

A longitudinal study of avian pox in a small passerine, the Dunnock (*Prunella modularis*)

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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* (APV). Despite its broad geographical distribution, there are few long-duration longitudinal studies of its epidemiology, and hence limited understanding of basic processes such as seasonality, and mortality rates of affected birds. Here, we report the results of a 15.5-year study of a wild population, involving 1549 captures of 588 Dunnocks *Prunella modularis*, a species recorded as affected by avian pox since the 1940s. Dunnocks were categorized as having avian pox if they were observed with skin lesions suggestive of that disease. The estimated lifetime prevalence of disease was 8.3% (annual range 0–25.8%) at a single site in the UK. No lesions suggestive of avian pox were seen in over 41 000 captures, of over 23 000 individual birds, of 50 other species at the site. No evidence of increased mortality was found in affected Dunnocks: apparent survival probability 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. Most Dunnocks that developed skin 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. In most years, the disease followed a seasonal pattern with a peak in late summer. The same APV DNA sequence was isolated from a skin lesion and from 50% (4/8) of the haematophagous ectoparasitic louse flies taken from apparently healthy Dunnocks at this site, including in years when no cases of avian pox were seen. The results of this study are consistent with APV circulating in Dunnocks with relatively minor adverse effects of avian pox on bird health.

Keywords: avian disease, *Avipoxvirus*, Hippoboscidae, survival, wildlife disease.

Infectious diseases are important determinants of bird 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 & Jeggo 2019) and emerging infectious diseases, such as trichomonosis in European Greenfinch *Chloris chloris* and Eurasian 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

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pathogens, especially those which may be zoonotic, without determining their effects on their host (Plaza *et al.* 2020).

Avian pox is caused by the double-stranded DNA viruses in the genus *Avipoxvirus* (APV) in the family Poxviridae. Currently, seven species of *Avipoxvirus* are recognized (International Committee on Taxonomy of Viruses 2024). Most of these seven species naturally infect only one or a small group of related bird species, although some have been shown to switch host species (Buenestado *et al.* 2004, Gyuranecz *et al.* 2013, 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 *et al.* 1999). The most widely studied is fowlpox virus because it primarily infects chickens and other domestic poultry (van Riper & 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 UK. Most long-term studies have taken place on the Hawaiian Islands, where non-native mosquitoes carrying APV were introduced, infecting both native and introduced species, with severe effects seen in some native species of conservation concern (van Riper *et al.* 2002, Vanderwerf 2009, VanderWerf & Young 2016, Samuel *et al.* 2018, VanderWerf *et al.* 2023). 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 USA an outbreak in Northern Bobwhite *Colinus virginianus* that began in July 1978 subsided in 9 months (Davidson *et al.* 1980) and on Marion Island in the Indian Ocean, where seabirds have been studied since the 1980s, a single case was detected in each of 2 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 5-year period (Young & VanderWerf 2008, VanderWerf & Young 2016). 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 across multiple years.

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 & Forrester 2007). Avian pox is often a seasonal disease in cooler regions where vectors are not active during the winter (van Riper & Forrester 2007, Lachish *et al.* 2012b). Avian pox is more likely to occur in immunologically naïve birds (van Riper *et al.* 2002, Lachish *et al.* 2012b, McGraw *et al.* 2022). Avian infections may be associated with periods of poorer immune function at times of stress, such as during the breeding season and moult (Sheldon & Verhulst 1996, Valdebenito *et al.* 2021).

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

Avian pox has two main presentations: a diphtheritic or 'wet' form affecting the respiratory and upper gastrointestinal tracts which can cause breathing 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). The precise nature and severity of lesions may vary with host species, the strain of the virus and locality. The appearance of 'wet pox', however, is non-specific as it can be similar to other infections such as trichomonosis, candidiasis and bacterial infections, as well

as vitamin A deficiency in aviary birds (Schmidt *et al.* 2015). Avian pox may also cause systemic infection (Schmidt *et al.* 2015). Confusion between avian pox lesions and other causes of swelling on birds' legs may have arisen in some studies due to the term papillomatosis being used to refer to both growths caused by papilloma viruses and wart-like lesions of unknown aetiology (Truchado *et al.* 2018).

Definitive veterinary diagnosis of avian pox relies on testing to confirm the diagnosis using laboratory techniques (Parker *et al.* 2011, Pérez-Tris *et al.* 2011, Alehegn *et al.* 2014), the results of which are generally highly correlated with the appearance of typical macroscopic appearance of skin lesions. The typical histology with Bollinger bodies was found in all of the 'charakteristischen pockenähnlichen Exantheme' ('characteristic pox-like lesions', the comparison being with small-pox lesions) seen in fowlpox (Bollinger 1873) and characteristic skin lesions examined in Great Tits (Lawson *et al.* 2012). Avian pox was confirmed in over 90% of suspected avian pox lesions in Hawaiian birds by a combination of histological examination and isolation of the virus on chorioallantoic membranes (van Riper *et al.* 2002). PCR has also been used to confirm the presence of APV in tissue samples, obtained from carcasses, swabs and biopsies (Senar & Conroy 2004, Parker *et al.* 2011, Lachish *et al.* 2012a, 2012b, Fukui *et al.* 2016, Ruiz-Martínez *et al.* 2016, Schoombie *et al.* 2018). The degree of correlation between the appearance of skin lesions and definitive testing may vary with the species and location as other studies have found lower levels of correlation. For example, in museum specimens from the Galapagos Islands collected over a 110-year period, only 35.6% of the specimens from birds with lesions consistent with avian pox were APV positive on PCR: other causes were identified as feather follicle cysts and post-mortem fungal colonization (Parker *et al.* 2011).

