	Kenfig NNR	5	3.xi.2021	Cetti's Warbler	*Cettia cetti*	Kenfig RG
5823	O.fringillina	ISLE OF MAN	♂		3	Calf of Man	80	12.ix.2021	Willow Warbler	*Phylloscopus trochilus*	Calf of Man Bird Observatory
5828	O.fringillina	ISLE OF MAN			3	Calf of Man	80	28.ix.2021	Goldcrest	*Regulus regulus*	Calf of Man Bird Observatory
5829	O.fringillina	ISLE OF MAN			3	Calf of Man	80	4.x.2021	Goldcrest	*Regulus regulus*	Calf of Man Bird Observatory
5830	O.fringillina	ISLE OF MAN			damaged	Calf of Man	80	10.x.2021	Goldfinch	*Carduelis carduelis*	Calf of Man Bird Observatory
5831	O.fringillina	ISLE OF MAN			3	Calf of Man	80	11.x.2021	Greenfinch	*Chloris chloris*	Calf of Man Bird Observatory
5832	O.fringillina	ISLE OF MAN			3	Calf of Man	80	13.x.2021	Dunnock	*Prunella modularis*	Calf of Man Bird Observatory
5861	O.fringillina	UNITED KINGDOM	♀	Suffolk	3	Felixstowe, Levington, Levington Reed Bed	5	18.viii.2021	Reed Warbler	*Acrocephalus scirpaceus*	Anna Alam/Mick Wright
5862	O.fringillina	UNITED KINGDOM	♀	Suffolk	3	Felixstowe, Levington, Levington Reed Bed	5	2.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Anna Alam/Mick Wright
5902	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Thetford	13	29.vi.2021	Blue Tit	*Cyanistes caeruleus*	Joanne Lashwood
5946	O.fringillina	UNITED KINGDOM	♀	Skye	3	Varagill	60	24.viii.2021			Jonathan Jones
5947	O.fringillina	UNITED KINGDOM	♂	Skye	3	Varagill	60	28.viii.2021	Goldcrest	*Regulus regulus*	Jonathan Jones
5955	O.fringillina	UNITED KINGDOM		Skye	3	Hungladder	40	28.viii.2021	Robin	*Erithacus rubecula*	Jonathan Jones
5956	O.fringillina	UNITED KINGDOM	♀	Skye	3	Hungladder	40	28.viii.2021			Jonathan Jones
5958	O.fringillina	UNITED KINGDOM	♀	Skye	3	Hungladder	40	2.ix.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
5981	O.fringillina	UNITED KINGDOM	♀	Skye	3	Hungladder	40	8.ix.2021	Great Tit	*Parus major*	Jonathan Jones

5985	O.fringillina	UNITED KINGDOM	♂	Skye	2	Hungladder	40	8.ix.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
5987	O.fringillina	UNITED KINGDOM		Skye	3	Hungladder	40	12.ix.2021	Robin	*Erithacus rubecula*	Jonathan Jones
5991	O.fringillina	UNITED KINGDOM		Skye	3	Varagill	60	14.ix.2021	Siskin	*Spinus spinus*	Jonathan Jones
5992	O.fringillina	UNITED KINGDOM	♂	Skye	3	Varagill	60	14.ix.2021	Goldcrest	*Regulus regulus*	Jonathan Jones
5993	O.fringillina	UNITED KINGDOM	♀	Skye	3	Varagill	60	16.ix.2021	Greenfinch	*Chloris chloris*	Jonathan Jones
5994	O.fringillina	UNITED KINGDOM	♀	Skye	3	Varagill	60	18.ix.2021	Treecreeper	*Certhia familiaris*	Jonathan Jones
5995	O.fringillina	UNITED KINGDOM		Skye	3	Portree	40	1.x.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
5996	O.fringillina	UNITED KINGDOM		Skye	3	Portree	40	2.x.2021	Greenfinch	*Chloris chloris*	Jonathan Jones
5997	O.fringillina	UNITED KINGDOM		Skye	3	Edinbane, Skye	5	5.x.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
6049	O.fringillina	ISLE OF MAN	♂		3	Calf of Man	80	25.viii.2021	Robin	*Erithacus rubecula*	Calf of Man Bird Observatory
6051	O.fringillina	ISLE OF MAN	♂		2	Calf of Man	80	27.viii.2021	Goldcrest	*Regulus regulus*	Calf of Man Bird Observatory
6054	O.fringillina	ISLE OF MAN	♂		3	Calf of Man	80	29.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Calf of Man Bird Observatory
6055	O.fringillina	ISLE OF MAN			2	Calf of Man	80	31.viii.2021	Goldcrest	*Regulus regulus*	Calf of Man Bird Observatory
6057	O.fringillina	ISLE OF MAN			3	Calf of Man	80	8.ix.2021	Willow Warbler	*Phylloscopus trochilus*	Calf of Man Bird Observatory
6059	O.fringillina	ISLE OF MAN			3	Calf of Man	80	10.ix.2021	Goldfinch	*Carduelis carduelis*	Calf of Man Bird Observatory
6060	O.fringillina	ISLE OF MAN	♀		3	Calf of Man	80	10.ix.2021			Calf of Man Bird Observatory
7001	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	26.vii.2021	Robin	*Erithacus rubecula*	A. Turner
7003	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	26.vii.2021	Dunnock	*Prunella modularis*	A. Turner
7004	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	27.vii.2021	House Sparrow	*Passer domesticus*	A. Turner
7011	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	30.vii.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7013	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	30.vii.2021			A. Turner
7017	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	3.viii.2021	Dunnock	*Prunella modularis*	A. Turner
7018	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	3.viii.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7021	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	5.viii.2021			A. Turner
7022	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	6.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7026	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire		Bancyffordd	205	7.viii.2021	Blue Tit	*Cyanistes caeruleus*	A. Turner
7027	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire		Bancyffordd	205	8.viii.2021	Dunnock	*Prunella modularis*	A. Turner
7029	O.fringillina	UNITED KINGDOM		Carmarthenshire		Bancyffordd	205	10.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7035	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire		Bancyffordd	205	15.viii.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7036	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	15.viii.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7037	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	15.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7038	O.fringillina	UNITED KINGDOM		Carmarthenshire	2	Bancyffordd	205	15.viii.2021	Dunnock	*Prunella modularis*	A. Turner
7161	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Inverness, Drummond	34	23.vii.2021	Chaffinch	*Fringilla coelebs*	Hugh Insley
7162	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Inverness, Drummond	34	23.vii.2021	Chaffinch	*Fringilla coelebs*	Hugh Insley
7164	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	24.vii.2021	Wren	*Troglodytes troglodytes*	Hugh Insley
7165	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	29.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley

7167	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	29.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7168	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	26.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7169	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	29.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7175	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	1.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7177	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	2&3	Carse of Ardersier	5	30.vii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7241	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	1.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7243	O.fringillina	UNITED KINGDOM	♂	Inverness-shire		Carse of Ardersier	5	1.viii.2021	House Sparrow	*Passer domesticus*	Hugh Insley
7246	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	2.viii.2021	Blackbird	*Turdus merula*	Hugh Insley
7247	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	3.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7248	O.fringillina	UNITED KINGDOM	♂	Inverness-shire		Carse of Ardersier	5	5.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7251	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	8.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7252	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	9.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7253	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	9.viii.2021	House Sparrow	*Passer domesticus*	Hugh Insley
7255	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7256	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7257	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7258	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7259	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7261	O.fringillina	UNITED KINGDOM	♂	Inverness-shire		Carse of Ardersier	5	13.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7262	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	13.viii.2021	Blackcap	*Sylvia atricapilla*	Hugh Insley
7263	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	13.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7264	O.fringillina	UNITED KINGDOM	♂	Inverness-shire		Carse of Ardersier	5	13.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7266	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	15.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7267	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	15.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7269	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	15.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7270	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	17.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7271	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	19.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7272	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	19.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7273	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	19.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7274	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	20.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7275	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	20.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7276	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	20.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7277	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	24.viii.2021	Bullfinch	*Pyrrhula pyrrhula*	Hugh Insley
7278	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	25.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7279	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	27.viii.2021	Blackbird	*Turdus merula*	Hugh Insley
7280	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	27.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley

7281	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	2.viii.2021	Greenfinch	*Chloris chloris*	Chris Dee
7287	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021	Blackcap	*Sylvia atricapilla*	Chris Dee
7289	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021	Goldfinch	*Carduelis carduelis*	Chris Dee
7290	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021	Greenfinch	*Chloris chloris*	Chris Dee
7291	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021			Chris Dee
7292	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021			Chris Dee
7293	O.fringillina	UNITED KINGDOM	♀	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021			Chris Dee
7294	O.fringillina	UNITED KINGDOM	♀	Devon		Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021			Chris Dee
7295	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	9.viii.2021			Chris Dee
7297	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	14.viii.2021			Chris Dee
7298	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	15.viii.2021	Greenfinch	*Chloris chloris*	Chris Dee
7299	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	25.viii.2021	Chaffinch	*Fringilla coelebs*	Chris Dee
7300	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	28.viii.2021	Robin	*Erithacus rubecula*	Chris Dee
7303	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	17.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7304	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	17.viii.2021			A. Turner
7305	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire		Bancyffordd	205	17.viii.2021			A. Turner
7306	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	17.viii.2021	Robin	*Erithacus rubecula*	A. Turner
7307	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	18.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7308	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	20.viii.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7312	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	22.viii.2021			A. Turner
7313	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	29.viii.2021	Dunnock	*Prunella modularis*	A. Turner
7314	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	29.viii.2021			A. Turner
7315	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	29.viii.2021	Dunnock	*Prunella modularis*	A. Turner
7316	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	31.viii.2021	Wren	*Troglodytes troglodytes*	A. Turner
7318	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	14.ix.2021	Dunnock	*Prunella modularis*	A. Turner
7319	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	14.ix.2021	Dunnock	*Prunella modularis*	A. Turner
7320	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	18.ix.2021	House Sparrow	*Passer domesticus*	A. Turner
7321	O.fringillina	UNITED KINGDOM	♂	Devon	2	Ilfracombe, West Down, Buttercombe Barton	160	28.viii.2021	Greenfinch	*Chloris chloris*	Chris Dee
7323	O.fringillina	UNITED KINGDOM	♂	Devon	2	Ilfracombe, West Down, Buttercombe Barton	160	28.viii.2021			Chris Dee
7324	O.fringillina	UNITED KINGDOM	♀	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	28.viii.2021	Greenfinch	*Chloris chloris*	Chris Dee
7325	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	29.viii.2021	Robin	*Erithacus rubecula*	Chris Dee
7326	O.fringillina	UNITED KINGDOM	♀	Devon	2&3	Ilfracombe, West Down, Buttercombe Barton	160	29.viii.2021			Chris Dee
7327	O.fringillina	UNITED KINGDOM	♀	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	3.ix.2021	Chaffinch	*Fringilla coelebs*	Chris Dee
7328	O.fringillina	UNITED KINGDOM	♀	Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	3.ix.2021	Goldfinch	*Carduelis carduelis*	Chris Dee
7329	O.fringillina	UNITED KINGDOM		Devon	3	Ilfracombe, West Down, Buttercombe Barton	160	3.ix.2021			Chris Dee
7381	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	2	Bancyffordd	205	18.ix.2021	Great Tit	*Parus major*	A. Turner

7382	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	2	Bancyffordd	205	21.ix.2021	Chaffinch	*Fringilla coelebs*	A. Turner
7383	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	2	Bancyffordd	205	22.ix.2021	Robin	*Erithacus rubecula*	A. Turner
7384	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	2	Bancyffordd	205	23.ix.2021	Dunnock	*Prunella modularis*	A. Turner
7443	O.fringillina	UNITED KINGDOM	♀	Warwickshire	3	Priors Marston	143	28.vii.2021	Dunnock	*Prunella modularis*	Northants RG
7449	O.fringillina	UNITED KINGDOM		Northamptonshire	2	Northhampton, Harrington Airfield	161	2.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Northants RG
7745	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	17.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7747	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	23.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7748	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	23.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7750	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	2	Carse of Ardersier	5	22.vii.2022	Dunnock	*Prunella modularis*	Hugh Insley
7752	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	22.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7753	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	17.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7755	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	2	Carse of Ardersier	5	17.vii.2022	Goldcrest	*Regulus regulus*	Hugh Insley
7758	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	23.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7759	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	23.vii.2022	Coal Tit	*Periparus ater*	Hugh Insley
7961	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	30.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7963	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	3.ix.2021	Blackcap	*Sylvia atricapilla*	Hugh Insley
7964	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	4.ix.2021	Dunnock	*Prunella modularis*	Hugh Insley
7965	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	4.ix.2021	Blackbird	*Turdus merula*	Hugh Insley
7967	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	8.ix.2021	Blackcap	*Sylvia atricapilla*	Hugh Insley
7969	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	8.ix.2021	Chaffinch	*Fringilla coelebs*	Hugh Insley
7972	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	20.ix.2021	Dunnock	*Prunella modularis*	Hugh Insley
7973	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	25.ix.2021	Robin	*Erithacus rubecula*	Hugh Insley
7974	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	17.x.2021	Goldcrest	*Regulus regulus*	Hugh Insley
7977	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	3	Carse of Ardersier	5	12.ix.2021	Meadow Pipit	*Anthus pratensis*	Hugh Insley
123A	O.fringillina	UNITED KINGDOM		Cumbria	2	Kirkbride	12	8.vii.2020	House Sparrow	*Passer domesticus*	Watchtree RG
123B	O.fringillina	UNITED KINGDOM	♂	Cumbria	2	Kirkbride	12	8.vii.2020	House Sparrow	*Passer domesticus*	Watchtree RG
172A	O.fringillina	UNITED KINGDOM	♂	County Durham	3	Butterknowle	208	24.vii.2020	Robin	*Erithacus rubecula*	John Black
172B	O.fringillina	UNITED KINGDOM	♂	County Durham		Butterknowle	208	24.vii.2020	Robin	*Erithacus rubecula*	John Black
2995A	O.fringillina	UNITED KINGDOM	♀	Norfolk	3	Walsey Hill	8	14.ix.2021	Reed Warbler	*Acrocephalus scirpaceus*	Norfolk Ornithologists Association
5123A	O.fringillina	UNITED KINGDOM		Suffolk	3	Brandon	15	20.viii.2021	Robin	*Erithacus rubecula*	Greg Conway
5123B	O.fringillina	UNITED KINGDOM		Suffolk	3	Brandon	15	20.viii.2021	Robin	*Erithacus rubecula*	Greg Conway
5123C	O.fringillina	UNITED KINGDOM	♀	Suffolk	3	Brandon	15	20.viii.2021	Robin	*Erithacus rubecula*	Greg Conway
5323B	O.fringillina	ISLE OF MAN	♂		3	Calf of Man	80	4.vii.2021			Calf of Man Bird Observatory
5528A	O.fringillina	ISLE OF MAN	♂		2	Calf of Man	80	22.vii.2021	Meadow Pipit	*Anthus pratensis*	Calf of Man Bird Observatory
5531A	O.fringillina	ISLE OF MAN	♀		3	Calf of Man	80	24.vii.2021			Calf of Man Bird Observatory
5531B	O.fringillina	ISLE OF MAN	♀		3	Calf of Man	80	24.vii.2021			Calf of Man Bird Observatory

5833A	O.fringillina	ISLE OF MAN	♀		3	Calf of Man	80	15.x.2021			Calf of Man Bird Observatory
5833B	O.fringillina	ISLE OF MAN	♀		3	Calf of Man	80	15.x.2021			Calf of Man Bird Observatory
7007A	O.fringillina	UNITED KINGDOM		Carmarthenshire	2	Bancyffordd	205	27.vii.2021	Robin	*Erithacus rubecula*	A. Turner
7007B	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	27.vii.2021	Robin	*Erithacus rubecula*	A. Turner
7007C	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	27.vii.2021	Robin	*Erithacus rubecula*	A. Turner
7023A	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	6.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7023B	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	6.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7039A	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	15.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7039B	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	15.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7040A	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	3	Bancyffordd	205	15.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7040B	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	15.viii.2021	House Sparrow	*Passer domesticus*	A. Turner
7254A	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7254B	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7254C	O.fringillina	UNITED KINGDOM		Inverness-shire	3	Carse of Ardersier	5	11.viii.2021	Robin	*Erithacus rubecula*	Hugh Insley
7260B-small	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	3	Carse of Ardersier	5	12.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7317A	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	3	Bancyffordd	205	1.ix.2021	Dunnock	*Prunella modularis*	A. Turner
7317B	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	1.ix.2021	Dunnock	*Prunella modularis*	A. Turner
7317C	O.fringillina	UNITED KINGDOM		Carmarthenshire	3	Bancyffordd	205	1.ix.2021	Dunnock	*Prunella modularis*	A. Turner
A74	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	3	Northampton, Harrington Airfield	150	7.ix.2020	Yellowhammer	*Emberiza citrinella*	Helen Franklin
C23	O.fringillina	UNITED KINGDOM		Northamptonshire	3	Greens Norton	95	27.viii.2020	Chiffchaff	*Phylloscopus collybita*	Chris Payne
D03	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	2	Flamborough	45	29.ix.2020	Yellowhammer	*Emberiza citrinella*	Andy Hood
E06	O.fringillina	UNITED KINGDOM		Cumbria	2	Kirkbride	14	20.viii.2021	Treecreeper	*Certhia familiaris*	Watchtree RG
E12	O.fringillina	UNITED KINGDOM		Cheshire	3	Mollington	33	16.ix.2020	Great Tit	*Parus major*	Phil Woollen
E14	O.fringillina	UNITED KINGDOM		Cheshire	3	Mollington	33	18.ix.2020	Goldfinch	*Carduelis carduelis*	Phil Woollen
FF101	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	23.vii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF102	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	23.vii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF105	O.fringillina	UNITED KINGDOM		Somerset	2	Minehead, Bratton	64	25.vii.2021	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
FF108	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	2.viii.2021	Dunnock	*Prunella modularis*	Denise Wawman
FF112	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	2.viii.2021			Denise Wawman
FF113	O.fringillina	UNITED KINGDOM	♂	Somerset	2	Minehead, Bratton	64	2.viii.2021			Denise Wawman
FF114	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	2.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF118	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	2.viii.2021			Denise Wawman
FF119	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	2.viii.2021			Denise Wawman
FF120	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	2.viii.2021			Denise Wawman
FF122	O.fringillina	UNITED KINGDOM	♂	Somerset	2	Minehead, Bratton	64	4.viii.2021	Dunnock	*Prunella modularis*	Denise Wawman
FF124	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	3.viii.2021			Denise Wawman

FF125	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	10.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF127	O.fringillina	UNITED KINGDOM		Somerset	2	Minehead, Bratton	64	12.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF128	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	12.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF130	O.fringillina	UNITED KINGDOM		Somerset	2	Minehead, Bratton	64	12.viii.2021			Denise Wawman
FF131	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	19.viii.2021	Siskin	*Spinus spinus*	Denise Wawman
FF132	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	19.viii.2021	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
FF133	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	22.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF134	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	22.viii.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF135	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	22.viii.2021			Denise Wawman
FF136	O.fringillina	UNITED KINGDOM		Somerset	2	Minehead, Bratton	64	22.viii.2021			Denise Wawman
FF139	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	3.ix.2021	Greenfinch	*Chloris chloris*	Denise Wawman
FF140	O.fringillina	UNITED KINGDOM	♂	Somerset		Minehead, Bratton	64	5.ix.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF141	O.fringillina	UNITED KINGDOM	♂	Somerset		Minehead, Bratton	64	21.ix.2021	Robin	*Erithacus rubecula*	Denise Wawman
FF142	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	21.ix.2021	Great Tit	*Parus major*	Denise Wawman
FF143	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	21.ix.2021	Great Tit	*Parus major*	Denise Wawman
FF144	O.fringillina	UNITED KINGDOM	♂	Somerset	2	Minehead, Bratton	64	25.ix.2021	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
FF145	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	23.x.2021	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF152	O.fringillina	UNITED KINGDOM	♂	Somerset		Minehead, Bratton	64	12.vi.2022	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
FF154	O.fringillina	UNITED KINGDOM	♂	Somerset	2	Minehead, Bratton	64	16.vi.2022	Great Tit	*Parus major*	Denise Wawman
FF158	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	15.vii.2022	Dunnock	*Prunella modularis*	Denise Wawman
FF162	O.fringillina	UNITED KINGDOM		Somerset	2	Webbers Post	246	20.vii.2022	Robin	*Erithacus rubecula*	Denise Wawman
FF165	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Webbers Post	245	29.vii.2022	Robin	*Erithacus rubecula*	Denise Wawman
FF166	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	30.vii.2022	Robin	*Erithacus rubecula*	Denise Wawman
FF169	O.fringillina	UNITED KINGDOM	♂	Somerset	2	Minehead, Bratton	64	30.vii.2022			Denise Wawman
FF22	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	7.viii.2013	Dunnock	*Prunella modularis*	Denise Wawman
FF24	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	16.viii.2014	Chiffchaff	*Phylloscopus collybita*	Denise Wawman
FF39	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	20.vii.2020			Denise Wawman
FF41	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	21.vii.2020			Denise Wawman
FF44	O.fringillina	UNITED KINGDOM		Somerset		Minehead, Bratton	64	24.vii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF46	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	24.vii.2020			Denise Wawman
FF47	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	24.vii.2020			Denise Wawman
FF51	O.fringillina	UNITED KINGDOM	♂	Somerset		Minehead, Bratton	64	2.viii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF57	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	8.viii.2020			Denise Wawman
FF58	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	8.viii.2020			Denise Wawman
FF61	O.fringillina	UNITED KINGDOM	♀	Somerset	2	Minehead, Bratton	64	17.viii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF64	O.fringillina	UNITED KINGDOM		Somerset	2	Minehead, Bratton	64	31.viii.2020	Dunnock	*Prunella modularis*	Denise Wawman