Licensing requirements, welfare concerns and other logistical challenges involved in taking tissue biopsies make strict diagnostic criteria unsuitable for use in living wild birds and necessitate a pragmatic approach to attempt to understand disease ecology. Given the characteristic appearance of skin lesions seen in avian pox, and the correlation with diagnosis by laboratory methods, many studies of the cutaneous form of avian pox in live wild bird populations classify cases as avian pox on the basis of external signs without laboratory confirmation of

all birds (Senar & Conroy 2004, Smits *et al.* 2005, Vanderwerf 2009, Lachish *et al.* 2012a, 2012b, Samuel *et al.* 2018, Schoombie *et al.* 2018). Some of these studies confirm the diagnosis in one or a few birds by PCR, histology or, in earlier studies, by incubation of the virus on chorioallantoic membranes (Senar & Conroy 2004, Smits *et al.* 2005, Lachish *et al.* 2012a, 2012b, Schoombie *et al.* 2018). Others rely on physical signs alone (Vanderwerf 2009, Samuel *et al.* 2018). However, reliance on external signs may miss all but the most severe cases of the diphtheritic form of the disease and all cases of septicaemia or systemic infection due to avian pox.

Disease surveillance has identified a limited number of causes of proliferative skin lesions affecting the legs of wild passerines in Europe. Knemidokoptosis (colloquially known as 'scaly leg'), due to mite infestation, usually has a chalky appearance due to grey or white debris (Pennycott 2003). Papillomatosis infection (colloquially known as 'spiky' or 'tassel feet') typically gives rise to rough, irregular lesions on the feet that may extend up the leg and is usually restricted to Eurasian Chaffinches (Pennycott 2003, Truchado *et al.* 2018). A study of proliferative leg skin lesions in finches in Great Britain diagnosed concurrent knemidokoptosis and *Fringilla coelebs* papillomavirus infection in 71% of cases, while all lesion samples tested for APV were PCR-negative (Lawson *et al.* 2018). In contrast, avian pox usually presents as discrete nodular lesions, on the bare areas of the feet and legs and around the base of the bill, which initially are usually the same colour as the surrounding skin, but may subsequently ulcerate, due to trauma or secondary infection, before scabbing over (Schmidt *et al.* 2015). Another possible cause of proliferative skin disease is neoplasia (Schmidt *et al.* 2015), but documented cases are rare in wild birds (Blackmore & Keymer 1969) and would probably be progressive, unlike avian pox which shows spontaneous resolution. Ticks *Ixodes* sp. have also been suggested as a possible source of confusion with avian pox lesions, but only when seen from a distance (Blackmore & Keymer 1969). If missing toes are included within criteria for suspected avian pox cases, as they are in some studies (van Riper *et al.* 2002, Vanderwerf 2009), other causes such as trauma or entanglement need to be considered.

The Dunnock *Prunella modularis* is a small, brown, predominantly insectivorous passerine,

with a mean body-weight of 21 g which, although common throughout Europe, is on the UK Amber List of Birds of Conservation Concern (British Trust for Ornithology 2023). Dunnock legs are not feathered. The sexes are similar in appearance and it is only possible to determine their sex in the hand during the breeding season when full brood patches or cloacal protuberances are present (Svensson 1992). In the UK, Dunnocks are a sedentary species: post-juvenile dispersal is rarely more than 2 km 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). Garden bird disease surveillance conducted across Great Britain since the early 1990s has regularly received disease incident reports consistent with avian pox in Dunnocks (Lawson *et al.* 2012, Garden Wildlife Health, unpublished data). The diagnosis of avian pox was confirmed in multiple Dunnocks through histological examination combined with Sanger sequencing of APV which clustered in the Canarypox virus subclade B1 (Lawson *et al.* 2012). Knemidokoptosis has been reported in two UK Dunnocks, but the scaly appearance and distribution of knemidokoptosis skin lesions was distinct from those of avian pox (Seilern-Moy *et al.* 2021). A literature review did not find any reports of proliferative skin lesions with other causes in Dunnocks, making them an ideal species for a study of avian pox based on the presence of characteristic lesions.

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. It compares survival probabilities of Dunnocks observed with and without lesions consistent with avian pox with the survival probability of the whole population, estimates the incidence and prevalence of disease, and examines the interactions between the annual number of cases, survival and population size (a proxy for population density). It also aims to explore the seasonality of avian pox, with references to the age structure of the population, breeding and moult cycles, as avian immunity may vary with age, reproductive status and other stressors. Additionally, it uses small numbers of ectoparasitic louse flies (Diptera: Hippoboscidae) collected from healthy Dunnocks for xenomonitoring. The authors discuss how the methods used

and the results obtained can be generalised to other diseases in populations of wild birds, and outline the limitations of this type of study.

METHODS

Data collection

Dunnocks were captured in mist-nets and ringed in a rural garden on the north-east edge of Exmoor, 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) licensed Retrapping Adults for Survival (RAS) Study (<https://www.bto.org/get-involved/volunteer/projects/bird-ringing-scheme/ringing-surveys/retrapping-adults-survival/about-ras>, last accessed on 19 February 2026). RAS studies aim to capture all adult birds of the study species in the study area each year and aim to keep the trapping effort constant across breeding seasons. Unlike many of the other species ringed at the site, Dunnocks could not be attracted to supplementary food, either in walk-in traps or at bird feeders. All birds were ringed with uniquely numbered BTO rings (Redfern & Clark 2001). From 30 September 2010 to 21 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.

At each capture, the age and sex of adults in the breeding season (together with codes for the presence or absence of cloacal protuberances and brood patches), and their moult status were recorded using BTO codes (Redfern & Clark 2001), and notes were made of any injury, external signs of disease or ectoparasite infestation seen, including the sites of lesions consistent with avian pox. In some years, ectoparasitic louse flies were collected and placed in 70% ethanol for identification and further testing, following methods previously described (Wawman *et al.* 2025).