FF65	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	31.viii.2020			Denise Wawman
FF66	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	31.viii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF67	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	31.viii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF68	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	31.viii.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF69	O.fringillina	UNITED KINGDOM		Somerset	3	Minehead, Bratton	64	10.ix.2020	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF70	O.fringillina	UNITED KINGDOM	♀	Somerset	3	Minehead, Bratton	64	10.ix.2020	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
MG02	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Hindolveston	66	4.viii.2018	Dunnock	*Prunella modularis*	Charles Dewhurst
MG16	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Field Dalling	50	1.ix.2019	Long-tailed Tit	*Aegithalos caudatus*	Charles Dewhurst
MG18A	O.fringillina	UNITED KINGDOM	♂	Norfolk	3	Field Dalling	50	26.vii.2020	Goldfinch	*Carduelis carduelis*	Charles Dewhurst
MG18B	O.fringillina	UNITED KINGDOM		Norfolk	2	Field Dalling	50	26.vii.2020	Goldfinch	*Carduelis carduelis*	Charles Dewhurst
MG22	O.fringillina	UNITED KINGDOM	♀	Norfolk	2	Field Dalling	50	16.viii.2020	Goldfinch	*Carduelis carduelis*	Charles Dewhurst
MG23	O.fringillina	UNITED KINGDOM		Norfolk	3	Field Dalling	50	24.viii.2020	Goldfinch	*Carduelis carduelis*	Charles Dewhurst
NW01	O.fringillina	UNITED KINGDOM	♀	Devon		Slapton Ley	4	6.ix.2020	Blackcap	*Sylvia atricapilla*	Nik Ward
NW05	O.fringillina	UNITED KINGDOM	♂	Devon	2	Slapton	10	5.ix.2021	Robin	*Erithacus rubecula*	Nik Ward
NW06	O.fringillina	UNITED KINGDOM	♀	Devon	2	Slapton	10	14.viii.2021	Linnet	*Linaria cannabina*	Nik Ward
NW07	O.fringillina	UNITED KINGDOM		Devon	3	Ide	20	24.ix.2021	Greenfinch	*Chloris chloris*	Nik Ward
NW08	O.fringillina	UNITED KINGDOM	♂	Devon	3	Ide	20	17.viii.2021			Nik Ward
NW09	O.fringillina	UNITED KINGDOM	♂	Devon	2	Slapton	10	23.viii.2021	Cetti's Warbler	*Cettia cetti*	Nik Ward
SB24	O.fringillina	IRELAND	♂	Cork	2	Enniskeane	99	15.vii.2021	Goldcrest	*Regulus regulus*	Sam Bayley
SB29	O.fringillina	IRELAND		Cork	3	Owenahincha, Little Island Wetland	0	26.viii.2021	Sedge Warbler	*Acrocephalus schoenobaenus*	Sam Bayley
SB36	O.fringillina	IRELAND	♂	Cork	3	Owenahincha, Little Island Wetland	0	26.viii.2021	Chiffchaff	*Phylloscopus collybita*	Sam Bayley
SB39	O.fringillina	IRELAND	♀	Cork	3	Owenahincha, Little Island Wetland	0	17.viii.2021	Robin	*Erithacus rubecula*	Sam Bayley
SB40	O.fringillina	IRELAND	♀	Cork	3	Owenahincha, Little Island Wetland	0	26.viii.2021	Chiffchaff	*Phylloscopus collybita*	Sam Bayley
SB59	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	31.viii.2021	Chaffinch	*Fringilla coelebs*	Sam Bayley
SB61	O.fringillina	IRELAND	♂	Cork	3	Enniskeane	99	24.viii.2021	Robin	*Erithacus rubecula*	Sam Bayley
SB62	O.fringillina	IRELAND	♂	Cork	3	Enniskeane	99	31.viii.2021	Robin	*Erithacus rubecula*	Sam Bayley
SB63	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	6.ix.2021	Great Tit	*Parus major*	Sam Bayley
SB64	O.fringillina	IRELAND		Cork	3	Enniskeane	99	22.xi.2021	Goldfinch	*Carduelis carduelis*	Sam Bayley
SB65	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	24.viii.2021			Sam Bayley
SB66	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	24.viii.2021	Chaffinch	*Fringilla coelebs*	Sam Bayley
SB67	O.fringillina	IRELAND	♀	Cork		Enniskeane	99	6.ix.2021	Chiffchaff	*Phylloscopus collybita*	Sam Bayley
SB69	O.fringillina	IRELAND		Cork		Enniskeane	99	5.xi.2021	Goldcrest	*Regulus regulus*	Sam Bayley
SB70	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	19.viii.2021	House Sparrow	*Passer domesticus*	Sam Bayley
SB71	O.fringillina	IRELAND		Cork	3	Enniskeane	99	31.viii.2021	Goldcrest	*Regulus regulus*	Sam Bayley
SB73	O.fringillina	IRELAND		Cork	3	Enniskeane	99	31.viii.2021	Willow Warbler	*Phylloscopus trochilus*	Sam Bayley
SB78	O.fringillina	IRELAND	♂	Cork		Enniskeane	99	8.viii.2021	Robin	*Erithacus rubecula*	Sam Bayley

SB80	O.fringillina	IRELAND	♂	Cork	3	Enniskeane	99	19.viii.2021	House Sparrow	*Passer domesticus*	Sam Bayley
SB81	O.fringillina	IRELAND	♂	Cork	3	Enniskeane	99	8.viii.2021	Robin	*Erithacus rubecula*	Sam Bayley
SB85	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	31.viii.2021	Blackcap	*Sylvia atricapilla*	Sam Bayley
SB86	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	10.viii.2021			Sam Bayley
SB88	O.fringillina	IRELAND		Cork	3	Enniskeane	99	24.viii.2021	Dunnock	*Prunella modularis*	Sam Bayley
SB89	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	31.viii.2021	Treecreeper	*Certhia familiaris*	Sam Bayley
SB91	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	31.vii.2021	Dunnock	*Prunella modularis*	Sam Bayley
SB92	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	31.viii.2021	Treecreeper	*Certhia familiaris*	Sam Bayley
SB93	O.fringillina	IRELAND	♀	Cork	3	Enniskeane	99	24.viii.2021	Song Thrush	*Turdus philomelos*	Sam Bayley
SB95	O.fringillina	IRELAND	♂	Cork	3	Enniskeane	99	23.vii.2021			Sam Bayley
FF170	O.fringillina	UNITED KINGDOM	♂	Somerset	3	Minehead, Bratton	64	1.viii.2022	Great Tit	*Parus major*	Denise Wawman
FF174	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	1.viii.2022	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
7188	O.fringillina	UNITED KINGDOM	♀	Norfolk	BSmart	Cranwich	10	23.vii.2022	Reed Warbler	*Acrocephalus scirpaceus*	Lee Barber
H181	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	23.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H182	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	27.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H183	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	28.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H184	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	27.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H185	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	5	28.vii.2022			Hugh Insley
H186	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	27.vii.2022	Robin	*Erithacus rubecula*	Hugh Insley
H189	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	27.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H191	O.fringillina	UNITED KINGDOM		Inverness-shire	BSmart	Carse of Ardersier	5	28.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H194	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	27.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H195	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	5	28.vii.2022	Chiffchaff	*Phylloscopus collybita*	Hugh Insley
H198	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	Hutson	Carse of Ardersier	5	28.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H200A	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	28.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H200B	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	ASmart	Carse of Ardersier	5	28.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7715	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	31.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7704	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	31.vii.2022	Goldcrest	*Regulus regulus*	Hugh Insley
7708	O.fringillina	UNITED KINGDOM		Inverness-shire	BSmart	Carse of Ardersier	5	31.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7709	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	31.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7713	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	31.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
FF175	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, North Hill	251	10.viii.2022	Stonechat	*Saxicola rubicola*	Denise Wawman
FF178	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Selworthy Beacon	290	27.viii.2022			Denise Wawman
7702	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	12.viii.2022	Blackcap	*Sylvia atricapilla*	Hugh Insley
7705	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	5	13.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7706	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	Hutson	Carse of Ardersier	5	13.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley

7707	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	5	13.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7712	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	13.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7928	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	34	15.viii.2022	Blue Tit	*Cyanistes caeruleus*	Hugh Insley
7716	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	22.viii.2022	Goldcrest	*Regulus regulus*	Hugh Insley
7717	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	5	22.viii.2022	Goldcrest	*Regulus regulus*	Hugh Insley
7719	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	24.viii.2022	Robin	*Erithacus rubecula*	Hugh Insley
7718	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	Hutson	Carse of Ardersier	5	24.viii.2022	Song Thrush	*Turdus philomelos*	Hugh Insley
H187	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	11.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H190	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	11.viii.2022	Chiffchaff	*Phylloscopus collybita*	Hugh Insley
H192	O.fringillina	UNITED KINGDOM		Inverness-shire		Carse of Ardersier	5	4.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H193	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	ASmart	Carse of Ardersier	5	4.viii.2022	Chiffchaff	*Phylloscopus collybita*	Hugh Insley
H196	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	5	11.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H197	O.fringillina	UNITED KINGDOM		Inverness-shire	ASmart	Carse of Ardersier	5	11.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H199	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	5	11.viii.2022	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
FF184	O.fringillina	UNITED KINGDOM	♂	Somerset	ASmart	Minehead, Bratton	64	1.ix.2022	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
7621	O.fringillina	UNITED KINGDOM	♀	Skye	Hutson	Portree	40	25.viii.2022	Siskin	*Spinus spinus*	Jonathan Jones
7622	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree	40	25.viii.2022	Goldfinch	*Carduelis carduelis*	Jonathan Jones
7627	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	3.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
7628	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill	60	6.ix.2022	Goldfinch	*Carduelis carduelis*	Jonathan Jones
7629	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill	60	6.ix.2022	Robin	*Erithacus rubecula*	Jonathan Jones
7630	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill	60	6.ix.2022	Great Tit	*Parus major*	Jonathan Jones
7633	O.fringillina	UNITED KINGDOM	♀	Skye	Hutson	Hungladder	40	28.viii.2022	Chaffinch	*Fringilla coelebs*	Jonathan Jones
7636	O.fringillina	UNITED KINGDOM	♂	Skye	ASmart	Varagill	60	4.ix.2022	Goldcrest	*Regulus regulus*	Jonathan Jones
7637	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Varagill	60	4.ix.2022	Great Tit	*Parus major*	Jonathan Jones
7638	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill	60	4.ix.2022	Bullfinch	*Pyrrhula pyrrhula*	Jonathan Jones
7639	O.fringillina	UNITED KINGDOM		Skye	BSmart	Varagill	60	4.ix.2022	Great Tit	*Parus major*	Jonathan Jones
7640	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill	60	4.ix.2022	Goldfinch	*Carduelis carduelis*	Jonathan Jones
7649	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Hungladder	40	31.vii.2022	Meadow Pipit	*Anthus pratensis*	Jonathan Jones
7652	O.fringillina	UNITED KINGDOM		Skye	damaged	Portree	40	9.viii.2022	Goldfinch	*Carduelis carduelis*	Jonathan Jones
7653	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Portree	40	11.viii.2022	Siskin	*Spinus spinus*	Jonathan Jones
7658	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree	40	11.viii.2022	Greenfinch	*Chloris chloris*	Jonathan Jones
7659	O.fringillina	UNITED KINGDOM		Skye	BSmart	Portree	40	20.viii.2022	Goldfinch	*Carduelis carduelis*	Jonathan Jones
7541	O.fringillina	UNITED KINGDOM	♀	Skye	damaged	Varagill	60	2.xi.2021	Chaffinch	*Fringilla coelebs*	Jonathan Jones
360	O.fringillina	UNITED KINGDOM	♀	Staffordshire	ASmart	Walsall, Daisybank	148	23.vii.2022	Long-tailed Tit	*Aegithalos caudatus*	David Clifton
348	O.fringillina	UNITED KINGDOM	♀	Warwickshire	ASmart	Hams Hall	72	27.vii.2022	Reed Warbler	*Acrocephalus scirpaceus*	David Clifton
352	O.fringillina	UNITED KINGDOM	♀	Warwickshire	ASmart	Hams Hall	72	5.viii.2022	Blackcap	*Sylvia atricapilla*	David Clifton

349	O.fringillina	UNITED KINGDOM	♂	Warwickshire	BSmart	Hams Hall	74	10.viii.2022			David Clifton
P33A	O.fringillina	UNITED KINGDOM	♂	Warwickshire	BSmart	Hams Hall	75	26.viii.2022	Reed Warbler	*Acrocephalus scirpaceus*	David Clifton
P33B	O.fringillina	UNITED KINGDOM	♀	Warwickshire	ASmart	Hams Hall	75	26.viii.2022	Reed Warbler	*Acrocephalus scirpaceus*	David Clifton
357	O.fringillina	UNITED KINGDOM	♀	Warwickshire	Hutson	Coleshill	76	24.ix.2022	Dunnock	*Prunella modularis*	David Clifton
344	O.fringillina	UNITED KINGDOM	♀	Staffordshire	ASmart	Walsall, Daisybank	148	11.x.2022	Goldfinch	*Carduelis carduelis*	David Clifton
7714	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	3	22.viii.2022	Blackcap	*Sylvia atricapilla*	Hugh Insley
7711	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	ASmart	Carse of Ardersier	3	30.viii.2022	Robin	*Erithacus rubecula*	Hugh Insley
7720	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	3	10.ix.2022	Great Tit	*Parus major*	Hugh Insley
H141	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	3	14.ix.2022	Goldcrest	*Regulus regulus*	Hugh Insley
H064	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	BSmart	Stranraer, Leswalt	35	8.viii.2022	Wren	*Troglodytes troglodytes*	Geoff & Jean Sheppard
H065	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	BSmart	Stranraer, Leswalt	35	8.viii.2022	Wren	*Troglodytes troglodytes*	Geoff & Jean Sheppard
H067	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	Hutson	Stranraer, Leswalt	35	12.viii.2022	Chaffinch	*Fringilla coelebs*	Geoff & Jean Sheppard
H069	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	BSmart	Stranraer, Leswalt	35	26.viii.2022	Lesser Redpoll	*Acanthis cabaret*	Geoff & Jean Sheppard
H070	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	BSmart	Stranraer, Leswalt	35	26.viii.2022	Siskin	*Spinus spinus*	Geoff & Jean Sheppard
H073	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	ASmart	Stranraer, Leswalt	35	2.ix.2022	Greenfinch	*Chloris chloris*	Geoff & Jean Sheppard
H074	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	BSmart	Stranraer, Leswalt	35	8.ix.2022	Great Tit	*Parus major*	Geoff & Jean Sheppard
H075	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	ASmart	Stranraer, Leswalt	35	8.ix.2022	Robin	*Erithacus rubecula*	Geoff & Jean Sheppard
3239	O.fringillina	UNITED KINGDOM	♂	Argyll	ASmart	Inveraray, Lagganbeg	93	10.viii.2022	House Sparrow	*Passer domesticus*	Rob Lightfoot
7332	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Ilfracombe, West Down, Buttercombe Barton	160	1.vii.2022	Chaffinch	*Fringilla coelebs*	Chris Dee
7336	O.fringillina	UNITED KINGDOM	♂	Devon	ASmart	Ilfracombe, West Down, Buttercombe Barton	160	7.vii.2022	Greenfinch	*Chloris chloris*	Chris Dee
7581	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Ilfracombe, West Down, Buttercombe Barton	160	1.viii.2022	Robin	*Erithacus rubecula*	Chris Dee
7583	O.fringillina	UNITED KINGDOM	♀	Devon	damaged	Ilfracombe, West Down, Buttercombe Barton	160	20.viii.2022			Chris Dee
547	O.fringillina	UNITED KINGDOM	♀	West Sussex	BSmart	Ladywell Valley	15	9.viii.2022			Clare Buckle
550	O.fringillina	UNITED KINGDOM	♀	West Sussex	ASmart	Ladywell Valley	15		Goldcrest	*Regulus regulus*	Clare Buckle
H005	O.fringillina	UNITED KINGDOM	♀	Suffolk	ASmart	Brandon	25	7.ix.2022	Goldfinch	*Carduelis carduelis*	Dr Greg Conway
5122	O.fringillina	UNITED KINGDOM	♀	Suffolk	ASmart	Brandon	25	4.x.2022	Siskin	*Spinus spinus*	Dr Greg Conway
7206	O.fringillina	UNITED KINGDOM	♀	Norfolk	BSmart	Rosedene	10	19.viii.2022	Reed Warbler	*Acrocephalus scirpaceus*	Lee Barber
7201	O.fringillina	UNITED KINGDOM	♀	Norfolk	BSmart	Cranwich	10	21.viii.2022	Reed Warbler	*Acrocephalus scirpaceus*	Lee Barber
7209	O.fringillina	UNITED KINGDOM	♀	Denibighshire	ASmart	Garth	200	28.viii.2022	Dunnock	*Prunella modularis*	Lee Barber
7203	O.fringillina	UNITED KINGDOM	♀	Norfolk	BSmart	Cranwich	10	4.ix.2022	Reed Warbler	*Acrocephalus scirpaceus*	Lee Barber
7212	O.fringillina	UNITED KINGDOM	♀	Norfolk	Hutson	Croxton Park	20	7.x.2022	Skylark	*Alauda arvensis*	Lee Barber
2942	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Camelby	120	1.ix.2022	Dunnock	*Prunella modularis*	Bob Medland
1566	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	ASmart	Stanford Reservoir	113	16.vii.2022	Dunnock	*Prunella modularis*	Stanford Ringing Group
1570	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	ASmart	Stanford Reservoir	113	6.viii.2022	Reed Warbler	*Acrocephalus scirpaceus*	Stanford Ringing Group
1571	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	Hutson	Stanford Reservoir	113	6.viii.2022	Whitethroat	*Curruca communis*	Stanford Ringing Group
1572	O.fringillina	UNITED KINGDOM	♀	Leicestershire	ASmart	Lutterworth, North Kilworth, Hanglands	151	16.viii.2022	Robin	*Erithacus rubecula*	Stanford Ringing Group