To reduce the risk of disease transmission associated with capture and handling, new birds with signs of avian pox ($n = 3$) were ringed outside, away from other birds, using separate equipment. Previously ringed birds with open, ulcerated or scabbed skin lesions consistent with avian pox were released at the net without further data collection: the age codes and moult status of 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 by using age codes from other captures of the same individual.

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 lesions were observed, and is hereafter referred to as ‘avian pox’. Photographs of typical avian pox lesions from Dunnocks at the study site are provided in Supporting Online Material S1, together with images of other skin diseases affecting birds at the site for comparison.

A diagnosis of avian pox was confirmed in a Dunnock from a skin lesion of typical appearance, shed by the bird at capture and therefore collected using non-invasive methods. The molecular protocols are described in Supporting Online Material S1. A sample of louse flies collected from apparently healthy Dunnocks was screened for APV using the same PCR protocol.

Data analysis

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 (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 additional package *scales* (Wickham & Seidel 2022).

Analyses of disease probabilities and seasonality

From the information in the BTO age codes, birds' ages were classed as ‘first calendar year’ (1cy), ‘second calendar year’ (2cy), ‘adult’ and ‘unknown’. Only one Dunnock was classed as unknown age due to the a priori decision to release severely diseased birds at the net.

Records of birds with suspected non-avian pox skin disease (knemidokoptosis, $n = 1$), 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 *et al.* 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 *et al.* 2002), it may also be due to injury and gives no information about the timing of the episode of disease. Several bird species in the study area often use sheep's wool in their nests, which sometimes tangles around their nestlings, resulting in injury to the nestlings' feet and legs, including loss of digits.

The lifetime prevalence (proportion of birds affected in the population over the duration of the study expressed as a percentage) of avian pox 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 in all age-classes after exclusions. The monthly incidence of 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 seven birds were captured both with and without observable pox lesions in the same month, as they progressed through the course of the disease.

Because the number of birds caught with avian pox lesions was zero in some months, which also gives a standard error of zero, the proportion of Dunnocks in the population with avian pox was estimated using a Bayesian model and is reported as the mean and 95% credible intervals. This was carried out in R, using the package *jagsUI* (Kellner & Meredith 2021), using a Poisson distribution and the uninformative priors in a uniform distribution of 1–10 000 for population size, and 0–1 for the proportion of birds with avian pox. The model was run with three Markov chains, for 10 000 iterations with iterations ‘burn-in’ 500. Convergence was judged to have been achieved when the R-hat values were 1.000 or 1.001, and the outputs 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. Further details of this model are given in the Supporting Online Material S2.

Analyses of survival and detection probabilities

Different age-classes of birds usually have different survival rates, with a high initial mortality seen in first-year birds (Beauchamp 2023), and in this study population, most cases of avian pox occurred

in first-year birds, with too few cases in adults for meaningful analysis of different age-classes. Consequently, data for first-year birds only were split into two subsets: birds which had avian pox at some point and those which were not detected as having avian pox ('pox' and 'no pox'). To compare the number of total captures per bird over the whole study period in the two groups of birds, the mean number of captures was compared using a Welch two-sample *t*-test.

To compare the survival and detection probabilities of 'pox' and 'no pox' groups, a Cormack–Jolly–Seber (CJS) model was used to calculate the apparent annual survival and annual detection probabilities. Resightings of colour-ringed birds were excluded as their disease status was unknown. 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 of being captured or resighted (whether it is diseased or not).
- That every individual has the same probability of survival 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 & Burnham 1999) and thus are only able to calculate apparent survival, with permanent emigrants assumed to be dead.

As avian pox showed a seasonal distribution with no cases in May or June in any year, the analyses were run in years from 1 June to 31 May, by using Julian Day 152, generated by the R package *lubridate* (Grolemund & Wickham 2011) as the start of each year. This avoided splitting avian pox seasons across 2 years and fits more closely with the age structure of the population than using calendar years, as most Dunnocks at the study location fledge between late May and mid-July. The data were analysed in Program MARK version 10.0 (White & Burnham 1999). Birds found dead were treated as birds alive in that year with no further captures. The final models were chosen based on the lowest Akaike information criterion (AIC). 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 due to the low numbers in the pox group so were rejected. The final accepted model estimated single survival and detection probabilities for the whole study period.

Analyses of the relationships between population size, prevalence of avian pox and survival

The second set of analyses used annual population size, the annual prevalence of avian pox and the estimated annual survival rate from a second CJS model to test the relationships between these variables. This model was run in Program MARK using the data from all capture records (no exclusions), for all age-classes, including colour-ring resightings, to obtain survival and detection probabilities for the whole population. Years were again split using Julian Day 152 as the start of each year and birds found dead were treated as birds alive in that year with no further captures. Unlike the previous analysis of first calendar year bird survival, the survival probability *P* and the detection probability *phi* were allowed to vary with time, to estimate separate survival probabilities for each year, to allow for differences in detection probabilities (due to varying ringing effort, changes in habitat, etc.) and changes in survival between years. The final models were chosen based on the lowest AIC.

Program MARK gave an estimate of the annual population size. The annual number of cases of avian pox was a count of the number of cases seen in a year (defined as starting on Julian Day 152) and the prevalence of avian pox was calculated by dividing the number of cases of avian pox by the annual population. A Spearman rank correlation test was used to check for correlation between pairs of variables: annual prevalence of avian survival with the number of cases of avian pox; annual prevalence of avian pox and the annual population of Dunnocks; and the annual prevalence of avian pox with the annual population. Graphs of these pairs of variables were plotted in base R.

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. Of the three birds with skin lesions present at first capture, two caught in 2017 had lesions in the late stages of healing, and a third with active skin lesions, caught during the period when colour-ringing was taking place, was ringed on the other leg and not colour-ringed.

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, which equates to 8.3% (46/554) of the total study population (annual range of 0–25.8%). If a less conservative approach had been adopted and the excluded birds – two Dunnocks with missing toes and two with slightly swollen toes – had been included, the total estimated lifetime prevalence would have been 8.9% (50/558). No other species were observed with skin lesions suggestive of avian pox (over 41 000 captures of over 23 000 individual birds of 50 other species).

The most common site for skin lesions was on the feet (27/46 Dunnocks, 58.7% of cases). Of diseased Dunnocks, 15.1% (7/46) had lesions on the head, at the base of the bill (Table S1.1). None of the lesions on the head were considered large enough to impair vision and, although some on the feet were up to 13 mm in diameter (Fig. 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 the diphtheritic (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. No bird was observed to have more than one episode of avian pox skin lesions.

The number of cases detected varied from year to year, with no cases in some years and up to 25.8% of the population observed with lesions in other years (Table S3.2). However, the sample sizes were generally low in each of the 15.5 years and many Dunnocks were only caught outside the main periods when avian pox was prevalent. Cases of avian pox were detected in each calendar year except 2014, but not in four of the years defined for data analysis purposes as starting from the end of June. Lower levels of detection occurred in some years when the population of Dunnocks was higher, for example, 1.4% when the population was at its peak in 2012–2013 (Table S3.2).

Avipoxvirus infection was confirmed by PCR of a skin lesion from one Dunnock with the sequence identified as APV clade B1 (see Supporting Online Information S1). An identical DNA sequence was detected in 50% (4/8) of the louse flies, *Ornithomya avicularia* and *O. fringillina*, taken from apparently healthy Dunnocks at the site, captured in the years 2013 (1/1 flies tested positive), 2020 (0/2), 2021 (1/2) and 2022 (2/3). However, no cases of avian pox were detected in Dunnocks in either the 2013 or 2022 louse fly seasons.

Disease rates and seasonality

Most (82.6%, 38/46) of the observed avian pox cases occurred in Dunnocks in their first year of life (Table 1). Avian pox was observed in 5.6% (52/927) of captures of birds in their first calendar year, 2.2% (6/270) captures of birds in their second calendar year, before their first post nuptial moult, and 3.6% (10/280) of adult captures (Table 2).

Cases occurred with a seasonal pattern, during 10 months of the year, with no cases detected in May and June despite 247 captures occurring in those months (Fig. 1a and 1b). Cases peaked in August when 45.6% (21/46) of all newly detected cases occurred, and 12.4% (35/282) of captures had avian pox (Table S3.1). While cases in juvenile (first-year) birds peaked in August (Fig. 2a), with a second peak in the February at the start of their second calendar year (Fig. 2b), those of adult birds showed a bimodal distribution with peaks in January and September (Fig. 2c), consistent with an association with the early part of their reproductive cycle and main period of moult (Fig. S3.1a and S3.1b). The number of cases per month and prevalence of avian pox are shown in Table S3.1.

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 of 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%

Survival and detection probabilities

The estimated mean annual survival and detection probabilities 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 probability was 0.32 (se 0.03, CI 0.27–0.37) for the population as a whole, 0.37 (se 0.12, CI 0.18–0.61, $n = 36$) for first-year birds with avian pox and 0.32 (se 0.03, CI 0.26–0.38, $n = 437$) for first-year birds without avian pox. The overlapping confidence intervals indicate that there was no difference in survival probability between the two groups.

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

Analyses of the relationships between population size, prevalence of avian pox and survival

Annual estimates of survival for the whole study population, with no exclusions, are shown in Table 4, together with the number of cases of avian pox and the estimated population sizes.

Spearman rank correlation tests (Table 5) showed very weak correlations (ρ) between

variables, with high S and P -values, suggesting that there was no statistically significant association between survival disease prevalence ($n = 15$, $\rho = 0.178$, $S = 460.1$, $P = 0.525$) or between survival and disease rates ($n = 15$, $\rho = 0.122$, $S = 491.69$, $P = 0.665$) or between survival and the size of the population ($n = 15$, $\rho = -0.170$, $S = 655.26$, $P = 0.545$) or between population sizes and the prevalence of avian pox ($n = 16$, $\rho = -0.070$, $S = 632.51$, $P = 0.797$). Plots of these pairs of variables showed no evident association (Fig. 3).