5294	O.fringillina	UNITED KINGDOM	♀	Derbyshire	ASmart	Markham Vale	97	29.viii.2022	Goldcrest	*Regulus regulus*	Bryn Roberts
H930	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham	10	16.viii.2022	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
H937	O.fringillina	UNITED KINGDOM	♀	East Sussex	damaged	Icklesham	10	12.ix.2022	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
H940	O.fringillina	UNITED KINGDOM	♀	East Sussex	Hutson	Icklesham	10	27.ix.2022	Cetti's Warbler	*Cettia cetti*	Rye Bay Ringing Group
A30	O.fringillina	UNITED KINGDOM	♂	Dumfries and Galloway	BSmart	RSPB Mersehead	0	6.viii.2022	Wren	*Troglodytes troglodytes*	ANON
1073	O.fringillina	UNITED KINGDOM	♀	Lincolnshire	BSmart	Owmby	19	15.vii.2022	Whitethroat	*Curruca communis*	Jenny Dunn
1069	O.fringillina	UNITED KINGDOM	♀	Lincolnshire	ASmart	Moorlands	23	22.vii.2022	Whitethroat	*Curruca communis*	Jenny Dunn
7587	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Ilfracombe, West Down, Buttercombe Barton	160	22.x.2022	Goldcrest	*Regulus regulus*	Chris Dee
SB37	O.fringillina	IRELAND	♀	Kerry	ASmart	Killarney National Park	50	11.vii.2022	Robin	*Erithacus rubecula*	Sam Bayley
SB83	O.fringillina	IRELAND	♀	Cork	Hutson	Owenahincha, Little Island Wetland	0	29.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Sam Bayley
SB68	O.fringillina	IRELAND	♀	Cork	BSmart	Owenahincha, Little Island Wetland	0	29.vii.2022	Treecreeper	*Certhia familiaris*	Sam Bayley
SB41	O.fringillina	IRELAND	♂	Kerry	BSmart	Killarney National Park	50	16.viii.2022	Goldcrest	*Regulus regulus*	Sam Bayley
SB30	O.fringillina	IRELAND		Kerry		Killarney National Park	50	25.xi.2022	Firecrest	*Regulus ignicapilla*	Sam Bayley
H081	O.fringillina	UNITED KINGDOM	♀	Dumfries and Galloway	ASmart	Toll	58	18.ix.2022	Robin	*Erithacus rubecula*	Tony Gibson
5202	O.fringillina	UNITED KINGDOM	♀	Derbyshire	ASmart	Moss Valley Meadows	189	9.viii.2022	Nuthatch	*Sitta europaea*	Ava Teasdale
H162	O.fringillina	UNITED KINGDOM	♀	Cumbria	ASmart	Kirkbride	10	28.vii.2022	Dunnock	*Prunella modularis*	Frank Mawby
H164	O.fringillina	UNITED KINGDOM		Cumbria	ASmart	Watchtree	70	13.viii.2022	Chaffinch	*Fringilla coelebs*	Frank Mawby
H165	O.fringillina	UNITED KINGDOM		Cumbria	BSmart	Watchtree	70	27.viii.2022			Frank Mawby
H166	O.fringillina	UNITED KINGDOM	♀	Cumbria	BSmart	Watchtree	70	27.viii.2022			Frank Mawby
432	O.fringillina	UNITED KINGDOM	♀	Norfolk	damaged	Burnham Deepdale	10	4.ix.2022	Robin	*Erithacus rubecula*	Denise Lamsdell
439	O.fringillina	UNITED KINGDOM	♀	Norfolk	BSmart	Little Snoring	50	16.ix.2022	Coal Tit	*Periparus ater*	Denise Lamsdell
H121	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill	60	4.ix.2022			Jonathan Jones
H122	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill	60	4.ix.2022			Jonathan Jones
H123	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Varagill	60	4.ix.2022			Jonathan Jones
H124	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill	60	4.ix.2022			Jonathan Jones
H125	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill	60	8.ix.2022	Goldcrest	*Regulus regulus*	Jonathan Jones
H126	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	15.ix.2022	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H127	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	15.ix.2022	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H128	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	15.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H129	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	16.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H130	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Portree	40	17.ix.2022	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H131	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	17.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H132	O.fringillina	UNITED KINGDOM	♀	Skye	damaged	Portree	40	17.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H133	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	18.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H134	O.fringillina	UNITED KINGDOM	♂	Skye	ASmart	Varagill	60	19.ix.2022	Long-tailed Tit	*Aegithalos caudatus*	Jonathan Jones
H135	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Edinbane	5	24.ix.2022	Great Tit	*Parus major*	Jonathan Jones

H136	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Portree	40	24.ix.2022	Siskin	*Spinus spinus*	Jonathan Jones
H137	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill	60	8.x.2022	Goldcrest	*Regulus regulus*	Jonathan Jones
H139	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Varagill	60	8.x.2022	Goldcrest	*Regulus regulus*	Jonathan Jones
H140	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Varagill	60	8.x.2022	Goldcrest	*Regulus regulus*	Jonathan Jones
7385	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	BSmart	Bancyffordd	205				A. Turner
7400A	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	ASmart	Bancyffordd	205	18.vii.2022	Dunnock	*Prunella modularis*	A. Turner
7400B	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	BSmart	Bancyffordd	205	18.vii.2022	Dunnock	*Prunella modularis*	A. Turner
H841	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	Hutson	Bancyffordd	205	22.ix.2022	Greenfinch	*Chloris chloris*	A. Turner
H645	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire		Bancyffordd	205	18.vii.2022	Dunnock	*Prunella modularis*	A. Turner
H650	O.fringillina	UNITED KINGDOM	♀	Carmarthenshire	ASmart	Bancyffordd	205	22.vii.2022	Wren	*Troglodytes troglodytes*	A. Turner
H651	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	ASmart	Bancyffordd	205	22.vii.2022			A. Turner
H652	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	BSmart	Bancyffordd	205	22.vii.2022			A. Turner
H660	O.fringillina	UNITED KINGDOM	♂	Carmarthenshire	BSmart	Bancyffordd	205	26.viii.2022	Robin	*Erithacus rubecula*	A. Turner
22NW02	O.fringillina	UNITED KINGDOM	♀	Devon	Hutson	Slapton Ley	4	3.ix.2022	Reed Warbler	*Acrocephalus scirpaceus*	Nik Ward
22NW03	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Slapton Ley	4	23.vii.2022	Reed Warbler	*Acrocephalus scirpaceus*	Nik Ward
22NW04	O.fringillina	UNITED KINGDOM		Devon	BSmart	Slapton Ley	4	16.vii.2022	Whitethroat	*Curruca communis*	Nik Ward
1581	O.fringillina	UNITED KINGDOM	♀	Isle of Wight	damaged	Bembridge	16	3.x.2022	Goldfinch	*Carduelis carduelis*	Isle of Wight Ringing Group
1888	O.fringillina	UNITED KINGDOM	♀	Isle of Wight	damaged	Bembridge	16	7.x.2022	Goldfinch	*Carduelis carduelis*	Isle of Wight Ringing Group
1885	O.fringillina	UNITED KINGDOM	♀	Isle of Wight	BSmart	Bembridge	16	27.x.2022	Goldfinch	*Carduelis carduelis*	Isle of Wight Ringing Group
7122	O.fringillina	UNITED KINGDOM	♀	Shropshire		Brownheath	90	18.ix.2022	Reed Bunting	*Emberiza schoeniclus*	Martin George
4323	O.fringillina	UNITED KINGDOM	♂	Surrey	ASmart	Leith Hill, Duke's Warren	258	1.viii.2022	Robin	*Erithacus rubecula*	Paul Stevenson
1449	O.fringillina	UNITED KINGDOM	♀	Pembrokeshire	ASmart	Skokholm Island	35	17.vi.2022	Wheatear	*Oenanthe oenanthe*	Skokholm Bird Observatory
1451	O.fringillina	UNITED KINGDOM	♀	Pembrokeshire	ASmart	Skokholm Island	35	12.vii.2022	Sedge Warbler	*Acrocephalus schoenobaenus*	Skokholm Bird Observatory
H311	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	8.x.2022	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
H302	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Bridford	244	22.x.2022	Robin	*Erithacus rubecula*	Samuel Gray
H305	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	14.xi.2022	Blue Tit	*Cyanistes caeruleus*	Samuel Gray
4958	O.fringillina	UNITED KINGDOM	♀	Rutland	BSmart	Rutland Water Nature Reserve	85	13.vii.2022	Goldcrest	*Regulus regulus*	Luke Nelson
B	O.fringillina	UNITED KINGDOM	♂	Rutland	BSmart	Rutland Water Nature Reserve	85	25.viii.2022	Blackcap	*Sylvia atricapilla*	Luke Nelson
A	O.fringillina	UNITED KINGDOM		Rutland	ASmart	Rutland Water Nature Reserve	84	26.viii.2022	Sedge Warbler	*Acrocephalus schoenobaenus*	Luke Nelson
4128	O.fringillina	UNITED KINGDOM	♂	Pembrokeshire	ASmart	Teifi	0	31.viii.2022	Goldcrest	*Regulus regulus*	Wendy James
4129	O.fringillina	UNITED KINGDOM	♂	Pembrokeshire	Hutson	Teifi Marshes, Pentood Marsh	0	3.x.2022	Blue Tit	*Cyanistes caeruleus*	Wendy James
RP01	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Exeter, Marsh Green	70	5.xii.2022	Blue Tit	*Cyanistes caeruleus*	Robin Pearson
3103	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Portishead, Gordano Valley	7	15.ix.2022	Wren	*Troglodytes troglodytes*	Gordano Valley RG
2115	O.fringillina	UNITED KINGDOM	♂	Gwynedd	Hutson	Rhostryfan	150	17.vii.2022	Willow Warbler	*Phylloscopus trochilus*	Adrienne Stratford
2116	O.fringillina	UNITED KINGDOM	♂	Gwynedd	Hutson	Rhostryfan	150	21.vii.2022	Robin	*Erithacus rubecula*	Adrienne Stratford
2117	O.fringillina	UNITED KINGDOM	♀	Gwynedd	Hutson	Rhostryfan	150	27.vii.2022	Whitethroat	*Curruca communis*	Adrienne Stratford

2120	O.fringillina	UNITED KINGDOM	♂	Gwynedd	Hutson	Rhostryfan	150	5.viii.2022	Goldcrest	*Regulus regulus*	Adrienne Stratford
H802	O.fringillina	UNITED KINGDOM	♀	Gwynedd	Hutson	Rhostryfan	150	25.viii.2002	Blackcap	*Sylvia atricapilla*	Adrienne Stratford
H804	O.fringillina	UNITED KINGDOM	♂	Gwynedd	Hutson	Rhostryfan	150	9.ix.2022	Chiffchaff	*Phylloscopus collybita*	Adrienne Stratford
H805	O.fringillina	UNITED KINGDOM	♀	Gwynedd	Hutson	Rhostryfan	150	14.ix.2022	Meadow Pipit	*Anthus pratensis*	Adrienne Stratford
H806	O.fringillina	UNITED KINGDOM	♀	Gwynedd	damaged	Rhostryfan	150	8.x.2022	Treecreeper	*Certhia familiaris*	Adrienne Stratford
2266	O.fringillina	UNITED KINGDOM	♂	Norfolk	BSmart	Holme, Holme, Holme Bird Observatory	2	14.vi.2022	Whitethroat	*Curruca communis*	Norfolk Ornithologists' Association
2265	O.fringillina	UNITED KINGDOM	♀	Norfolk	Hutson	Holme, Holme, Holme Bird Observatory	2	23.vii.2022	Whitethroat	*Curruca communis*	Norfolk Ornithologists' Association
2267	O.fringillina	UNITED KINGDOM		Norfolk	damaged	Holme, Holme, Holme Bird Observatory	2	29.ix.2022	Blue Tit	*Cyanistes caeruleus*	Norfolk Ornithologists' Association
FF194	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	7.vii.2023	House Sparrow	*Passer domesticus*	Denise Wawman
FF213	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	15.vii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF215	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	18.vii.2023			Denise Wawman
FF216	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	18.vii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF217	O.fringillina	UNITED KINGDOM	♀	Somerset	Hutson	Minehead, Bratton	64	18.vii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF218	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	18.vii.2023	House Sparrow	*Passer domesticus*	Denise Wawman
FF225	O.fringillina	UNITED KINGDOM	♂	Somerset	ASmart	Minehead, Bratton	64	18.vii.2023	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
FF232	O.fringillina	UNITED KINGDOM	♂	Somerset	ASmart	Minehead, Bratton	64	20.vii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF233	O.fringillina	UNITED KINGDOM	♂	Somerset	Hutson	Minehead, Bratton	64	20.vii.2023	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
H306	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Bridford	244	23.vi.2023	Blackcap	*Sylvia atricapilla*	Samuel Gray
FF240	O.fringillina	UNITED KINGDOM	♀	Somerset		Minehead, Bratton	64	25.vii.2023	Robin	*Erithacus rubecula*	Denise Wawman
7976	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	14.vii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
7938	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	14.vii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H147A	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	15.vii.2023	Dunnock	*Prunella modularis*	Hugh Insley
H147B	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	15.vii.2023	Dunnock	*Prunella modularis*	Hugh Insley
H154	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	15.vii.2023	Dunnock	*Prunella modularis*	Hugh Insley
H152	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	15.vii.2023	Dunnock	*Prunella modularis*	Hugh Insley
H155	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	15.vii.2023	Siskin	*Spinus spinus*	Hugh Insley
H151	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	17.vii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H148	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	19.vii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H149	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	19.vii.2023	Robin	*Erithacus rubecula*	Hugh Insley
H159	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	19.vii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
H142	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	19.vii.2023	Song Thrush	*Turdus philomelos*	Hugh Insley
H157	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	20.vii.2023	Siskin	*Spinus spinus*	Hugh Insley
X395	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	21.vii.2023	Blackcap	*Sylvia atricapilla*	Hugh Insley
FF421	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	26.vii.2023	Dunnock	*Prunella modularis*	Denise Wawman
A50	O.fringillina	UNITED KINGDOM	♀	Norfolk	ASmart	Anmer, Crow Hill Cottage	70	21.vii.2023	Tree Sparrow	*Passer montanus*	Denise Lamsdell
FF242	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	27.vii.2023	Blue Tit	*Cyanistes caeruleus*	Denise Wawman

X278	O.fringillina	UNITED KINGDOM	♂	Northamptonshire	BSmart	Stanford Reservoir	113	26.vii.2023	Chiffchaff	*Phylloscopus collybita*	Stanford Ringing Group
X280	O.fringillina	UNITED KINGDOM	♂	Northamptonshire	ASmart	Corby	90	28.vii.2023	Dunnock	*Prunella modularis*	Adam Homer
FF246	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	9.viii.2023	Siskin	*Spinus spinus*	Denise Wawman
FF247	O.fringillina	UNITED KINGDOM	♂	Somerset	ASmart	Minehead, Bratton	64	11.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF248	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	11.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF249	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	11.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF250	O.fringillina	UNITED KINGDOM	♂	Somerset	ASmart	Minehead, Bratton	64	11.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF251	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	16.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF252	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	16.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF253	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	16.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF254	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	16.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF256	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	16.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
X467	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	11	31.vii.2023	Blue Tit	*Cyanistes caeruleus*	Hugh Insley
X462	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	31.vii.2023	Robin	*Erithacus rubecula*	Hugh Insley
X461	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Inverness, Drummond	29	31.vii.2023	Dunnock	*Prunella modularis*	Hugh Insley
H146	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	1.viii.2023	Goldcrest	*Regulus regulus*	Hugh Insley
X464	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	2.viii.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X468	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	2.viii.2023	Siskin	*Spinus spinus*	Hugh Insley
H158	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	3.viii.2023	Dunnock	*Prunella modularis*	Hugh Insley
X459	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	3.viii.2023	Blackcap	*Sylvia atricapilla*	Hugh Insley
X455	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Inverness, Drummond	29	5.viii.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X456	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	5.viii.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X470	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	5.viii.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X458	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Inverness, Drummond	29	5.viii.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X453	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	BSmart	Carse of Ardersier	11	7.viii.2023	Goldcrest	*Regulus regulus*	Hugh Insley
X460	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	damaged	Carse of Ardersier	11	7.viii.2023	Willow Warbler	*Phylloscopus trochilus*	Hugh Insley
X451	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Carse of Ardersier	11	10.viii.2023	Blackbird	*Turdus merula*	Hugh Insley
X452	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	Hutson	Carse of Ardersier	11	13.viii.2023	Goldcrest	*Regulus regulus*	Hugh Insley
X454	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	13.viii.2023	Robin	*Erithacus rubecula*	Hugh Insley
X465	O.fringillina	UNITED KINGDOM	♂	Inverness-shire	ASmart	Carse of Ardersier	11	13.viii.2023	Robin	*Erithacus rubecula*	Hugh Insley
X466	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	damaged	Carse of Ardersier	11	14.viii.2023	Goldcrest	*Regulus regulus*	Hugh Insley
X706	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	ASmart	Inverness, Drummond	29	16.viii.2023	Blue Tit	*Cyanistes caeruleus*	Hugh Insley
H255	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	19.vii.2023	Blue Tit	*Cyanistes caeruleus*	Jonathan Jones
H284	O.fringillina	UNITED KINGDOM	♀	Skye		Portree	40	3.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H286	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	25.vii.2023	House Sparrow	*Passer domesticus*	Jonathan Jones
H294	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree	40	14.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones

H295	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	15.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H297	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree	40	15.viii.2023	Blue Tit	*Cyanistes caeruleus*	Jonathan Jones
H299	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill	60	17.viii.2023	Robin	*Erithacus rubecula*	Jonathan Jones
H300	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill	60	17.viii.2023	Robin	*Erithacus rubecula*	Jonathan Jones
FF257	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	20.viii.2023	House Sparrow	*Passer domesticus*	Denise Wawman
FF258	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	20.viii.2023	Goldfinch	*Carduelis carduelis*	Denise Wawman
FF260	O.fringillina	UNITED KINGDOM	♀	Somerset	Hutson	Withiel Florey	265	21.viii.2023	Great Tit	*Parus major*	Denise Wawman
FF265	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	25.viii.2023			Denise Wawman
FF261	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	25.viii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF262	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	25.viii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF263	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	25.viii.2023	Dunnock	*Prunella modularis*	Denise Wawman
FF264	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	25.viii.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF266	O.fringillina	UNITED KINGDOM	♂	Somerset	BSmart	Minehead, Bratton	64	25.viii.2023			Denise Wawman
X362	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	21.vii.2023	Robin	*Erithacus rubecula*	Samuel Gray
X369	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	21.vii.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X365	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Bridford	244	25.vii.2023	Whitethroat	*Curruca communis*	Samuel Gray
X361	O.fringillina	UNITED KINGDOM	♀	Devon	Hutson	Bridford	244	25.vii.2023	Blackcap	*Sylvia atricapilla*	Samuel Gray
X367	O.fringillina	UNITED KINGDOM	♀	Devon	Hutson	Bridford	244	26.vii.2023	Linnet	*Linaria cannabina*	Samuel Gray
X368	O.fringillina	UNITED KINGDOM	♂	Devon	Hutson	Bridford	244	28.vii.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X355	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	8.viii.2023	Wren	*Troglodytes troglodytes*	Samuel Gray
X352	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	10.viii.2023	Robin	*Erithacus rubecula*	Samuel Gray
X360	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	15.viii.2023	Willow Warbler	*Phylloscopus trochilus*	Samuel Gray
X358	O.fringillina	UNITED KINGDOM	♀	Devon	damaged	Bridford	244	15.viii.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X357	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	22.viii.2023	Robin	*Erithacus rubecula*	Samuel Gray
FF268	O.fringillina	UNITED KINGDOM	♀	Somerset	damaged	Minehead, Bratton	64	7.ix.2023	Blue Tit	*Cyanistes caeruleus*	Denise Wawman
X571	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Ilfracombe, West Down, Buttercombe Barton	160	8.viii.2023	Goldfinch	*Carduelis carduelis*	Chris Dee
X573	O.fringillina	UNITED KINGDOM	♀	Devon	damaged	Ilfracombe, West Down, Buttercombe Barton	160	1.ix.2023	Goldfinch	*Carduelis carduelis*	Chris Dee
7595	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Ilfracombe, West Down, Buttercombe Barton	160	21.vii.2023			Chris Dee
7598	O.fringillina	UNITED KINGDOM	♀	Devon	Hutson	Ilfracombe, West Down, Buttercombe Barton	160	29.vii.2023	Dunnock	*Prunella modularis*	Chris Dee
3286	O.fringillina	UNITED KINGDOM	♀	Kirkcudbrightshire	BSmart	Mossdale	55	25.vii.2023			Tony Gibson
FF269	O.fringillina	UNITED KINGDOM	♀	Somerset	BSmart	Minehead, Bratton	64	21.ix.2023	Robin	*Erithacus rubecula*	Denise Wawman
FF270	O.fringillina	UNITED KINGDOM	♀	Somerset	ASmart	Minehead, Bratton	64	21.ix.2023	Robin	*Erithacus rubecula*	Denise Wawman
H274	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	29.viii.2023	Coal Tit	*Periparus ater*	Hugh Insley
H268	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	damaged	Carse of Ardersier	11	31.viii.2023	Sparrowhawk	*Accipiter nisus*	Hugh Insley
X601	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	15.ix.2023	Goldcrest	*Regulus regulus*	Hugh Insley
H541	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill	60	17.viii.2023	Goldcrest	*Regulus regulus*	Jonathan Jones