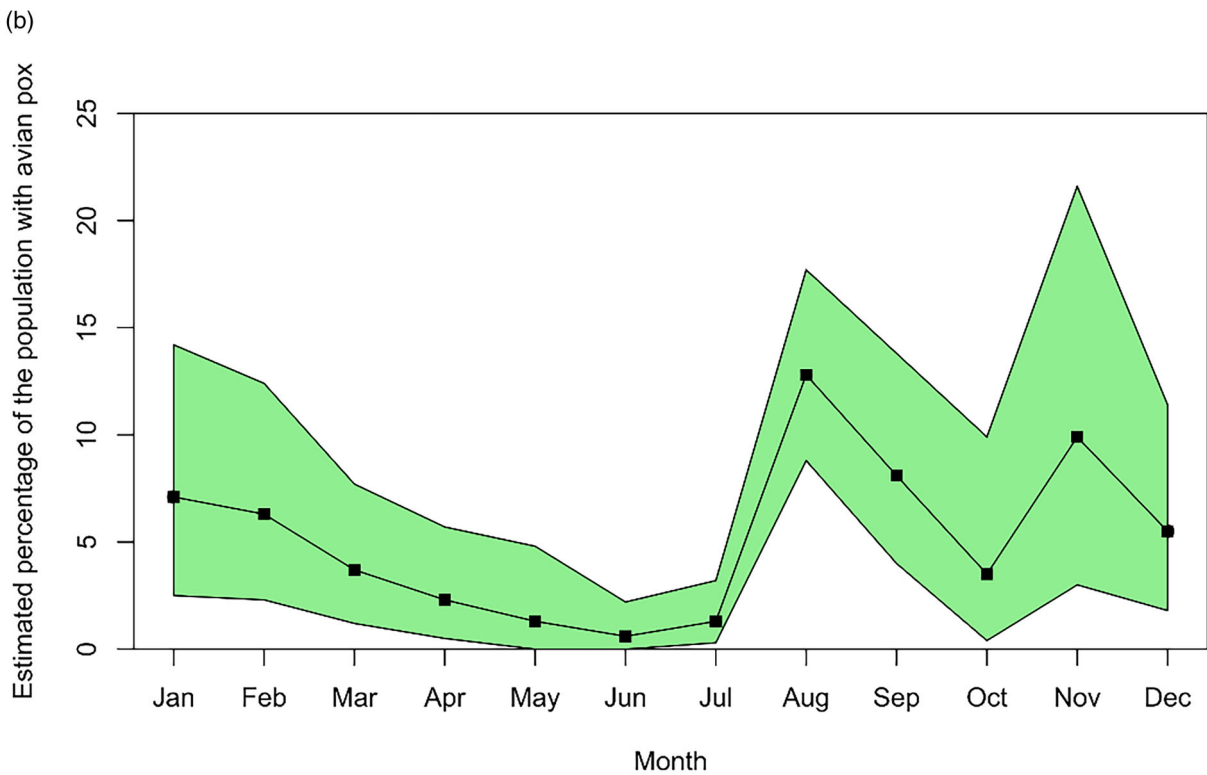
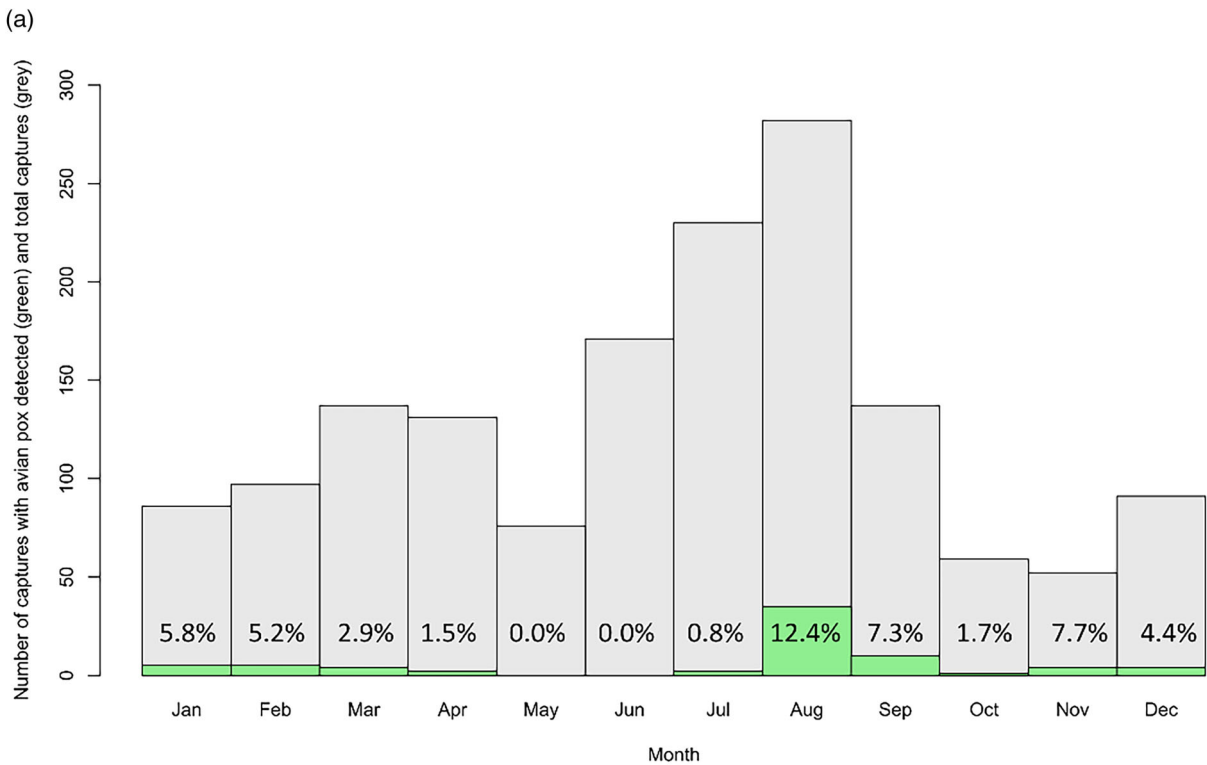
Only 10 Dunnocks were found dead during the course of the study, none of which had skin lesions consistent with avian pox.

DISCUSSION

This 15.5-year study found a lifetime prevalence of avian pox-like lesions of 8.3% of Dunnocks, mainly in juveniles in August, but with no significant difference between the survival probabilities of first-year Dunnocks with and without signs of avian pox. *Avipoxvirus* infection was confirmed by PCR in a skin lesion typical of those seen in other birds in the study. The same APV sequence was detected in 50% (4/8) of the louse flies taken from apparently healthy Dunnocks at the site.

The prevalence of avian pox in this study is similar to the prevalence of observed lesions reported in some other studies of endemic disease in small passerines, for example, 7.2% of House Finches (McGraw *et al.* 2022) and 6.1% of Henslow's Sparrows *Centronyx henslowii* in the USA (Ellison *et al.* 2014). However, this prevalence is higher than in some studies of endemic avian pox in passerines that report a prevalence of 0.0–3.7% (Williams *et al.* 2021). Studies of populations of passerines where avian pox has been introduced or switched to new host species often find far higher prevalences than is seen in endemic pox. For example, avian pox affected 40% of Hawaii 'Elepaio *Chasiempis sandwichensis*, a small monarch flycatcher, in some areas of Hawaii where avian pox was introduced to naïve populations over 100 years ago (Vanderwerf 2001), and 50% of

Figure 1. Seasonality of avian pox in Dunnocks: (a) the number of captures with avian pox (green shaded bar) and total number of captures (grey bar) with figures giving the percentage of captures of Dunnocks with avian pox shown in each month; (b) an estimate of the percentage of Dunnocks in the population with avian pox shown with the mean and 95% credible interval derived from the Bayesian model described in the Methods.