H542	O.fringillina	UNITED KINGDOM	♀	Skye	Hutson/BSmart	Varagill		60	17.viii.2023	Goldcrest	*Regulus regulus*	Jonathan Jones
H543	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill		60	17.viii.2023			Jonathan Jones
H544	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Varagill		60	17.viii.2023	Robin	*Erithacus rubecula*	Jonathan Jones
H545	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill		60	17.viii.2023			Jonathan Jones
H546	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Varagill		60	17.viii.2023	Goldcrest	*Regulus regulus*	Jonathan Jones
H549	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Portree		40	24.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H550	O.fringillina	UNITED KINGDOM	♀	Ross and Cromarty		Avoch		115	20.viii.2023			Jonathan Jones
H551	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	24.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H552	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree		40	24.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H553	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	24.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H554	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree		40	24.viii.2023	House Sparrow	*Passer domesticus*	Jonathan Jones
H555	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree		40	24.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H556	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Varagill		60	27.viii.2023	Goldcrest	*Regulus regulus*	Jonathan Jones
H557	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill		60	27.viii.2023	Great Tit	*Parus major*	Jonathan Jones
H558	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Varagill		60	27.viii.2023	Coal Tit	*Periparus ater*	Jonathan Jones
H560	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	27.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H981	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	28.viii.2023	Dunnock	*Prunella modularis*	Jonathan Jones
H982	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	28.viii.2023	Dunnock	*Prunella modularis*	Jonathan Jones
H983	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree		40	29.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H984	O.fringillina	UNITED KINGDOM	♂	Skye	Hutson	Portree		40	30.viii.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H985	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree		40	30.viii.2023			Jonathan Jones
H986	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	5.ix.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H987	O.fringillina	UNITED KINGDOM	♀	Skye	BSmart	Portree		40	5.ix.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
H988	O.fringillina	UNITED KINGDOM	♀	Skye	ASmart	Portree		40	7.ix.2023	Chaffinch	*Fringilla coelebs*	Jonathan Jones
2419	O.fringillina	UNITED KINGDOM	♀	Cheshire	ASmart	Hoylake		6	21.vi.2023	Robin	*Erithacus rubecula*	Jane Turner
X037	O.fringillina	UNITED KINGDOM	♀	Cheshire	BSmart	Hoylake		6	26.vii.2023	Goldfinch	*Carduelis carduelis*	Jane Turner
X044	O.fringillina	UNITED KINGDOM	♀	Cheshire	ASmart	Hoylake		6	26.vii.2023	Robin	*Erithacus rubecula*	Jane Turner
X045	O.fringillina	UNITED KINGDOM	♀	Cheshire	Hutson/BSmart	Hoylake		6	1.ix.2023	Robin	*Erithacus rubecula*	Jane Turner
5257	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham		10	16.viii.2023	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
5250	O.fringillina	UNITED KINGDOM	♂	East Sussex	BSmart	Icklesham		10	..2023			Rye Bay Ringing Group
X783	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham		10	19.viii.2023	Whitethroat	*Curruca communis*	Rye Bay Ringing Group
X800	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham		10	7.ix.2023	Reed Warbler	*Acrocephalus scirpaceus*	Rye Bay Ringing Group
X791	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham		10	14.ix.2023			Rye Bay Ringing Group
X795	O.fringillina	UNITED KINGDOM	♀	East Sussex	ASmart	Icklesham		10	17.ix.2023	Cetti's Warbler	*Cettia cetti*	Rye Bay Ringing Group
X780	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Icklesham		10	28.ix.2023	Chiffchaff	*Phylloscopus collybita*	Rye Bay Ringing Group
X764	O.fringillina	UNITED KINGDOM	♀	East Sussex	ASmart	Icklesham		10	19.x.2023	Goldfinch	*Carduelis carduelis*	Rye Bay Ringing Group

X532	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	22.viii.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X543	O.fringillina	UNITED KINGDOM	♀	Devon	ASmart	Bridford	244	23.viii.2023	Willow Warbler	*Phylloscopus trochilus*	Samuel Gray
X541	O.fringillina	UNITED KINGDOM	♂	Devon	Hutson	Bridford	244	23.viii.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X533	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	24.viii.2023	Goldcrest	*Regulus regulus*	Samuel Gray
X526	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	12.ix.2023	Goldcrest	*Regulus regulus*	Samuel Gray
X550	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	12.ix.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X548	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	13.ix.2023	Blackcap	*Sylvia atricapilla*	Samuel Gray
X535	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	15.ix.2023	Blackcap	*Sylvia atricapilla*	Samuel Gray
X527	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	15.ix.2023	Coal Tit	*Periparus ater*	Samuel Gray
X536	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Bridford	244	25.ix.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X538	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Bridford	244	1.x.2023	Chiffchaff	*Phylloscopus collybita*	Samuel Gray
X545	O.fringillina	UNITED KINGDOM	♂	Devon	Hutson	Bridford	244	1.x.2023	Long-tailed Tit	*Aegithalos caudatus*	Samuel Gray
X524	O.fringillina	UNITED KINGDOM	♂	Devon	ASmart	Bridford	244	6.x.2023	Firecrest	*Regulus ignicapilla*	Samuel Gray
701	O.fringillina	UNITED KINGDOM	♀	Norfolk		Little Snoring	55	1.xi.2023	Blue Tit	*Cyanistes caeruleus*	Denise Lamsdell
197	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	damaged	Flamborough	45	28.vii.2023	Whitethroat	*Curruca communis*	Andy Hood
198	O.fringillina	UNITED KINGDOM	♂	East Riding of Yorkshire	ASmart	Flamborough	45	28.vii.2023	Whitethroat	*Curruca communis*	Andy Hood
D05	O.fringillina	UNITED KINGDOM	♂	East Riding of Yorkshire	Hutson	Flamborough	45	15.viii.2023	Robin	*Erithacus rubecula*	Andy Hood
D07	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	BSmart	Flamborough	45	15.viii.2023	Willow Warbler	*Phylloscopus trochilus*	Andy Hood
D08	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	ASmart	Flamborough	45	21.viii.2023	Tree Sparrow	*Passer montanus*	Andy Hood
1464	O.fringillina	UNITED KINGDOM	♂	Pembrokeshire	Hutson	Skokholm Island	30	23.viii.2023	Pied Wagtail	*Motacilla alba*	Skokholm Bird Observatory
551	O.fringillina	UNITED KINGDOM	♀	East Sussex	BSmart	Wivelsfield	40	25.x.2023	Blue Tit	*Cyanistes caeruleus*	Clare Buckle
H275	O.fringillina	UNITED KINGDOM	♀	Inverness-shire	BSmart	Carse of Ardersier	11	26.x.2023	Chaffinch	*Fringilla coelebs*	Hugh Insley
X503	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	ASmart	Bempton Cliffs	92	7.ix.2023	Goldfinch	*Carduelis carduelis*	David Aitken
X519	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	ASmart	Bempton Cliffs	92	7.ix.2023	Goldfinch	*Carduelis carduelis*	David Aitken
X512	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	ASmart	Bempton Cliffs	92	17.ix.2023	Great Tit	*Parus major*	David Aitken
X471	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	ASmart	Stanford Reservoir	113	29.vii.2023	Reed Warbler	*Acrocephalus scirpaceus*	Stanford Ringing Group
X472	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Corby	90	31.vii.2023	Dunnock	*Prunella modularis*	Adam Homer
X475	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Stanford Reservoir	113	12.viii.2023	Whitethroat	*Curruca communis*	Stanford Ringing Group
X481	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Stanford Reservoir	113	20.viii.2023	Willow Warbler	*Phylloscopus trochilus*	Stanford Ringing Group
X482	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Stanford Reservoir	113	25.viii.2023	Whitethroat	*Curruca communis*	Stanford Ringing Group
X483	O.fringillina	UNITED KINGDOM	♂	Northamptonshire	ASmart	Stanford Reservoir	113	26.viii.2023	Reed Warbler	*Acrocephalus scirpaceus*	Stanford Ringing Group
1544	O.fringillina	UNITED KINGDOM	♀	Huntingdonshire	BSmart	Woodwalton Fen	2	31.viii.2023	Sedge Warbler	*Acrocephalus schoenobaenus*	Stanford Ringing Group
X487	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	ASmart	Stanford Reservoir	113	9.ix.2023	Blackcap	*Sylvia atricapilla*	Stanford Ringing Group
X488	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Stanford Reservoir	113	9.ix.2023	Blackcap	*Sylvia atricapilla*	Stanford Ringing Group
3664	O.fringillina	UNITED KINGDOM	♀	Suffolk	ASmart	Languard Bird Observatory	0	30.ix.2023	Blue Tit	*Cyanistes caeruleus*	Languard Bird Observatory
7693	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Buckfastleigh, Brook Manor,	100	2.ix.2023	Goldcrest	*Regulus regulus*	Ellie Ness & Robbie Phillips

7466	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Buckfastleigh, Brook Manor,	100	3.ix.2023	Chiffchaff	*Phylloscopus collybita*	Ellie Ness & Robbie Phillips
7470	O.fringillina	UNITED KINGDOM	♀	Devon	BSmart	Buckfastleigh, Brook Manor,	100	30.ix.2023	Blue Tit	*Cyanistes caeruleus*	Ellie Ness & Robbie Phillips
7472	O.fringillina	UNITED KINGDOM	♂	Devon	BSmart	Buckfastleigh, Brook Manor,	100	1.x.2023	Goldcrest	*Regulus regulus*	Ellie Ness & Robbie Phillips
7479	O.fringillina	UNITED KINGDOM	♀	Devon	Hutson	Buckfastleigh, Brook Manor,	100	1.x.2023	Goldcrest	*Regulus regulus*	Ellie Ness & Robbie Phillips
H049	O.fringillina	UNITED KINGDOM	♀	Hertfordshire		Benington	105	8.x.2023	Yellowhammer	*Emberiza citrinella*	Paul Roper
X057	O.fringillina	UNITED KINGDOM	♀	Argyll	BSmart	Glen Euchar	104	10.ix.2023	Robin	*Erithacus rubecula*	Rob Lightfoot
2010	O.fringillina	UNITED KINGDOM	♀	Angus		Montrose, Wellington Park	8	5.x.2023	Goldfinch	*Carduelis carduelis*	Ben Herschell
X346	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	Hutson	Stanford Reservoir	113	16.ix.2023	Blackcap	*Sylvia atricapilla*	Stanford Ringing Group
H171	O.fringillina	UNITED KINGDOM	♀	Cumbria	ASmart	Kirkbride	13	10.vii.2023	Blackbird	*Turdus merula*	Frank Mawby
2124	O.fringillina	UNITED KINGDOM	♀	Stirlingshire	BSmart	Dunblane, Kinbuck	98	13.viii.2023	Chaffinch	*Fringilla coelebs*	Liam Reid
H202	O.fringillina	UNITED KINGDOM	♀	Northamptonshire	BSmart	Pitsford Reservoir	88	31.viii.2023	Whitethroat	*Curruca communis*	Northants Ringing Group
H689	O.fringillina	UNITED KINGDOM	♂	East Riding of Yorkshire	Hutson	Flamborough, South Landing	34	17.viii.2023	Tree Sparrow	*Passer montanus*	Jo Hood
H682	O.fringillina	UNITED KINGDOM	♀	East Riding of Yorkshire	BSmart	Flamborough, South Landing	34	27.viii.2023	Lesser Redpoll	*Acanthis cabaret*	Jo Hood
GRIEV1	O.fringillina	UNITED KINGDOM	♂	Lanarkshire	BSmart	Biggar, Symington	220	.ix.2023	Dunnock	*Prunella modularis*	David Grieve
1110A	O.fringillina	UNITED KINGDOM	♀	Lincolnshire	ASmart	Nocton Fen, Wasps Nest	10	31.vii.2023	Linnet	*Linaria cannabina*	Carl Soulsbury
1110B	O.fringillina	UNITED KINGDOM	♀	Lincolnshire	BSmart	Nocton Fen, Wasps Nest	10	31.vii.2023	Linnet	*Linaria cannabina*	Carl Soulsbury
H812	O.fringillina	UNITED KINGDOM	♂	Gwynedd	Hutson	Rhostryfan	150	29.vii.2023	Chiffchaff	*Phylloscopus collybita*	Adrienne Stratford
H813	O.fringillina	UNITED KINGDOM	♀	Gwynedd	BSmart	Rhostryfan	150	7.viii.2023	Blackcap	*Sylvia atricapilla*	Adrienne Stratford
4860	O.fringillina	UNITED KINGDOM	♀	Powys	BSmart	Brecon, Llangorse Lake	160	28.vii.2023	Reed Warbler	*Acrocephalus scirpaceus*	Llangorse Ringing Group
4846	O.fringillina	UNITED KINGDOM	♀	Powys	ASmart	Brecon, Llangorse Lake	160	27.viii.2023	Spotted Flycatcher	*Muscicapa striata*	Llangorse Ringing Group
4848	O.fringillina	UNITED KINGDOM	♀	Powys	BSmart	Brecon, Llangorse Lake	160	14.ix.2023	Blackcap	*Sylvia atricapilla*	Llangorse Ringing Group
4849	O.fringillina	UNITED KINGDOM	♀	Powys	BSmart	Brecon, Llangorse Lake	160	6.x.2023	Blue Tit	*Cyanistes caeruleus*	Llangorse Ringing Group
4850	O.fringillina	UNITED KINGDOM	♀	Powys	BSmart	Brecon, Llangorse Lake	160	6.x.2023	Goldcrest	*Regulus regulus*	Llangorse Ringing Group
5129	O.fringillina	UNITED KINGDOM	♀	Suffolk	damaged	Brandon	25	2.xii.2022	Blue Tit	*Cyanistes caeruleus*	Dr Greg Conway
5138	O.fringillina	UNITED KINGDOM	♀	Suffolk	damaged	Brandon	25	20.xi.2022	Blue Tit	*Cyanistes caeruleus*	Dr Greg Conway
H018	O.fringillina	UNITED KINGDOM	♀	Suffolk	ASmart	Brandon	25	5.viii.2023	Blue Tit	*Cyanistes caeruleus*	Dr Greg Conway
SB26	O.fringillina	IRELAND	♂	Cork	BSmart	Clonakilty, Clogheen Marsh	5	25.vii.2023	Wren	*Troglodytes troglodytes*	Sam Bayley
H989	O.fringillina	UNITED KINGDOM	♂	Skye	BSmart	Portree	40	17.x.2023			Jonathan Jones
WWFF01	O.fringillina	UNITED KINGDOM	♀	Berkshire	ASmart	Oxford, Wytham Woods		15.i.2024	Great Tit	*Parus major*	Kyu Min Huh & Keith Mc Mahon

Table S2. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of two morphotypes of *Ornithomya fringillina*

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Fly wing	-0.19688	0.290685	-0.61492	-0.13575	0.026845	-0.61596	0.313605	-0.04136
Scutellar bristles	0.038708	-0.17843	-0.25172	-0.1607	**0.899187**	0.106544	-0.23971	0.010969
Fly sex	0.318961	**-0.55652**	-0.18567	0.295966	0.044378	0.102641	**0.672535**	-0.04092
Latitude	**0.633488**	0.273895	0.014031	-0.13291	0.019847	-0.08264	0.042753	**0.704812**
Longitude	-0.4249	0.272585	-0.35607	0.276818	-0.01672	**0.602872**	0.140257	0.397913
Altitude	-0.45929	-0.55462	0.140913	-0.05817	-0.05272	-0.32878	-0.0875	**0.582814**
Julian Day	-0.25476	0.290205	**0.590708**	-0.1775	0.359869	-0.02122	**0.583053**	0.022985
Host mass	-0.01742	-0.18112	-0.1681	**-0.85963**	-0.23625	0.346234	0.150925	-0.03463

Figure S1. PCA Scree plot for the two morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.

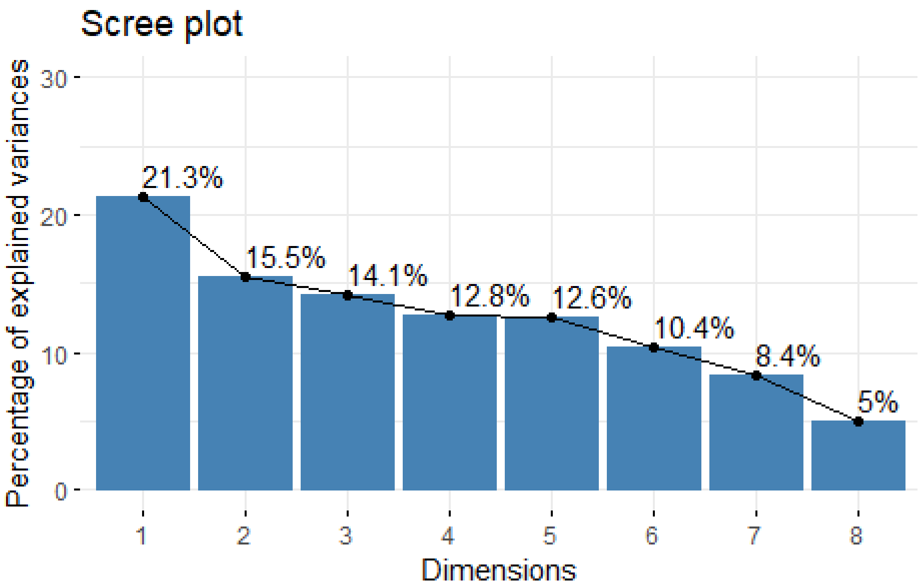
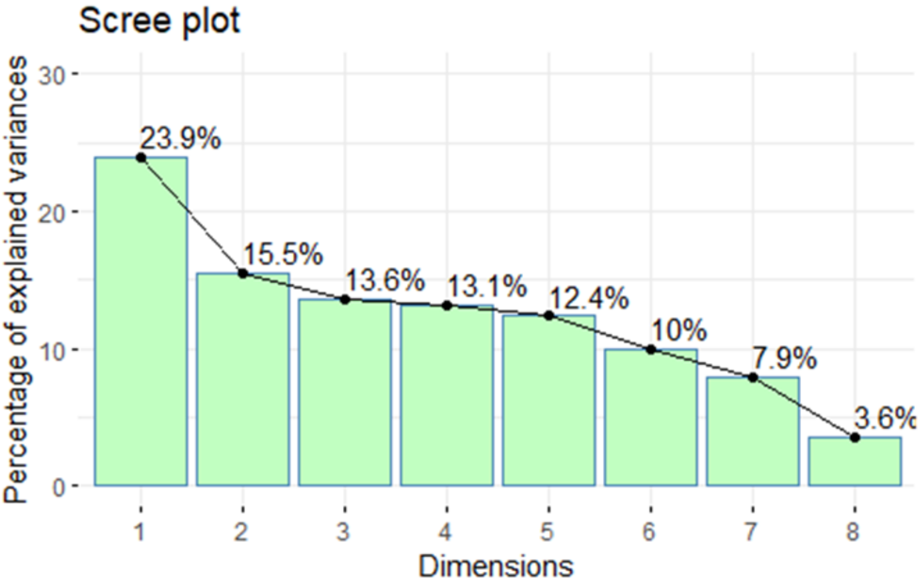


Table S3. Contributions of the variables to the principal components (loadings), with values over 0.5 highlighted in bold typeface, for the analysis of three morphotypes of *Ornithomya fringillina*

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Fly wing	-0.18512	**0.594653**	-0.00992	0.204191	0.224839	**0.663969**	-0.28091	-0.00298
Scutellar bristles	0.048662	-0.0316	-0.27951	**0.836367**	0.290779	-0.18391	0.316687	0.018134
Latitude	**0.628791**	0.145387	-0.2264	-0.09226	0.043162	0.048709	-0.00835	**-0.7207**
Longitude	-0.44598	0.303067	0.197818	-0.04102	0.322081	**-0.58989**	-0.23355	-0.40273
Altitude	-0.46519	-0.45001	0.129226	0.210677	-0.29056	0.340544	0.080832	**-0.55953**
Julian Day	-0.1992	-0.20506	**-0.79322**	-0.05744	-0.05949	-0.06804	**-0.52542**	0.03929
Host Mass	0.117181	0.329418	0.122548	0.369097	**-0.77106**	-0.23099	-0.2793	0.024391
Fly sex	0.315072	-0.42348	0.412883	0.254336	0.277111	0.032032	**-0.63685**	0.053343

Figure S2. PCA Scree plot for the three morphotypes analysis showing the percentage contribution of the eigenvalue of each principal component.