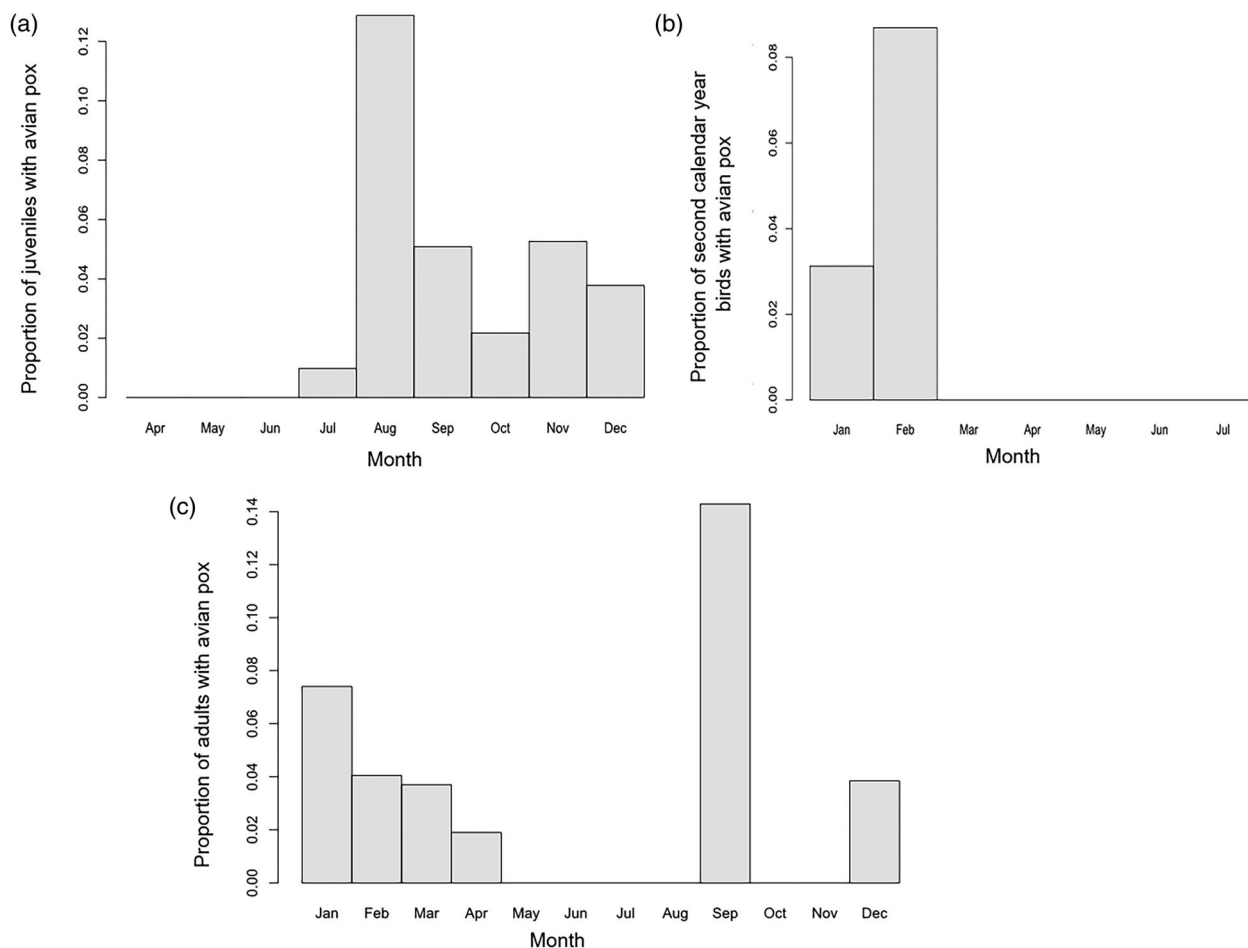


Figure 2. Proportions of Dunnocks detected with avian pox each month in each age-class for all years combined. (a) Juveniles (first calendar year birds), (b) second calendar year birds, (c) adults.

Table 3. Results of a Cormack–Jolly–Sieber model showing survival and detection probabilities of Dunnocks, for the first calendar year (1cy) aged Dunnocks with avian pox lesions (pox) and birds that were not detected as having avian pox (no pox) after exclusions, and for the whole study population (all birds of all ages, no exclusions), given to three decimal places, with standard errors (se), lower confidence intervals (LCI) and upper confidence intervals (UCI). The first two groups' survival and detection estimates are based only on trapping data, whereas the final group includes field observations of colour-ringed birds.

Group	Statistics	Estimate	se	LCI	UCI	Number
Pox 1cy	Survival (Φ)	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 (Φ)	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 (Φ)	0.315	0.026	0.265	0.368	588
All birds	Detection probability (P)	0.579	0.061	0.456	0.692	588

Mediterranean Short-toed Larks *Alaudula rufescens* and 28% of Berthelot's Pipits *Anthus berthelotii* in the Canary Islands where APV is believed to have switched hosts (Smits *et al.* 2005).

A molecular study has shown that a high proportion of some species of wild birds are infected with APV: PCR detected APV in the spleens of 43% of wild birds, mostly waterfowl and other

Table 4. Annual Dunnock study population count, proportion with avian pox (annual prevalence) 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). One Dunnock from the study population, captured after the end of May 2023, is not included in these totals because its capture occurred after the stated 12-month period.

Year from June	Year to end May	Pox cases	Total population	Pox proportion or annual prevalence	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

Table 5. The results of a series of Spearman rank coefficient tests, comparing pairs of variables: annual survival and number of cases of avian pox observed in the population, the annual prevalence of avian pox and the annual population; the prevalence of avian pox and the annual population. The Spearman coefficients and *P*-values have been rounded to three decimal places.

Variable 1	Annual survival rate	Annual survival rate	Annual survival rate	Annual pox prevalence
Variable 2	Number of cases of pox	Annual pox prevalence	Annual population	Annual population
Pairs of variables	15	15	15	16
rho, Spearman coefficient	0.178	0.122	-0.170	0.070
S sum of squares	460.1	491.69	655.26	632.51
<i>P</i> -value	0.525	0.665	0.545	0.797

larger species, in Italy (Bertelloni *et al.* 2022), suggesting that APV infection may go undetected. There is also evidence of widespread undetected exposure to APV: 69.2% of a mixture of introduced species in New Zealand were seropositive for avian pox (Ha *et al.* 2013).

APV was detected in 50% of louse flies which had been feeding on apparently healthy Dunnocks at the site. Although this was only a small sample, the absence of skin lesions on these Dunnocks and the detection of APV in louse flies in years when no avian pox cases were observed in birds at the site are further evidence that APV may be circulating at higher levels than detected in this study and may not result in externally visible disease; however, without further testing of Dunnocks, it

is not possible to determine whether subclinical infection occurred. A sample of louse flies from Dunnocks across the UK tested positive for the same strain of APV at sites where avian pox was not observed by bird ringers (Wawman *et al.* 2025). The same strain was found in seven Dunnocks with skin lesions (Lawson *et al.* 2012).

In this study, the annual detection probability calculated by the CJS model was slightly lower in the avian pox group of first-year Dunnocks (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 for birds without avian pox) and the increased frequency of capture may have increased

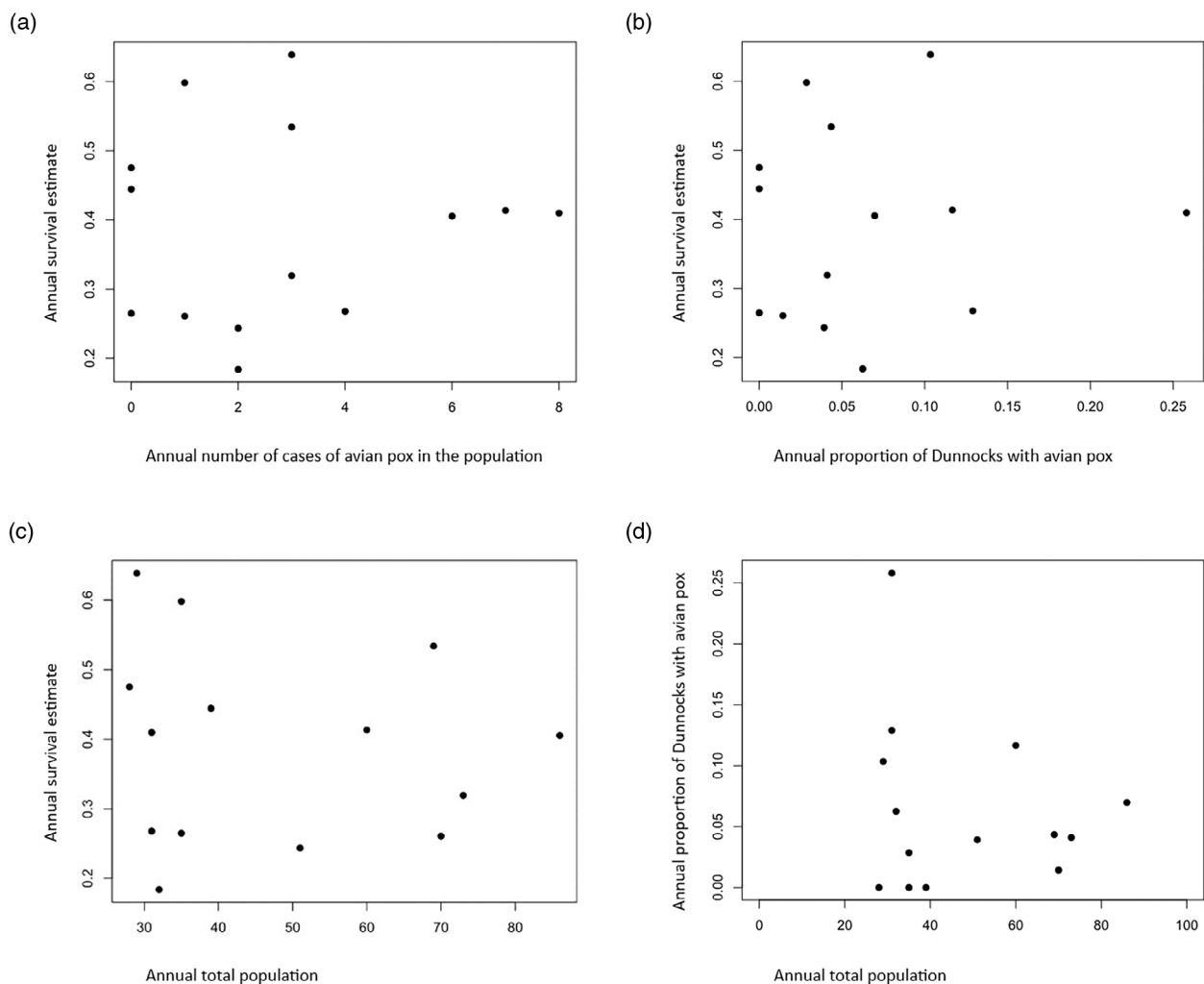


Figure 3. (a–d) Plots of the survival estimate (probability), proportion of Dunnocks with avian pox and size of study population of Dunnocks, showing the absence of any correlation. (a) Annual survival estimate (probability) plotted against annual number of cases of avian pox in the population. (b) Annual survival estimate (probability) plotted against annual proportion of Dunnocks with avian pox. (c) Annual survival estimate (probability) plotted against annual total population. (d) Annual proportion of Dunnocks with avian pox plotted against total annual population.