SUPPORTING INFORMATION

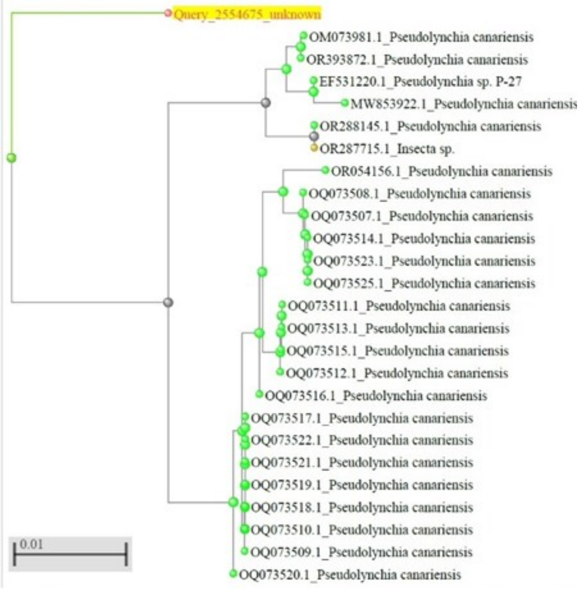
CHAPTER 2.2

Figure 1. Phylogeny for the genus Pseudolynchia produced used GenBank Tree Viewer

Supporting Information Chapter 2.2

Figure S1. Phylogeny for genus Pseudolynchia produced from all the specimens in the GenBank database plus the specimen of *Pseudolynchia garzettae* (Query_2554675_unknown highlighted in yellow) produced using GenBank Tree Viewer 1.20.

Link to tree produced in GenBank:
https://www.ncbi.nlm.nih.gov/projects/treeview/tv.html?edgehighlight=overview&generateoverview=with-image&renderer=rect&renderscale=false&autoaspectratio=true&pctmaxzoom=0&returntreedict=true&nodereturndistthreshold=3&margins=3&maxdim=1000&appname=ncbiblast&btc_id=NCID_1_29646647_130.14.18.128_9147_1735755522_296332365_0MetA0__S_NC_PhyloTree&fontface=Times-Roman&fontsize=12&labelspacing=1.2&horizspacing=5.8&nodesize=4&linewidth=1&rotatedlabels=false&collapsednodeIDs=&selectednodeIDs=1&nodereturnmode=full&distmode=true&renderclientoverlap=client&clientviewportx=0&clientviewporty=0&sortreturnednodes=true&postype=global&clientviewportwidth=1035&clientviewportheight=373&width=1036&height=373&tilewidth=518&tileheight=373&silent_urls=&upperScaleMark=false&totalx=0&totaly=0&vertzoom=false&user_provided_vertzoom=true&featnames=id,organism,leaf-count&clickableLabels=true&maxwidth=3106&maxheight=1120&minwidth=1035&minheight=373&pctoptimalzoom=3&numtilesx=2&numtilesy=1&horisontalVieports=2&verticalVieports=1&panx=50&pany=50&centerpointx=518&centerpointy=184&toolbar=maszopthuref&nodeaction=bsrc&use_distance=true



SUPPORTING INFORMATION

CHAPTER 3.1

Additional references and acknowledgements

Supporting information Chapter 3.1

Additional references and acknowledgements not included in the main text

Original species descriptions

Ornithomya biloba (Dufour, 1827)

Pseudolynchia canariensis (Marquart, 1839)

Pseudolynchia garzettae (Rondani, 1879)

Sources of information checked for species records

Publications

Early systematic work by entomologists and museum curators, who examined large numbers of louse flies, which had been collected over previous decades (Thompson, 1953, 1954, 1955; Bequaert, 1954; Hill, 1962; Hutson, 1984).

Small more intense studies of single species of flies on suitable hosts, for example, Crataerina (Stenepteryx) hirundinis on Hirundines (Summers, 1975).

Grey literature, that is, literature which has not been through peer review, including bird observatory reports (Williamson, 1950, 1952, 1954; Butterfield, 1951; Edwards, 1951, 1952; Thompson, 1952, 1964; Stansfield, 1954; Corbet, 1955; Ennion, 1955; G. Stansfield, 1955; Geoffrey Stansfield, 1955; Thompson and Beaumont, 1968) other bird reports (Denton, 1974, 1975, 1976, 1977, 1978, 1979, 1980) and reports of Diptera (Waterson, 1910; Ash, 1952, 1955; Ash and Monk, 1959; Beaumont, 1965; Cutts, 1971; Sellers and Redgate, 1992; Emley, 1992; Hancock, 1995, 1996; Johnson, 2020; Chandler, 2021b, 2021a).

Online recording schemes and record collections

GBIF Global Biodiversity Information Facility https://www.gbif.org (last accessed 06-05-2023)

NBN atlas https://nbnatlas.org (last accessed 06-05-2023)

Local Environmental Records Centres Records

Requests for copies of all records of Hippoboscidae were sent to all Local Environmental Records Centres (LERC) in the United Kingdom, with at least two follow up emails sent if there was no response. Some centres had no relevant data but records of Hippoboscidae were supplied by:

The Environmental Records Centre for Cornwall and the Isles of Scilly, Devon Biological Records Centre, Somerset Environmental Records Centre, Wiltshire and Swindon Biological Records Centre, Dorset Environmental Records Centre, Isle of Wight Natural History and Archaeological Society, Hampshire Biodiversity Information Centre, Sussex Biodiversity Record Centre, Surrey Biodiversity Information Centre, Essex Field Club, Essex Wildlife Trust Biological Records Centre, Thames Valley Environmental Records Centre, Buckinghamshire and Milton Keynes Environmental Records Centre, Norfolk

Biodiversity Information Service, Cambridgeshire and Peterborough Environmental Records Centre, Gloucestershire Centre for Environmental Records, South East Wales Biodiversity Records Centre, Herefordshire Biological Records Centre, Warwickshire Biological Records Centre, Staffordshire Ecological Record, Biodiversity Information Service for Powys and Brecon Beacons Beacons National Park, West Wales Biodiversity Information Centre, Cofnod (North Wales Environmental Information), Greater Lincolnshire Nature Partnership, Leicestershire & Rutland Environmental Records Centre, Nottinghamshire Biological & Geological Records Centre, RECORD LRC, Merseyside Biobank, Greater Manchester Local Environmental Records Centre, Environmental Records Centre for the North East of England, West Yorkshire Ecology, Cumbria Biodiversity Information Centre, South West Scotland Environmental Information Centre, Greenspace Development Service North Lanarkshire Council, The Wildlife Information Centre, Tayshire Biodiversity Records, North East Scotland Biological Records Centre, Argyll Biological Records Centre, Orkney Wildlife Information and Records Centre, Guernsey Biological Records Centre, Jersey Biodiversity Centre

Other sources of records

Glasgow Museum, Liverpool Museum, Perth Museum, The Box Plymouth, John Flynn for supplying Dennis Hill's original records, Tanyptera Project, Dipterists Forum Field Meeting Records, Sorby Invertebrate Group Diptera Recording Scheme, Dave Brice, Norman Cobley, Mike Denton, A.P. Foster, Andrew Grayson, Andrew Halstead, Geoff Hancock, Roger Morris, Malcolm Storey

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Ringing groups (RG): Belvide RG, Borders RG, Clyde RG, East Dales RG, Gordano Valley RG, Gower RG, Isle of Wight RG, Kenfig RG, Llangorse RG, Lundy Field Society, Merseyside RG, Mid-Wales RG, Northants RG, Northern England Raptor Group, Peak District Raptor Monitoring Group, Rye Bay RG, Shropshire RG, Stanford RG, Steyning RG, Watchtree RG.

Bird observatories: Bardsey Bird Observatory, Calf of Man Bird Observatory, Dungeness Bird Observatory, Fair Isle Bird Observatory, Hilbre Bird Observatory, Isle of May Bird

Observatory RG, Landguard Bird Observatory, Norfolk Ornithologists Association, North Ronaldsay Bird Observatory, Portland Bird Observatory, Sandwich Bay Bird Observatory, Skokholm Bird Observatory.

Those who wished to remain anonymous and all those who tried but failed to catch any flies.

With sincere apologies to anyone I have missed off this list.

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SUPPORTING INFORMATION

CHAPTER 3.2

Figure SOM1. Map of sites at which Hippoboscidae were collected for the study

Figure SOM2. Maxent model outputs used to check for random distributions of collection sites

Figure SOM3. Kernal Densities for all flies in the study

Figure SOM4. Boxplot showing altitudes at which different species were collected

Supporting Information Chapter 3.2

Figure SOM1: All sites from which Hippoboscids were collected for the study. UK sites are plotted as white squares at 1km^2 resolution and Irish sites in purple

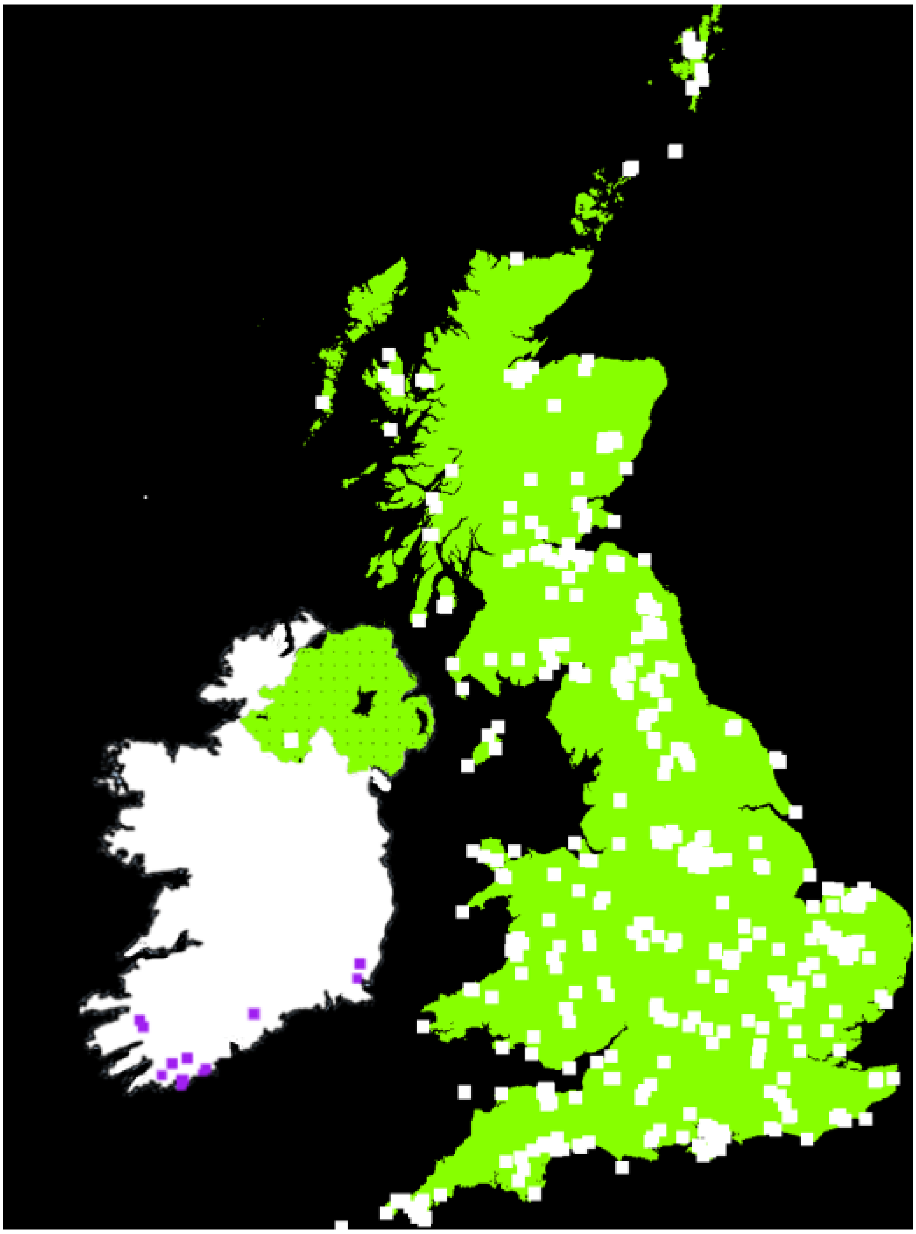

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Figure SOM2: Maps showing the distribution of capture sites for all flies in the study, as Maxent model outputs predicting the likelihood of a Hippoboscid in the project being collected at a site, relative to a) the proportion of urban land-cover in that 1km^2, b) the proportion of protected land-cover and c) the proportions of both urban and protected land-cover. Warmer (redder) colours predict a higher probability that a fly will be found at a site. The areas under the receiver operator curve, and the high proportion of green in these maps indicate that the sites are almost randomly distributed with respect to both urban and protected area land-cover.

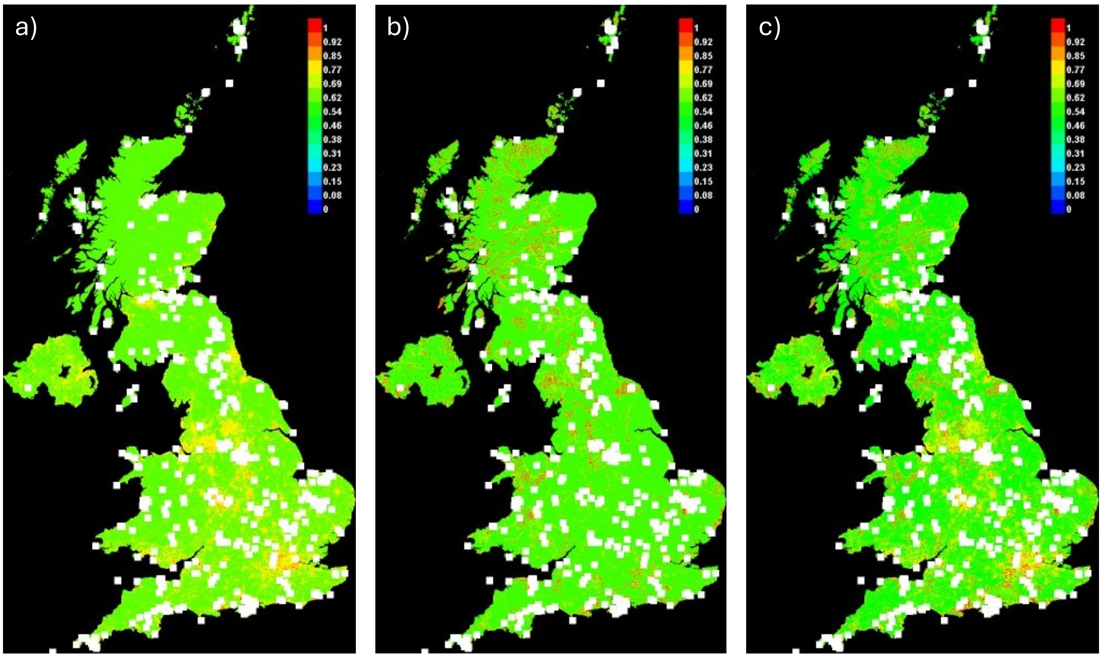


Figure SOM3: Kernel densities for all flies in the study. The kernel densities are plotted plot at 95% predicted probability (dark red), 75% probability and 50% probability of a fly being caught at a given location, during the study, based entirely on latitude, longitude and presence data.

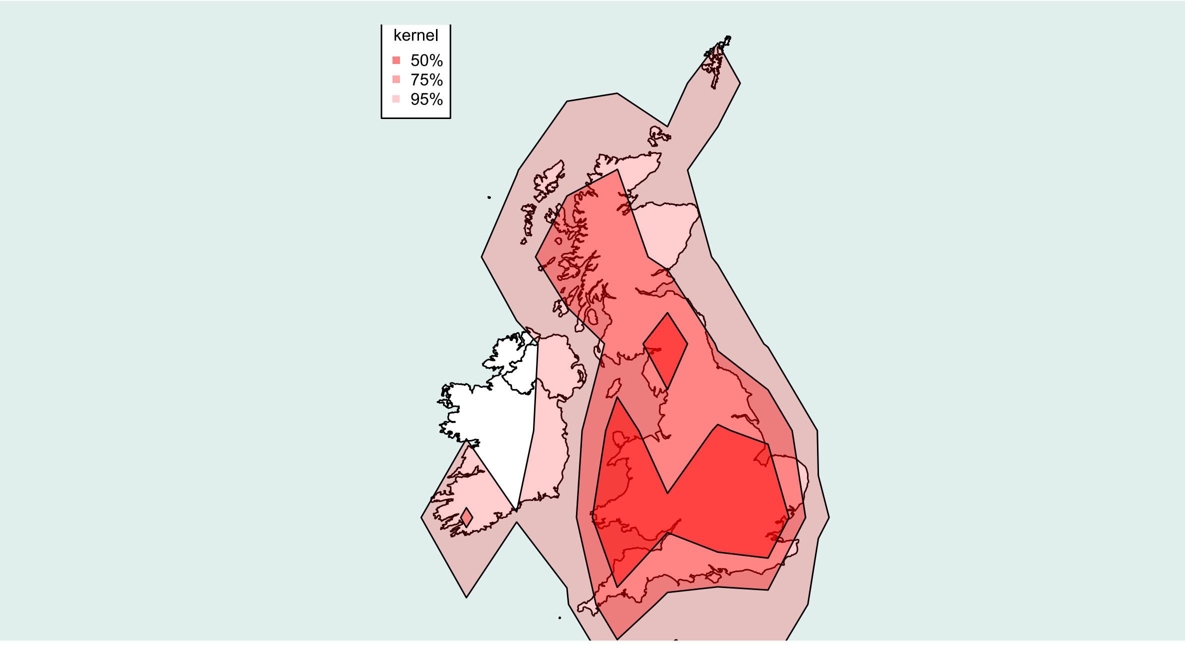
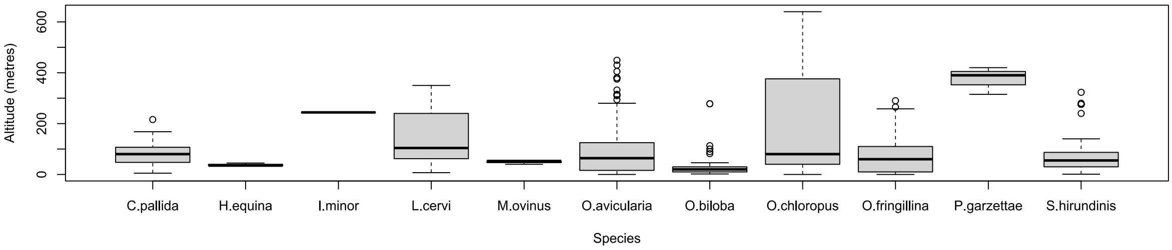


Figure SOM4: Boxplots showing the altitude ranges of all of the species of Hippoboscid received during the study period. *Ornithomya chloropus* occurs over a wider altitude range than the other *Ornithomya* sp.



SUPPORTING INFORMATION

CHAPTER 3.3

S1. Sources of information checked for host species records.

S2. Table of host species and their masses used in the models.

S3. Table of known host-Hippoboscid interactions from the United Kingdom, Republic of Ireland and Isle of Man.

S4. A table of the network metrics calculated by the Bipartite package for all species of Hippoboscid in the current study: a) species metrics, b) network metrics.

S5. A table comparing the network metrics calculated by the Bipartite package the three generalist species in the genus *Ornithomya* (*O. avicularia, O. chloropus* and *O. fringillina*) from the 1960s study (Hill, 1962a) and the current study: a) species metrics, b) network metrics.

S1. Sources of information checked for host species records

Publications

Early systematic work by entomologists and museum curators, who examined large numbers of louse flies, which had been collected over previous decades (Thompson, 1953, 1954b, 1954a, 1955b, 1955c, 1955a; Bequaert, 1954; Hill, 1962; Hutson, 1984; O'Connor and Sleeman, 1987).

Small more intense studies of single species of flies on suitable hosts, for example, *Crataerina (Stenepteryx) hirundinis* on Hirundines (Summers, 1975) and Crataerina pallida on Swift *Apus apus* (Hutson, 1981).

Reports of new species in the United Kingdom and Republic of Ireland (Graham *et al.*, 1954; Lloyd-Evans, 1967; Thompson, 1968; Palmer, 1987; Harrow, 2021; Wawman, 2024).

Other peer reviewed literature: (Curtis, 1836; SMART, 1945; Kettle and Utsi, 1955; G. B. Corbet, 1956; Gordon B. Corbet, 1956; Hill, Wilson and Corbet, 1967; Smiddy, 1997; Denton, 2004; Smiddy and Sleeman, 2004; Turner and Mann, 2004; Harris, 2009; Gibson, Pilkington and Pemberton, 2010; Macdonald, 2022)

Books: (Theobald, 1896; Smart, 1939)

Letters: (White, 1789a, 1789b, 1789c)

Other published reports (grey literature, that is, literature which has not been through peer review). Only those with reports of Hippoboscidae are included:

Bird observatory reports (Williamson, 1949, 1950, 1952, 1954; Butterfield, 1951; Edwards, 1951, 1952; Thompson, 1952, 1964; Stansfield, 1954; Corbet, 1955; Ennion, 1955; G. Stansfield, 1955; Geoffrey Stansfield, 1955; Thompson and Beaumont, 1968; Waine, 1993, 1997, 1999, 2000, 2001, 2002, 2004, 2005, 2007, 2008, 2009, 2013, 2014).

Other bird reports, often from ringing groups, (Lloyd-Evans, 1967; Burn, 1968, 1969, 1970, 1971, 1972, 1973, 1974; Denton, 1977, 1978, 1979, 1980, 1974, 1975, 1976)

Reports of Diptera (Waterson, 1910; Ash, 1952, 1955; Ash and Monk, 1959; Beaumont, 1965; Cutts, 1971; Lane, 1978; Sellers and Redgate, 1992; Emley, 1992; Hancock, 1996, 1995; Chandler, 2009, 2021, 2023; Johnson, 2020).

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S2. Table of host species used in the models, with their masses (in grams), families and merged groupings

Binomial	Species	Family	Order	merged Passerines	Merged Waders, Passerines, Seabirds	Host mass
Branta bernicla	Brent Goose	Anatidae	Anseriformes	Anatidae	ANAT	1236
Branta canadensis	Canada Goose	Anatidae	Anseriformes	Anatidae	ANAT	4128
Branta leucopsis	Barnacle Goose	Anatidae	Anseriformes	Anatidae	ANAT	1895
Anser anser	Greylag Goose	Anatidae	Anseriformes	Anatidae	ANAT	3362
Anser fabalis	Taiga Bean Goose	Anatidae	Anseriformes	Anatidae	ANAT	
Anser brachyrhynchus	Pink-footed Goose	Anatidae	Anseriformes	Anatidae	ANAT	2547
Anser albifrons	White-fronted Goose	Anatidae	Anseriformes	Anatidae	ANAT	2542
Cygnus olor	Mute Swan	Anatidae	Anseriformes	Anatidae	ANAT	9605
Cygnus columbianus	Bewick's Swan	Anatidae	Anseriformes	Anatidae	ANAT	6048
Cygnus cygnus	Whooper Swan	Anatidae	Anseriformes	Anatidae	ANAT	8893
Alopochen aegyptiaca	Egyptian Goose	Anatidae	Anseriformes	Anatidae	ANAT	2528
Tadorna tadorna	Shelduck	Anatidae	Anseriformes	Anatidae	ANAT	1220
Aix galericulata	Mandarin Duck	Anatidae	Anseriformes	Anatidae	ANAT	623
Spatula querquedula	Garganey	Anatidae	Anseriformes	Anatidae	ANAT	353
Spatula clypeata	Shoveler	Anatidae	Anseriformes	Anatidae	ANAT	639
Mareca strepera	Gadwall	Anatidae	Anseriformes	Anatidae	ANAT	803
Mareca penelope	Wigeon	Anatidae	Anseriformes	Anatidae	ANAT	740
Anas platyrhynchos	Mallard	Anatidae	Anseriformes	Anatidae	ANAT	1211
Anas acuta	Pintail	Anatidae	Anseriformes	Anatidae	ANAT	938
Anas crecca	Teal	Anatidae	Anseriformes	Anatidae	ANAT	321
Aythya ferina	Pochard	Anatidae	Anseriformes	Anatidae	ANAT	1065
Aythya fuligula	Tufted Duck	Anatidae	Anseriformes	Anatidae	ANAT	797
Aythya marila	Scaup	Anatidae	Anseriformes	Anatidae	ANAT	
Somateria mollissima	Eider	Anatidae	Anseriformes	Anatidae	ANAT	1878
Melanitta fusca	Velvet Scoter	Anatidae	Anseriformes	Anatidae	ANAT	
Melanitta nigra	Common Scoter	Anatidae	Anseriformes	Anatidae	ANAT	
Clangula hyemalis	Long-tailed Duck	Anatidae	Anseriformes	Anatidae	ANAT	
Bucephala clangula	Goldeneye	Anatidae	Anseriformes	Anatidae	ANAT	679
Mergellus albellus	Smew	Anatidae	Anseriformes	Anatidae	ANAT	
Mergus merganser	Goosander	Anatidae	Anseriformes	Anatidae	ANAT	1214
Mergus serrator	Red-breasted Merganser	Anatidae	Anseriformes	Anatidae	ANAT	
Oxyura jamaicensis	Ruddy Duck	Anatidae	Anseriformes	Anatidae	ANAT	
Tetrao urogallus	Capercaillie	Phasianidae	Galliformes	Phasianidae	Phasianidae	3150
Lyrurus tetrix	Black Grouse	Phasianidae	Galliformes	Phasianidae	Phasianidae	1050
Lagopus muta	Ptarmigan	Phasianidae	Galliformes	Phasianidae	Phasianidae	450
Lagopus lagopus	Red Grouse	Phasianidae	Galliformes	Phasianidae	Phasianidae	600
Alectoris rufa	Red-legged Partridge	Phasianidae	Galliformes	Phasianidae	Phasianidae	450
Perdix perdix	Grey Partridge	Phasianidae	Galliformes	Phasianidae	Phasianidae	414
Coturnix coturnix	Quail	Phasianidae	Galliformes	Phasianidae	Phasianidae	119
Phasianus colchicus	Pheasant	Phasianidae	Galliformes	Phasianidae	Phasianidae	1190
Chrysolophus pictus	Golden Pheasant	Phasianidae	Galliformes	Phasianidae	Phasianidae	
Chrysolophus amherstiae	Lady Amherst's Pheasant	Phasianidae	Galliformes	Phasianidae	Phasianidae	
Gallus gallus domesticus	Chicken	Phasianidae	Galliformes	Phasianidae	Phasianidae	2000

Caprimulgus europaeus	Nightjar	Caprimulgidae	Caprimulgiformes	Caprimulgidae	Caprimulgidae	73
Apus apus	Swift	Apodidae	Apodiformes	Apodidae	Apodidae	40
Cuculus canorus	Cuckoo	Cuculidae	Cucliformes	Cuculidae	Cuculidae	115
Columba livia	Rock Dove	Columbidae	Columbiformes	Columbidae	Columbidae	351
Columba livia domestica	feral pigeon	Columbidae	Columbiformes	Columbidae	Columbidae	300
Columba oenas	Stock Dove	Columbidae	Columbiformes	Columbidae	Columbidae	327
Columba palumbus	Woodpigeon	Columbidae	Columbiformes	Columbidae	Columbidae	515
Streptopelia turtur	Turtle Dove	Columbidae	Columbiformes	Columbidae	Columbidae	156
Streptopelia decaocto	Collared Dove	Columbidae	Columbiformes	Columbidae	Columbidae	204
Rallus aquaticus	Water Rail	Rallidae	Gruiformes	Rallidae	Rallidae	125
Crex crex	Corncrake	Rallidae	Gruiformes	Rallidae	Rallidae	168
Porzana porzana	Spotted Crake	Rallidae	Gruiformes	Rallidae	Rallidae	85.5
Gallinula chloropus	Moorhen	Rallidae	Gruiformes	Rallidae	Rallidae	364
Fulica atra	Coot	Rallidae	Gruiformes	Rallidae	Rallidae	868
Grus grus	Crane	Gruidae	Gruiformes	Gruidae	GRUI	
Tachybaptus ruficollis	Little Grebe	Podicipedidae	Podicipediformes	Podicipedidae	PODI	220
Podiceps grisegena	Red-necked Grebe	Podicipedidae	Podicipediformes	Podicipedidae	PODI	
Podiceps cristatus	Great Crested Grebe	Podicipedidae	Podicipediformes	Podicipedidae	PODI	920
Podiceps auritus	Slavonian Grebe	Podicipedidae	Podicipediformes	Podicipedidae	PODI	446
Podiceps nigricollis	Black-necked Grebe	Podicipedidae	Podicipediformes	Podicipedidae	PODI	
Burhinus oedicnemus	Stone-curlew	Burhinidae	Charadriformes	Burhinidae	Waders	431
Haematopus ostralegus	Oystercatcher	Haematopodidae	Charadriformes	Haematopodidae	Waders	538
Recurvirostra avosetta	Avocet	Recurvirostridae	Charadriiformes	Recurvirostridae	Waders	340
Vanellus vanellus	Lapwing	Charadriidae	Charadriiformes	Charadriidae	Waders	236
Pluvialis apricaria	Golden Plover	Charadriidae	Charadriiformes	Charadriidae	Waders	192
Pluvialis squatarola	Grey Plover	Charadriidae	Charadriiformes	Charadriidae	Waders	226
Charadrius hiaticula	Ringed Plover	Charadriidae	Charadriiformes	Charadriidae	Waders	65
Charadrius dubius	Little Ringed Plover	Charadriidae	Charadriiformes	Charadriidae	Waders	37
Charadrius morinellus	Dotterel	Charadriidae	Charadriiformes	Charadriidae	Waders	115
Numenius phaeopus	Whimbrel	Scolopacidae	Charadriiformes	Scolopacidae	Waders	440
Numenius arquata	Curlew	Scolopacidae	Charadriiformes	Scolopacidae	Waders	786
Limosa lapponica	Bar-tailed Godwit	Scolopacidae	Charadriiformes	Scolopacidae	Waders	293
Limosa limosa	Black-tailed Godwit	Scolopacidae	Charadriiformes	Scolopacidae	Waders	301
Arenaria interpres	Turnstone	Scolopacidae	Charadriiformes	Scolopacidae	Waders	107
Calidris canutus	Knot	Scolopacidae	Charadriiformes	Scolopacidae	Waders	137
Calidris pugnax	Ruff	Scolopacidae	Charadriiformes	Scolopacidae	Waders	164
Calidris ferruginea	Curlew Sandpiper	Scolopacidae	Charadriiformes	Scolopacidae	Waders	66
Calidris temminckii	Temminck's Stint	Scolopacidae	Charadriiformes	Scolopacidae	Waders	
Calidris alba	Sanderling	Scolopacidae	Charadriiformes	Scolopacidae	Waders	56
Calidris alpina	Dunlin	Scolopacidae	Charadriiformes	Scolopacidae	Waders	49
Calidris maritima	Purple Sandpiper	Scolopacidae	Charadriiformes	Scolopacidae	Waders	70
Calidris minuta	Little Stint	Scolopacidae	Charadriiformes	Scolopacidae	Waders	27
Scolopax rusticola	Woodcock	Scolopacidae	Charadriiformes	Scolopacidae	Waders	325
Lymnocryptes minimus	Jack Snipe	Scolopacidae	Charadriiformes	Scolopacidae	Waders	59
Gallinago media	Great Snipe	Scolopacidae	Charadriiformes	Scolopacidae	Waders	175
Gallinago gallinago	Snipe	Scolopacidae	Charadriiformes	Scolopacidae	Waders	109
Phalaropus lobatus	Red-necked Phalarope	Scolopacidae	Charadriiformes	Scolopacidae	Waders	
Phalaropus fulicarius	Grey Phalarope	Scolopacidae	Charadriiformes	Scolopacidae	Waders	

Actitis hypoleucos	Common Sandpiper	Scolopacidae	Charadriiformes	Scolopacidae	Waders	57
Tringa ochropus	Green Sandpiper	Scolopacidae	Charadriiformes	Scolopacidae	Waders	83
Tringa totanus	Redshank	Scolopacidae	Charadriiformes	Scolopacidae	Waders	150
Tringa glareola	Wood Sandpiper	Scolopacidae	Charadriiformes	Scolopacidae	Waders	55.7
Tringa erythropus	Spotted Redshank	Scolopacidae	Charadriiformes	Scolopacidae	Waders	155
Tringa nebularia	Greenshank	Scolopacidae	Charadriiformes	Scolopacidae	Waders	191
Rissa tridactyla	Kittiwake	Laridae	Charadriiformes	Laridae	Laridae	365
Chroicocephalus ridibundus	Black-headed Gull	Laridae	Charadriiformes	Laridae	Laridae	289
Hydrocoloeus minutus	Little Gull	Laridae	Charadriiformes	Laridae	Laridae	110
Ichthyaetus melanocephalus	Mediterranean Gull	Laridae	Charadriiformes	Laridae	Laridae	330
Larus canus	Common Gull	Laridae	Charadriiformes	Laridae	Laridae	405
Larus marinus	Great Black-backed Gull	Laridae	Charadriiformes	Laridae	Laridae	1538
Larus hyperboreus	Glaucous Gull	Laridae	Charadriiformes	Laridae	Laridae	
Larus glaucoides	Iceland Gull	Laridae	Charadriiformes	Laridae	Laridae	
Larus argentatus	Herring Gull	Laridae	Charadriiformes	Laridae	Laridae	940
Larus michahellis	Yellow-legged Gull	Laridae	Charadriiformes	Laridae	Laridae	
Larus fuscus	Lesser Black-backed Gull	Laridae	Charadriiformes	Laridae	Laridae	822
Hydroprogne caspia	Caspian Tern	Laridae	Charadriiformes	Laridae	Laridae	
Thalasseus sandvicensis	Sandwich Tern	Laridae	Charadriiformes	Laridae	Laridae	236
Sternula albifrons	Little Tern	Laridae	Charadriiformes	Laridae	Laridae	55
Sterna dougallii	Roseate Tern	Laridae	Charadriiformes	Laridae	Laridae	115
Sterna hirundo	Common Tern	Laridae	Charadriiformes	Laridae	Laridae	129
Sterna paradisaea	Arctic Tern	Laridae	Charadriiformes	Laridae	Laridae	272
Chlidonias niger	Black Tern	Laridae	Charadriiformes	Laridae	Laridae	
Stercorarius skua	Great Skua	Stercorariidae	Charadriiformes	STE	Stercorariidae	1331
Stercorarius parasiticus	Arctic Skua	Stercorariidae	Charadriiformes	STE	Stercorariidae	420
Uria aalge	Common Guillemot	Alcidae	Charadriiformes	Alcidae	SEAB	923
Alca torda	Razorbill	Alcidae	Charadriiformes	Alcidae	SEAB	614
Cepphus grylle	Black Guillemot	Alcidae	Charadriiformes	Alcidae	SEAB	406
Fratercula arctica	Puffin	Alcidae	Charadriiformes	Alcidae	SEAB	383
Gavia stellata	Red-throated Diver	Phaethontidae	Phaethonidae	PHAE	SEAB	1665
Gavia arctica	Black-throated Diver	Phaethontidae	Phaethonidae	PHAE	SEAB	
Gavia immer	Great Northern Diver	Phaethontidae	Phaethonidae	PHAE	SEAB	
Hydrobates pelagicus	Storm Petrel	Hydrobatidae	Procellariformes	Hydrobatidae	SEAB	25
Oceanodroma leucorhoa	Leach's Petrel	Hydrobatidae	Procellariformes	Hydrobatidae	SEAB	43
Fulmarus glacialis	Fulmar	Procellariidae	Procellariformes	Procellariidae	SEAB	779
Puffinus puffinus	Manx Shearwater	Procellariidae	Procellariformes	Procellariidae	SEAB	392
Morus bassanus	Gannet	Sulidae	Suliformes	Sulidae	SEAB	2990
Phalacrocorax carbo	Cormorant	Phalacrocoracidae	Phalacrocoracidae	Phalacrocoracidae	SEAB	2702
Phalacrocorax aristotelis	Shag	Phalacrocoracidae	Phalacrocoracidae	Phalacrocoracidae	SEAB	1780
Plegadis falcinellus	Glossy Ibis	Theskiornithidae	Pelecaniformes	Theskiornithidae	THES	
Platalea leucorodia	Spoonbill	Theskiornithidae	Pelecaniformes	Theskiornithidae	THES	
Botaurus stellaris	Bittern	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	1250
Ixobrychus minutus	Little Bittern	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	
Bubulcus ibis	Cattle Egret	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	
Ardea cinerea	Grey Heron	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	1675
Ardea purpurea	Purple Heron	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	1250
Ardea alba	Great White Egret	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	

Egretta garzetta	Little Egret	Ardeidae	Pelecaniformes	Ardeidae	Ardeidae	488
Pandion haliaetus	Osprey	Pandionidae	Acciptriformes	PAND	Pandionidae	1372.5
Pernis apivorus	Honey-buzzard	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	
Aquila chrysaetos	Golden Eagle	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	4550
Accipiter nisus	Sparrowhawk	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	181
Accipiter gentilis	Goshawk	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	1040
Circus aeruginosus	Marsh Harrier	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	
Circus cyaneus	Hen Harrier	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	490
Circus pygargus	Montagu's Harrier	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	
Milvus milvus	Red Kite	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	929
Haliaeetus albicilla	White-tailed Eagle	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	
Buteo lagopus	Rough-legged Buzzard	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	
Buteo buteo	Buzzard	Accipitridae	Acciptriformes	Accipitridae	Accipitridae	917
Tyto alba	Barn Owl	Tytonidae	Strigiformes	Tytonidae	Tytonidae	339
Athene noctua	Little Owl	Strigidae	Strigiformes	Strigidae	Strigidae	190
Asio otus	Long-eared Owl	Strigidae	Strigiformes	Strigidae	Strigidae	288
Asio flammeus	Short-eared Owl	Strigidae	Strigiformes	Strigidae	Strigidae	358
Strix aluco	Tawny Owl	Strigidae	Strigiformes	Strigidae	Strigidae	481
Upupa epops	Hoopoe	Upupidae	Coraciiformes	Upupidae	UPUP	
Alcedo atthis	Kingfisher	Alcedinidae	Coraciiformes	Alcedinidae	ALCE	39
Merops apiaster	Bee-eater	Meropidae	Coraciiformes	Meropidae	MERO	
Jynx torquilla	Wryneck	Picidae	Coraciiformes	Picidae	Picidae	33
Dryobates minor	Lesser Spotted Woodpecker	Picidae	Coraciiformes	Picidae	Picidae	20
Dendrocopos major	Great Spotted Woodpecker	Picidae	Coraciiformes	Picidae	Picidae	78
Picus viridis	Green Woodpecker	Picidae	Coraciiformes	Picidae	Picidae	189
Falco tinnunculus	Kestrel	Falconidae	Falconiformes	Falconidae	Falconidae	204
Falco vespertinus	Red-footed Falcon	Falconidae	Falconiformes	Falconidae	Falconidae	
Falco columbarius	Merlin	Falconidae	Falconiformes	Falconidae	Falconidae	213
Falco subbuteo	Hobby	Falconidae	Falconiformes	Falconidae	Falconidae	257
Falco peregrinus	Peregrine	Falconidae	Falconiformes	Falconidae	Falconidae	1063
Psittacula krameri	Ring-necked Parakeet	Psittaculidae	Psittaciformes	Psittaculidae	Psittaculidae	142
Lanius collurio	Red-backed Shrike	Laniidae	Passeriformes	Passeriformes	Passeriformes	28
Lanius excubitor	Great Grey Shrike	Laniidae	Passeriformes	Passeriformes	Passeriformes	62.7
Oriolus oriolus	Golden Oriole	Oriolidae	Passeriformes	Passeriformes	Passeriformes	67
Garrulus glandarius	Jay	Corvidae	Passeriformes	Passeriformes	Passeriformes	167
Pica pica	Magpie	Corvidae	Passeriformes	Passeriformes	Passeriformes	210
Pyrrhocorax pyrrhocorax	Chough	Corvidae	Passeriformes	Passeriformes	Passeriformes	325
Coloeus monedula	Jackdaw	Corvidae	Passeriformes	Passeriformes	Passeriformes	230
Corvus frugilegus	Rook	Corvidae	Passeriformes	Passeriformes	Passeriformes	440
Corvus corone	Carrion Crow	Corvidae	Passeriformes	Passeriformes	Passeriformes	511
Corvus cornix	Hooded Crow	Corvidae	Passeriformes	Passeriformes	Passeriformes	529
Corvus corax	Raven	Corvidae	Passeriformes	Passeriformes	Passeriformes	1222.5
Bombycilla garrulus	Waxwing	Bombycillidae	Passeriformes	Passeriformes	Passeriformes	58
Periparus ater	Coal Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	9
Lophophanes cristatus	Crested Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	10
Poecile palustris	Marsh Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	10
Poecile montanus	Willow Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	10
Cyanistes caeruleus	Blue Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	10

Parus major	Great Tit	Paridae	Passeriformes	Passeriformes	Passeriformes	18
Panurus biarmicus	Bearded Tit	Panuridae	Passeriformes	Passeriformes	Passeriformes	15
Lullula arborea	Woodlark	Alaudidae	Passeriformes	Passeriformes	Passeriformes	29
Alauda arvensis	Skylark	Alaudidae	Passeriformes	Passeriformes	Passeriformes	38
Eremophila alpestris	Shore Lark	Alaudidae	Passeriformes	Passeriformes	Passeriformes	35
Riparia riparia	Sand Martin	Hirundinidae	Passeriformes	Passeriformes	Passeriformes	13
Hirundo rustica	Swallow	Hirundinidae	Passeriformes	Passeriformes	Passeriformes	19
Delichon urbicum	House Martin	Hirundinidae	Passeriformes	Passeriformes	Passeriformes	17
Cettia cetti	Cetti's Warbler	Cettiidae	Passeriformes	Passeriformes	Passeriformes	13
Aegithalos caudatus	Long-tailed Tit	Aegithalidae	Passeriformes	Passeriformes	Passeriformes	7
Phylloscopus sibilatrix	Wood Warbler	Phylloscopidae	Passeriformes	Passeriformes	Passeriformes	9
Phylloscopus trochilus	Willow Warbler	Phylloscopidae	Passeriformes	Passeriformes	Passeriformes	8
Phylloscopus collybita	Chiffchaff	Phylloscopidae	Passeriformes	Passeriformes	Passeriformes	7
Acrocephalus paludicola	Aquatic Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	12.9
Acrocephalus schoenobaenus	Sedge Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	11
Acrocephalus agricola	Paddyfield Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	
Acrocephalus scirpaceus	Reed Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	11
Acrocephalus palustris	Marsh Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	13
Hippolais icterina	Icterine Warbler	Acrocephalidae	Passeriformes	Passeriformes	Passeriformes	13
Locustella luscinioides	Savi's Warbler	Locustellidae	Passeriformes	Passeriformes	Passeriformes	15
Locustella naevia	Grasshopper Warbler	Locustellidae	Passeriformes	Passeriformes	Passeriformes	13
Sylvia atricapilla	Blackcap	Sylviidae	Passeriformes	Passeriformes	Passeriformes	17
Sylvia borin	Garden Warbler	Sylviidae	Passeriformes	Passeriformes	Passeriformes	17
Curruca nisoria	Barred Warbler	Sylviidae	Passeriformes	Passeriformes	Passeriformes	24.3
Curruca curruca	Lesser Whitethroat	Sylviidae	Passeriformes	Passeriformes	Passeriformes	11
Curruca communis	Whitethroat	Sylviidae	Passeriformes	Passeriformes	Passeriformes	13
Curruca undata	Dartford Warbler	Sylviidae	Passeriformes	Passeriformes	Passeriformes	9
Regulus ignicapilla	Firecrest	Regulidae	Passeriformes	Passeriformes	Passeriformes	5
Regulus regulus	Goldcrest	Regulidae	Passeriformes	Passeriformes	Passeriformes	5
Troglodytes troglodytes	Wren	Troglodytidae	Passeriformes	Passeriformes	Passeriformes	9
Sitta europaea	Nuthatch	Sittidae	Passeriformes	Passeriformes	Passeriformes	22
Certhia familiaris	Treecreeper	Certhiidae	Passeriformes	Passeriformes	Passeriformes	8
Sturnus vulgaris	Starling	Sturnidae	Passeriformes	Passeriformes	Passeriformes	83
Zoothera aurea	White's Thrush	Turdidae	Passeriformes	Passeriformes	Passeriformes	
Turdus torquatus	Ring Ouzel	Turdidae	Passeriformes	Passeriformes	Passeriformes	105
Turdus merula	Blackbird	Turdidae	Passeriformes	Passeriformes	Passeriformes	101
Turdus pilaris	Fieldfare	Turdidae	Passeriformes	Passeriformes	Passeriformes	108
Turdus iliacus	Redwing	Turdidae	Passeriformes	Passeriformes	Passeriformes	65
Turdus philomelos	Song Thrush	Turdidae	Passeriformes	Passeriformes	Passeriformes	74
Turdus viscivorus	Mistle Thrush	Turdidae	Passeriformes	Passeriformes	Passeriformes	125
Muscicapa striata	Spotted Flycatcher	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	14
Erithacus rubecula	Robin	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	19
Luscinia svecica	Bluethroat	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	16.7
Luscinia megarhynchos	Nightingale	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	21
Ficedula hypoleuca	Pied Flycatcher	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	13
Phoenicurus ochruros	Black Redstart	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	16
Phoenicurus phoenicurus	Redstart	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	14
Saxicola rubetra	Whinchat	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	16

Saxicola rubicola	Stonechat	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	15.4
Oenanthe oenanthe	Wheatear	Muscicapidae	Passeriformes	Passeriformes	Passeriformes	28
Cinclus cinclus	Dipper	Cinclidae	Passeriformes	Passeriformes	Passeriformes	63
Passer domesticus	House Sparrow	Passeridae	Passeriformes	Passeriformes	Passeriformes	27
Passer montanus	Tree Sparrow	Passeridae	Passeriformes	Passeriformes	Passeriformes	21
Prunella modularis	Dunnock	Prunellidae	Passeriformes	Passeriformes	Passeriformes	21
Motacilla flava	Yellow Wagtail	Motacillidae	Passeriformes	Passeriformes	Passeriformes	17
Motacilla citreola	Citrine Wagtail	Motacillidae	Passeriformes	Passeriformes	Passeriformes	
Motacilla cinerea	Grey Wagtail	Motacillidae	Passeriformes	Passeriformes	Passeriformes	18
Motacilla alba	Pied Wagtail	Motacillidae	Passeriformes	Passeriformes	Passeriformes	23
Anthus pratensis	Meadow Pipit	Motacillidae	Passeriformes	Passeriformes	Passeriformes	18
Anthus trivialis	Tree Pipit	Motacillidae	Passeriformes	Passeriformes	Passeriformes	21
Anthus spinoletta	Water Pipit	Motacillidae	Passeriformes	Passeriformes	Passeriformes	24
Anthus petrosus	Rock Pipit	Motacillidae	Passeriformes	Passeriformes	Passeriformes	25
Fringilla coelebs	Chaffinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	21
Fringilla montifringilla	Brambling	Fringillidae	Passeriformes	Passeriformes	Passeriformes	24
Coccothraustes coccothraustes	Hawfinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	52
Pyrrhula pyrrhula	Bullfinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	22
Carpodacus erythrinus	Common Rosefinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	
Chloris chloris	Greenfinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	87
Linaria flavirostris	Twite	Fringillidae	Passeriformes	Passeriformes	Passeriformes	16
Linaria cannabina	Linnet	Fringillidae	Passeriformes	Passeriformes	Passeriformes	18
Acanthis flammea	Redpoll	Fringillidae	Passeriformes	Passeriformes	Passeriformes	
Loxia pytyopsittacus	Parrot Crossbill	Fringillidae	Passeriformes	Passeriformes	Passeriformes	50
Loxia scotica	Scottish Crossbill	Fringillidae	Passeriformes	Passeriformes	Passeriformes	
Loxia curvirostra	Crossbill	Fringillidae	Passeriformes	Passeriformes	Passeriformes	40
Carduelis carduelis	Goldfinch	Fringillidae	Passeriformes	Passeriformes	Passeriformes	15
Serinus serinus	Serin	Fringillidae	Passeriformes	Passeriformes	Passeriformes	11
Spinus spinus	Siskin	Fringillidae	Passeriformes	Passeriformes	Passeriformes	12
Calcarius lapponicus	Lapland Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	26
Plectrophenax nivalis	Snow Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	33
Emberiza calandra	Corn Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	46
Emberiza citrinella	Yellowhammer	Calcariidae	Passeriformes	Passeriformes	Passeriformes	25
Emberiza hortulana	Ortolan Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	
Emberiza cirlus	Cirl Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	24
Emberiza schoeniclus	Reed Bunting	Calcariidae	Passeriformes	Passeriformes	Passeriformes	19
Rangifer tarandus	Reindeer	Cervidae	Mammaliaformes	Cervidae	Cervidae	170
Dama dama	Fallow Deer	Cervidae	Mammaliaformes	Cervidae	Cervidae	65000
Capreolus capreolus	Roe Deer	Cervidae	Mammaliaformes	Cervidae	Cervidae	25
Cervus nippon	Sika Deer	Cervidae	Mammaliaformes	Cervidae	Cervidae	42000
Cervus elaphus	Red Deer	Cervidae	Mammaliaformes	Cervidae	Cervidae	200000
Ovis aries	Sheep	Bovidae	Mammaliaformes	Bovidae	Bovidae	80000
Bos taurus	Cattle	Bovidae	Mammaliaformes	Bovidae	Bovidae	510000
Equus ferus caballus	Horse	Equidae	Mammaliaformes	Equidae	Equidae	450000
Meles Meles	Badger	Mustelidae	Mammaliaformes	Mustelidae	Mustelidae	15000
Canis familiaris	Dog	Canidae	Mammaliaformes	Canidae	Canidae	40000
Homo sapiens	Human	Hominidae	Mammaliaformes	Hominidae	Hominidae	70000

S3. Table of known host-Hippoboscid interactions from the United Kingdom, Republic of Ireland and Isle of Man.

The numbers in the columns refer to the references for the original report (listed below), if it is available, or attributed to the paper in which the references can be found, Those listed as “NEW” are interactions first reported in this study.

Unfortunately, it was necessary to exclude many of the earlier published host-parasite interactions because *Ornithomya chloropus* was not recognised as a separate species and records were included with those of *O. fringillina*.

	Generalists			Stenoxenous louse flies					Vagrant louse flies					Keds				
Host British vernacular name	***Ornithomya avicularia***	***Ornithomya chloropus***	***Ornithomya fringillina***	***Ornithomya biloba***	***Crataerina pallida***	***Stenepteryx hirundinis***	***Pseudolynchia canariensis***	***Pseudolynchia garzettae***	***Ornithophila gestroi***	***Ornithophila metallica***	***Icosta ardae***	***Icosta minor***	***Olfersia spinifera***	***Hippobosca longipennis***	***Hippobosca equina***	***Lipoptena cervi***	***Melophagus ovinus***	***Host scientific name***
Black Grouse	2	13	21															*Lyrurus tetrix*
Ptarmigan		13																*Lagopus muta*
Red Grouse	2	2																*Lagopus lagopus*
Red-legged Partridge	21																	*Alectoris rufa*
Grey Partridge	2	13	21															*Perdix perdix*
Pheasant	2																	*Phasianus colchicus*
Chicken	33															33		*Gallus gallus domest*
Nightjar	NEW							34										*Caprimulgus europae*
Swift					35	1												*Apus apus*
Cuckoo	2	25																*Cuculus canorus*
Rock Dove	2		NEW															*Columba livia*
feral pigeon	2						NEW											*Columba livia domes*
Stock Dove	NEW	NEW																*Columba oenas*
Woodpigeon	2																	*Columba palumbus*
Turtle Dove	2																	*Streptopelia turtur*
Collared Dove	2																	*Streptopelia decaoct*
Water Rail	27	13																*Rallus aquaticus*
Corncrake			2									28						*Crex crex*
Moorhen	2	42																*Gallinula chloropus*
Oystercatcher		40	NEW															*Haematopus ostraleg*
Lapwing		13																*Vanellus vanellus*
Golden Plover		13																*Pluvialis apricaria*
Ringed Plover	2	40																*Charadrius hiaticula*
Curlew		41																*Numenius arquata*
Black-tailed Godwit		NEW																*Limosa limosa*
Turnstone		NEW																*Arenaria interpres*
Dunlin		13																*Calidris alpina*
Woodcock	13	8																*Scolopax rusticola*
Jack Snipe		NEW																*Lymnocryptes minim*

Great Snipe		NEW							*Gallinago media*
Snipe	2	40							*Gallinago gallinago*
Common Sandpiper	NEW	2							*Actitis hypoleucos*
Green Sandpiper		25							*Tringa ochropus*
Redshank		13							*Tringa totanus*
Great Black-backed Gull		NEW							*Larus marinus*
Herring Gull	NEW								*Larus argentatus*
Lesser Black-backed Gull	NEW								*Larus fuscus*
Arctic Tern		NEW							*Sterna paradisaea*
Great Skua		NEW							*Stercorarius skua*
Arctic Skua		27							*Stercorarius parasitic*
Ascension Frigatebird							36		*Fregata aquila*
Bittern						5			*Botaurus stellaris*
Little Bittern						5			*Ixobrychus minutus*
Grey Heron	2								*Ardea cinerea*
Purple Heron						5			*Ardea purpurea*
Osprey	NEW								*Pandion haliaetus*
Golden Eagle		NEW							*Aquila chrysaetos*
Sparrowhawk	2	22	NEW	NEW					*Accipiter nisus*
Goshawk	NEW								*Accipiter gentilis*
Hen Harrier		NEW							*Circus cyaneus*
Montagu's Harrier		41							*Circus pygargus*
Red Kite	NEW								*Milvus milvus*
Buzzard	2								*Buteo buteo*
Barn Owl	2	NEW		NEW					*Tyto alba*
Tawny Owl	2	2							*Strix aluco*
Little Owl	2	30							*Athene noctua*
Long-eared Owl	2	22	13						*Asio otus*
Short-eared Owl	13	15							*Asio flammeus*
Wryneck		NEW							*Jynx torquilla*
Great Spotted Woodpecker	2				NEW				*Dendrocopos major*
Green Woodpecker	5								*Picus viridis*
Kestrel	2	13							*Falco tinnunculus*
Red-footed Falcon		13							*Falco vespertinus*
Merlin	25	38							*Falco columbarius*
Hobby	NEW			NEW					*Falco subbuteo*
Peregrine	2								*Falco peregrinus*
Ring-necked Parakeet	32								*Psittacula krameri*
Red-backed Shrike	2	13							*Lanius collurio*
Jay	2								*Garrulus glandarius*
Magpie	2								*Pica pica*
Chough	NEW								*Pyrrhocorax pyrrhoco*
Jackdaw	2								*Coloeus monedula*
Rook	2								*Corvus frugilegus*
Carrion Crow	2	13							*Corvus corone*
Hooded Crow	NEW	NEW							*Corvus cornix*
Coal Tit			NEW					NEW	*Periparus ater*
Willow Tit			NEW						*Poecile montanus*

Blue Tit	19	NEW	41							*Cyanistes caeruleus*
Great Tit	2	23	26							*Parus major*
Skylark		13	29							*Alauda arvensis*
Sand Martin		6	6	7		1				*Riparia riparia*
Swallow	8	13	6	9	6	10				*Hirundo rustica*
House Martin	1		2		2	11				*Delichon urbicum*
Cetti's Warbler			NEW							*Cettia cetti*
Long-tailed Tit	12		8							*Aegithalos caudatus*
Willow Warbler	13	13	14							*Phylloscopus trochilu*
Chiffchaff			5							*Phylloscopus collybit*
Sedge Warbler	NEW	15	13					NEW		*Acrocephalus schoenobaenus*
Paddyfield Warbler				7						*Acrocephalus agricol*
Reed Warbler	16		13							*Acrocephalus scirpac*
Icterine Warbler		13								*Hippolais icterina*
Grasshopper Warbler	NEW	NEW								*Locustella naevia*
Blackcap	NEW	NEW	13							*Sylvia atricapilla*
Garden Warbler	NEW	18	17							*Sylvia borin*
Barred Warbler			13							*Curruca nisoria*
Lesser Whitethroat	2		19							*Curruca curruca*
Whitethroat	2	13	17				20			*Curruca communis*
Dartford Warbler		13	21							*Curruca undata*
Firecrest			NEW							*Regulus ignicapilla*
Goldcrest		22	13						NEW	*Regulus regulus*
Wren		13	23							*Troglodytes troglody*
Nuthatch	41		41							*Sitta europaea*
Treecreeper			23							*Certhia familiaris*
Starling	2	2	14							*Sturnus vulgaris*
White's Thrush		13								*Zoothera aurea*
Ring Ouzel		24								*Turdus torquatus*
Blackbird	2	22	NEW							*Turdus merula*
Redwing	13	25							NEW	*Turdus iliacus*
Song Thrush	2	13	NEW							*Turdus philomelos*
Mistle Thrush	41									*Turdus viscivorus*
Spotted Flycatcher	41	13	21							*Muscicapa striata*
Robin	2	23	26							*Erithacus rubecula*
Bluethroat		13								*Luscinia svecica*
Pied Flycatcher	NEW	13								*Ficedula hypoleuca*
Redstart	NEW	13	NEW							*Phoenicurus phoenic*
Whinchat		13								*Saxicola rubetra*
Stonechat	21	NEW	13							*Saxicola rubicola*
Wheatear	2	27	2							*Oenanthe oenanthe*
House Sparrow	2	38	13							*Passer domesticus*
Tree Sparrow	9	23	23							*Passer montanus*
Dunnock	2	13	17							*Prunella modularis*
Yellow Wagtail		13	13							*Motacilla flava*
Citrine Wagtail		25								*Motacilla citreola*
Pied Wagtail	23	13	14							*Motacilla alba*
Meadow Pipit	NEW	27	2							*Anthus pratensis*

Tree Pipit	NEW	22	2			28					*Anthus trivialis*
Rock Pipit	29	27	29								*Anthus petrosus*
Chaffinch	41	NEW	2								*Fringilla coelebs*
Bullfinch	13	23	NEW								*Pyrrhula pyrrhula*
Greenfinch	19	NEW	19								*Chloris chloris*
Twite	25	27									*Linaria flavirostris*
Linnet	19	23	19								*Linaria cannabina*
Redpoll		30	NEW								*Acanthis flammea*
Crossbill	NEW	13									*Loxia curvirostra*
Goldfinch	NEW	NEW	21								*Carduelis carduelis*
Siskin	NEW	NEW	NEW								*Spinus spinus*
Corn Bunting	21										*Emberiza calandra*
Yellowhammer	NEW	13	26								*Emberiza citrinella*
Reed Bunting	NEW	31	13								*Emberiza schoeniclus*
Sheep										28	*Ovis aries*
Reindeer									37		*Rangifer tarandus*
Fallow Deer									3		*Dama dama*
Roe Deer									3		*Capreolus capreolus*
Sika Deer									28		*Cervus nippon*
Red Deer									3		*Cervus elaphus*
Cattle								4			*Bos taurus*
Horse								4	NEW		*Equus ferus caballus*
Badger									28		*Meles Meles*
Dog								4	28		*Canis familiaris*
Human	21	NEW	21	2				28	28		*Homo sapiens*
ACCIDENTAL IMPORTS											
Pekin Robin/Red-billed Leiothrix					28						*Leiothrix lutea*
Ring-necked Parakeet					28						*Psittiacula krameri*
Cheetah							39				*Acinonyx jubatus*

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S4. Network metrics for all species from the current study

a) Species metrics

	O. avicularia	***O. biloba***	***O. chloropus***	***O. fringillina***	***C. pallida***	***S. hirundinis***
degree	74	2	64	47	5	5
normalised degree	0.637931034	0.017241379	0.551724138	0.405172414	0.043103448	0.043103448
species strength	44.58614419	0.837092732	34.94085136	24.60112686	1.228254546	1.944106069
interaction push pull	0.589001948	-0.081453634	0.530325803	0.502151635	0.045650909	0.188821214
nestedrank	0	0.545454545	0.090909091	0.181818182	0.454545455	0.363636364
PDI	0.965716538	0.999613527	0.970885093	0.947891963	0.999248524	0.998269112
resource range	0.365217391	0.991304348	0.452173913	0.6	0.965217391	0.965217391
species specificity index	0.255011782	0.958022234	0.297781907	0.240189123	0.920794233	0.845365189
PSI	0.763759715	0.757905402	0.691391516	0.653482991	0.912538744	0.951856639
node specialisation index NSI	1.1	1.7	1.3	1.3	1.7	1.6
betweenness	0.550438596	0	0.103070175	0.103070175	0	0.006578947
weighted betweenness	0.459349593	0	0.113821138	0.134146341	0	0.146341463
closeness	0.125	0.089912281	0.111842105	0.111842105	0.089912281	0.096491228
weighted closeness	0.003414942	0.003190928	0.003400286	0.003408246	0.003030389	0.003170291
Fisher alpha	NA	NA	NA	NA	NA	NA
partner diversity	3.215848312	0.175975125	2.983992958	3.027604097	0.379240079	0.528876185
effective partners	24.92442662	1.192408397	19.76658643	20.64770338	1.46117379	1.697024096
proportional generality	0.540122337	0.025839969	0.428349868	0.447444027	0.031664223	0.036775194
proportional similarity	0.568767004	0.024270655	0.482515997	0.418222766	0.083858009	0.082523326
d	0.588972467	0.915978748	0.558245396	0.620026734	0.91906373	0.963452836

	P. canariensis	***P. garzettae***	***I. minor***	***H. equina***	***L. cervi***	***M. ovinus***
degree	1	1	1	1	8	1
normalised degree	0.00862069	0.00862069	0.00862069	0.00862069	0.068965517	0.00862069
species strength	0.857142857	0.6	0.083333333	0.666666667	4.655281385	1
interaction push pull	-0.142857143	-0.4	-0.916666667	-0.333333333	0.456910173	0
nestedrank	0.727272727	0.909090909	1	0.818181818	0.272727273	0.636363636
PDI	1	1	1	1	0.987198068	1
resource range	1	1	1	1	0.939130435	1
species specificity index	1	1	1	1	0.508277217	1
PSI	0.857142857	0.6	0.083333333	0.666666667	0.935520697	1
node specialisation index NSI	2	2	1.8	2.5	1.6	NA
betweenness	0	0	0	0	0.236842105	0
weighted betweenness	0	0	0	0	0.146341463	0
closeness	0.070175439	0.070175439	0.083333333	0.059210526	0.092105263	0
weighted closeness	0.002647297	0.001529727	0.000649137	0.001674691	0.002920682	0
Fisher alpha	NA	NA	NA	NA	NA	NA
partner diversity	0	0	0	0	1.519280007	0
effective partners	1	1	1	1	4.56893441	1
proportional generality	0.021670402	0.021670402	0.021670402	0.021670402	0.099010644	0.021670402
proportional similarity	0.001716107	0.001225791	0.002941898	0.001470949	0.036487242	0.013483697
d	0.971652831	0.909317326	0.581491958	0.927157521	0.965575898	1

b) Network metrics all species

connectance	0.062056738
web asymmetry	-0.91836735
links per species	0.714285714
number of compartments	2
compartment diversity	1.487469234
cluster coefficient	0.012411348
modularity Q	0.541110205
nestedness	0.328057014
NODF	8.027472217
weighted nestedness	0.696069989
weighted NODF	4.226329785
interaction strength asymmetry	-0.40715892
specialisation asymmetry	0.388362937
linkage density	10.66744442
weighted connectance	0.036283825
Fisher alpha	46.90793502
Shannon diversity	4.280137048
interaction evenness	0.526668532
Alatalo interaction evenness	0.56546745
H2	0.698574421
Number of species HL	12
Number of species LL	282
Mean number of shared partners HL	1.984848485
Mean number of shared partners LL	0.147573257
Cluster coefficient HL	0.199396146
Cluster coefficient LL	0.203031789
Weighted cluster coefficient HL	0.311972002
Weighted cluster coefficient LL	0.902750337
Niche overlap HL	0.013151516
Niche overlap LL	0.360204403
Togetherness HL	0.025680401
Togetherness LL	0.038647615
C score HL	0.769453565
C score LL	0.35483654
V ratio HL	48.21679688
V ratio LL	1.881055034
Discrepancy HL	150
Discrepancy LL	71
Extinction slope HL	0.319090285
Extinction slope LL	0.525437841
Robustness HL	0.221368562
Robustness LL	0.298146446
Functional complementarity HL	1940.015143
Functional complementarity LL	2519.633151
Partner diversity HL	2.763589388
Partner diversity LL	0.448329122
Generality HL	19.65590981
Vulnerability LL	1.678979035

S5. A comparison of the network and species metrics from Hill (1962) with the current study for the three generalist Ornithomya species

a) Species Metrics

	Hill, 1962			**Current study**		
	O. avicularia	***O. chloropus***	***O. fringillina***	***O. avicularia***	***O. chloropus***	***O. fringillina***
degree	43	56	25	74	64	47
normalised degree	0.483146067	0.629213483	0.280898876	0.678899083	0.587155963	0.431192661
species strength	30.15866039	42.27262843	16.56871117	47.30966764	36.69991057	24.99042179
interaction push pull	0.678108381	0.737011222	0.622748447	0.625806319	0.557811103	0.510434506
nestedrank	0.5	0	1	0	0.5	1
PDI	0.972348485	0.964022727	0.992272727	0.963494461	0.968998016	0.94451459
resource.range	0.522727273	0.375	0.727272727	0.324074074	0.416666667	0.574074074
species specificity index	0.437585506	0.416682865	0.620386913	0.253985425	0.296925685	0.239090571
PSI	0.84244066	0.930199012	0.910756303	0.769052816	0.695710484	0.656085624
node specialisation index NSI	1	1	1	1	1	1
betweenness	0	0	0	0	0	0
weighted betweenness	0	1	0	0	0	0
closeness	0.333333333	0.333333333	0.333333333	0.333333333	0.333333333	0.333333333
weighted closeness	0.253978868	0.46213907	0.482473842	0.605720071	0.39969812	0.471838586
Fisher alpha	9.069509294	10.59316743	5.824961963	15.9467077	15.36664586	10.4658841
partner diversity	2.119669196	1.985464436	1.522202484	3.215848312	2.983992958	3.027604097
effective partners	8.328381969	7.28242882	4.582306544	24.92442662	19.76658643	20.64770338
proportional generality	0.541491216	0.473485876	0.297930469	0.626289828	0.49668593	0.518826242
proportional similarity	0.426183914	0.641212223	0.141755961	0.63214889	0.518457245	0.470453937
d	0.747958646	0.821632863	0.939128446	0.527611754	0.522059746	0.584157452

b) Network Metrics, calculated using the same species matrix for both studies.

	Hill, 1962	**Current Study**
connectance	0.146572104	0.218676123
web asymmetry	-0.978947368	-0.978947368
links per species	0.435087719	0.649122807
number of compartments	1	1
compartment diversity	NA	NA
cluster coefficient	0.15248227	0.226950355
modularity Q	0.479253993	0.436534141
nestedness	4.919740816	10.0260877
NODF	3.660295146	8.035314201
weighted nestedness	0.239844204	0.165464041
weighted NODF	1.557977547	4.294901663
interaction strength asymmetry	-0.544433976	-0.468035443
specialisation asymmetry	0.48201482	0.541496903
linkage density	4.238152126	12.06025872
weighted connectance	0.014870709	0.042316697
Fisher alpha	25.01211869	41.5232781
Shannon diversity	2.89353342	4.1651485
interaction evenness	0.429274551	0.61792694
Alatalo interaction evenness	0.621777808	0.557740323
H2	0.824823549	0.543455919
number of species HL	3	3
number of species LL	282	282
mean number of shared partners HL	13.66666667	33.33333333
mean number of shared partners LL	0.069230963	0.146336539
cluster coefficient HL	0.17207364	0.227621835
cluster coefficient LL	0.547787527	0.798188508
weighted cluster coefficient HL	0.091204409	0.31147565
weighted cluster coefficient LL	1	1
niche overlap HL	0.073456872	0.240820641
niche overlap LL	0.415990723	0.444655954
togetherness HL	0.229193005	0.456852064
togetherness LL	0.033656394	0.033038035
C score HL	0.403565891	0.190309325
C score LL	0.468410226	0.473389356
V ratio HL	8.759036145	6.576470588
V ratio LL	1.455003747	1.840723959
discrepancy HL	133	129
discrepancy LL	45	49
extinction slope HL	0.271424641	0.395856508
extinction slope LL	0.556650332	0.732943629
robustness HL	0.088833727	0.132927502
robustness LL	0.307458194	0.38040196
functional complementarity HL	2373.055928	1253.841098
functional complementarity LL	2366.931756	1989.0383
partner diversity HL	1.969517898	3.102749946
partner diversity LL	0.16043579	0.481358158
generality HL	7.266374585	22.38518181
vulnerability LL	1.209929668	1.735335617

SUPPORTING INFORMATION

CHAPTER 4.1

Table S4.1. Monthly incidence, prevalence and number of captures – all years combined

Figure S4.1 plots of monthly proportions of adult Dunnocks with brood patches, and all birds in moult

Table S4.2. Annual population, proportion of Dunnocks with Avian Pox, survival and detection rates from CJS model

Figures S4.2 Plots comparing annual incidence, survival and study population size.

Table S4.3 Results, given to three decimal places, of fit for models comparing survival rates, avian pox rates and population size.

Supplementary Information Chapter 4

S4 Additional tables and plots

Table S4.1. Monthly incidence, prevalence and numbers of captures with avian pox for all years of the study combined. The p value given is for the proportion of captures with avian pox (prevalence) per month.

Month	New cases per month (incidence)	Proportion of annual new cases detected in each month	Ongoing case per month	Number of captures with avian pox	Total number of captures	Proportion of captures with avian pox (prevalence)	P value
1	3	0.065	3	5	86	**0.058**	**<0.01**
2	3	0.065	4	5	97	**0.052**	**0.83**
3	1	0.022	2	4	137	**0.029**	**0.31**
4	1	0.022	2	2	131	**0.015**	**0.14**
5	0	0	0	0	76	**0**	**0.07**
6	0	0	0	0	171	**0**	**<0.05**
7	2	0.043	2	2	230	**0.008**	**0.06**
8	21	0.456	22	35	282	**0.124**	**<0.01**
9	7	0.152	9	10	137	**0.073**	**0.60**
10	1	0.022	1	1	59	**0.017**	**0.24**
11	4	0.087	4	4	52	**0.077**	**0.24**
12	3	0.065	3	4	91	**0.044**	**0.65**
Total	46		52	72	1549	**0.046**	

Figure S4.1 Month of detection of definite brood patches consistent with egg-laying, in all adult Dunnocks, defined as BTO/EURING brood patch code, BP=2. It is not possible to determine the sex of Dunnocks outside of their breeding attempts. b) Proportion of Dunnocks in moult per month for all years of the study combined. This includes all stage of post-juvenile and post-nuptial moult.

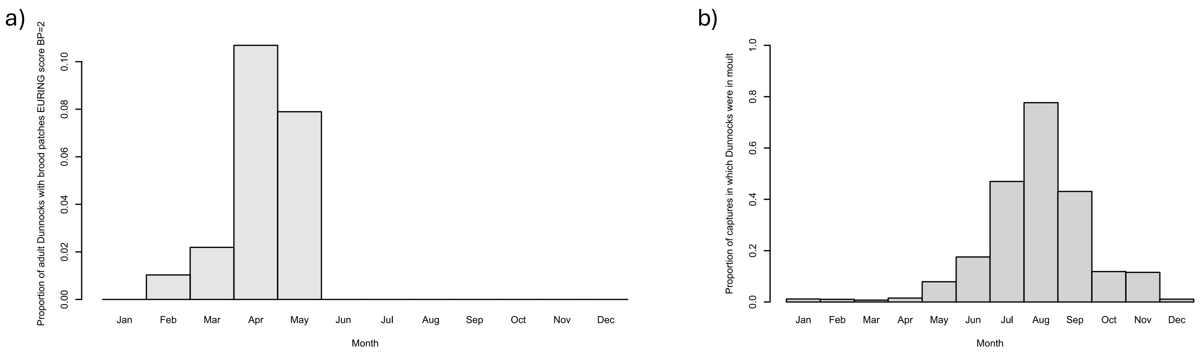
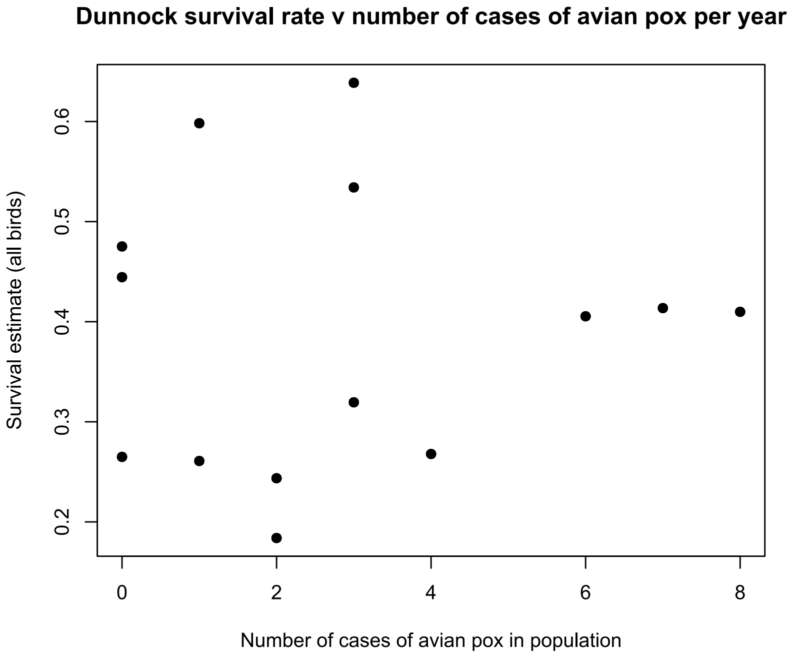


Table S4.2 Annual Dunnock study population count, proportion with avian pox and survival (Phi) and detection estimates (p) from the CJS model, given to three decimal places, with standard errors (SE) lower confidence intervals (LCI) and upper confidence intervals (UCI).

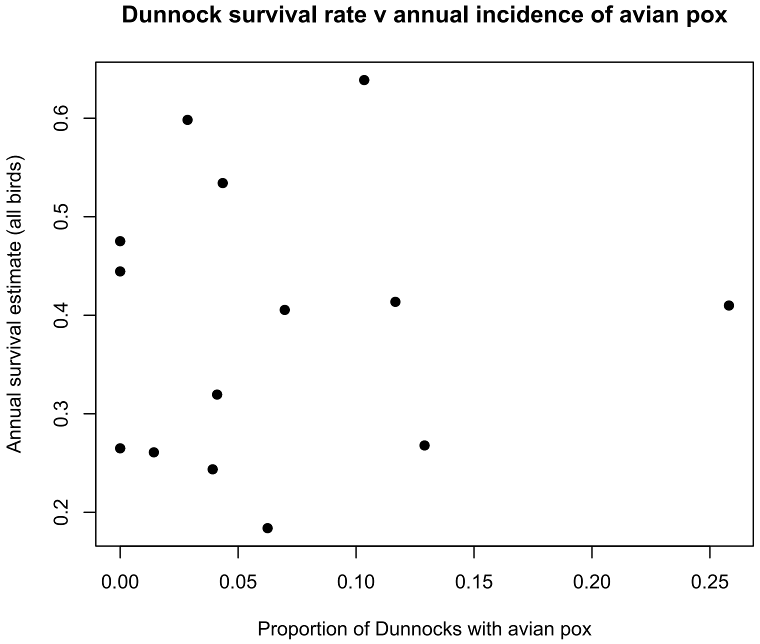
YEAR From June	**YEAR To end May**	**pox cases**	**Total population**	**Pox Proportion**	**Survival Estimate (Phi)**	**SE_phi**	**LCI_phi**	**UCI_phi**	**Detection Probability (p)**	**SE_p**	**LCI_p**	**UCI_p**
2007	2008	0	23	**0**	**n/a**	n/a	n/a	n/a	**n/a**	n/a	n/a	n/a
2008	2009	6	51	**0.117**	**1**	1E-07	1	1	**0.522**	0.104	0.325	0.712
2009	2010	3	73	**0.041**	**0.319**	0.069	0.200	0.468	**0.858**	0.127	0.440	0.979
2010	2011	5	86	**0.058**	**0.405**	0.072	0.274	0.552	**0.813**	0.114	0.501	0.950
2011	2012	3	69	**0.043**	**0.534**	0.116	0.315	0.741	**0.531**	0.124	0.299	0.749
2012	2013	1	70	**0.014**	**0.260**	0.053	0.171	0.377	**1**	0	1	1
2013	2014	0	35	**0**	**0.265**	0.091	0.127	0.473	**0.485**	0.179	0.189	0.792
2014	2015	0	39	**0**	**0.444**	0.148	0.198	0.721	**0.606**	0.194	0.239	0.882
2015	2016	1	35	**0.029**	**0.598**	0.259	0.153	0.925	**0.286**	0.143	0.092	0.612
2016	2017	2	51	**0.039**	**0.244**	0.093	0.107	0.465	**0.746**	0.203	0.265	0.960
2017	2018	7	60	**0.117**	**0.414**	0.153	0.170	0.709	**0.667**	0.241	0.193	0.944
2018	2019	8	31	**0.258**	**0.410**	0.276	0.069	0.867	**0.253**	0.184	0.048	0.695
2019	2020	3	29	**0.103**	**0.639**	0.814	0.001	0.999	**0.121**	0.159	0.007	0.718
2020	2021	2	32	**0.063**	**0.184**	0.193	0.018	0.737	**0**	0	0	0
2021	2022	4	31	**0.129**	**0.268**	0.129	0.092	0.570	**0.613**	0.266	0.150	0.934
2022	2023	0	28	**0**	**0.475**	236.671	0	1	**0.475**	236.686	0	1

Figures S4.2 a-d). Plots numbers and incidence of avian pox, survival and study population of Dunnocks. a) Survival rate against number of cases of avian pox per year. b) Survival rate against annual proportion (incidence) of cases per year. c) Annual survival rate against total population. d) Incidence of avian pox against total population of Dunnocks.

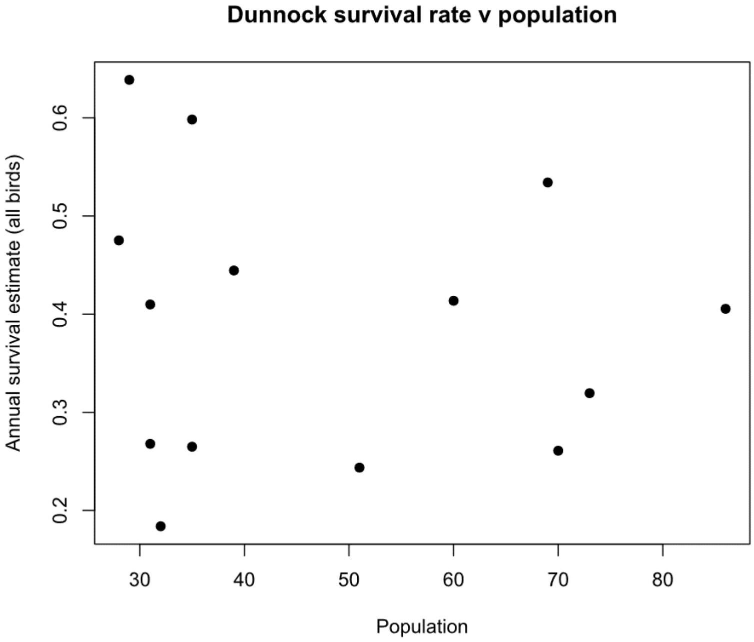
a)



b)



c)


Dunnock survival rate v population
Annual survival estimate (all birds)
0.2
0.3
0.4
0.5
0.6
30
40
50
60
70
80
Population

d)

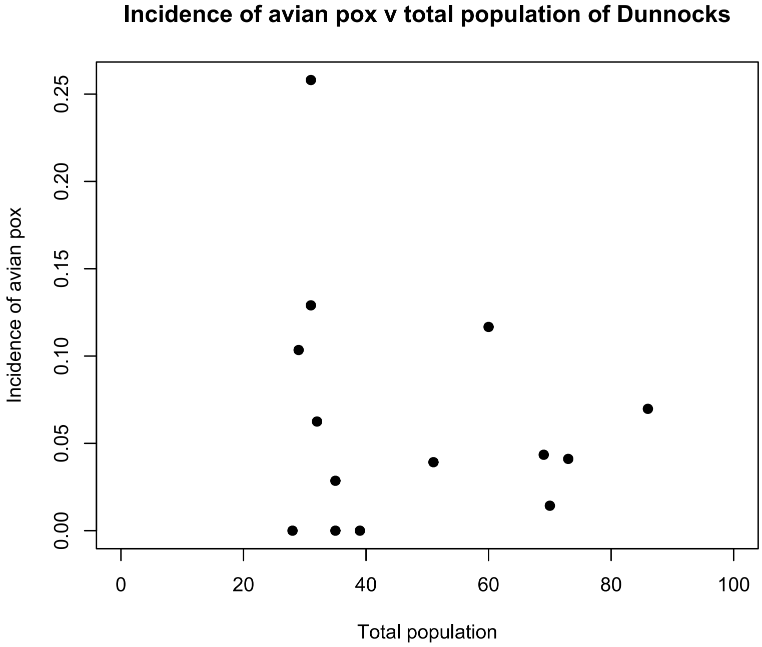

Incidence of avian pox v total population of Dunnocks
Incidence of avian pox
0.00
0.05
0.10
0.15
0.20
0.25
0
20
40
60
80
100
Total population

Table S4.3 Results, given to three decimal places, of fit for models comparing survival rates, avian pox rates and population size.

Model	adjusted R-squared	F-statistic	p-values
model1<-lm(survival estimate ~ annual pox cases)	-0.080	0.039	0.847
model2<-lm(survival estimate ~ annual pox cases/total population	-0.178	0.018	0.982
model3<-lm(survival estimate ~total population)	-0.069	0.157	0.699
model4<-lm((pox cases/total population)~total population)	-0.048	0.410	0.534

SUPPORTING INFORMATION

CHAPTER 5

There is no additional information for this chapter

SUPPORTING INFORMATION

CHAPTER 6

There is no additional information for this chapter