the probability that the disease would be observed in these Dunnocks. If the duration of observed disease in Dunnocks could be as short as 36 days (Wawman 2025) or the 2.5 months reported for complete resolution of lesions in the 1940s (Edwards 1955), it is entirely possible that disease may not have been detected, especially in Dunnocks caught less frequently, as they may have developed lesions and recovered between captures. A study of Red-legged Partridges *Alectoris rufa* in Spain found that individuals that were inspected for pox lesions more than once during the study

period had a 75% prevalence of avian pox compared to a prevalence of 41.4% of the whole population (Buenestado *et al.* 2004).

While the apparent similarity in survival probabilities between birds with and without observed avian pox may indicate failure to detect avian pox, it might suggest that avian pox in Dunnocks has a low case mortality rate. The observation that none of the lesions appeared to impair vision or feeding supports the hypothesis that endemic avian pox is typically a disease with a lower case-fatality rate in UK Dunnocks than in some other species, as does

the lack of evidence of a relationship between the survival rate and infection rate. Studies in other European wild bird populations have found higher mortality rates. For example, in 1996, a single outbreak of avian pox in European Serins *Serinus serinus* in north-eastern Spain reported a survival rate of 0.46 in birds with avian pox compared to 0.87 in healthy birds (Senar & Conroy 2004).

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 species (van Riper & Forrester, 2007).

It is possible that the CJS model failed to detect a real difference in the survival probabilities 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 & 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 birds with avian pox 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 & Conroy 2004) possibly due to sick birds being less able to leave the area.

As in a previous UK study that examined the occurrence of non-Paridae pox, in which 49.5% of incidents were in Dunnocks (Lawson *et al.* 2012), the largest peak in observed cases occurred from late July to mid-September. The peak of cases in autumn might be due partly 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 probably due to 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 first-year birds, although analyses of annual population size and 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 also likely to be 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 *et al.* 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 the mite *Dermanyssus gallinae* (Shirinov *et al.* 1972, Huong *et al.* 2014), stable flies *Stomoxys calcitrans* (Alehegn *et al.* 2014), fleas (Smits *et al.* 2005), midges (Lee *et al.* 2017) and the louse flies *Ornithomya avicularia* and *O. fringillina* (Wawman *et al.* 2025).

Cases of avian pox in adult Dunnocks had a bimodal distribution, with peaks in January and September. While it is possible that the lesions observed early in the year had developed in the previous year and gone undetected, these peaks correlate with increased periods of stress and hormonal changes which can result in poorer immune responses. This could reflect 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 & Verhulst 1996) or moult (Hamilton & 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, has been shown to lower the immune response to infection (Folstad & Karter 1992). In females, some modulation of immune activity within the reproductive tract is required to avoid immune-mediated damage to spermatozoa and the developing embryo (Wigby *et al.* 2019). In domestic hens, a decrease in immunity as hens come into lay has been associated with a transient increase in *Salmonella enterica* serovars Enteritidis and Pullorum numbers in the spleen and translocation to the reproductive tract (Wigley *et al.* 2005, Johnston *et al.* 2012). 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 & Clark 2001) – roughly corresponds to the start of egg laying (Hinde 1961, Jones 1971), and in this population, brood patches in this state were present from February to May.

CONCLUSIONS

The uncertainty around the possibility of subclinical APV 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 invasive sampling to determine the immunological status of birds and the role of vectors in disease transmission. Serial inspection for avian pox lesions combined with 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 infections. It would also allow exploration of the immunological response to infection and how this varies between birds and throughout the year. Louse flies in the genus *Ornithomya* collected from known individual Dunnocks could be used to detect APV, and regular sampling of mosquitoes, midges, ticks and biting flies throughout the year could enhance knowledge about how APV is circulating in potential vector populations. While the gold standard to establish the incubation period would be studies on captive Dunnocks, these would be ethically challenging, and aspects such as survival rates might not be generalizable to wild populations exposed to a wide range of climatic conditions, predators, parasites and other infectious diseases.

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 demographic rates. Although colour-ringing of individuals so that they can be resighted without being recaptured may boost survival estimates, it is not helpful if birds need to be categorized as either clinically sick or healthy at each capture. Our results provide foundations for future studies by demonstrating the prevalence of avian pox in Dunnocks and its seasonality and demography that could be generalized to other species, including the use of ectoparasitic louse flies for xenomonitoring.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ETHICAL NOTE

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

AUTHOR CONTRIBUTIONS

Denise C. Wawman: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision; resources. **Steven R. Fiddaman:** Visualization; investigation; writing – review and editing. **Becki Lawson:** Writing – review and editing. **Maria D. Christodoulou:** Validation; writing – review and editing. **Ben C. Sheldon:** Writing – review and editing; supervision. **Adrian L. Smith:** Resources; supervision; writing – review and editing.

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DATA AVAILABILITY STATEMENT

The dataset is available in ORA, the University of Oxford Research Archive, as Wawman, DC. 2026. Avian Pox in Dunnocks Capture Data. University of Oxford. <https://doi.org/10.5287/ora-44gndqb92>. The *Avipoxvirus* sequence from the lesion is available at GenBank (<https://www.ncbi.nlm.nih.gov/genbank>. Last accessed on 20 March 2025) with accession number PP756527, and those from the louse flies with accession numbers PQ790031, PQ790032, PQ790033 and PQ790034.

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SUPPORTING INFORMATION

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

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

Figure S1.1. Skin lesions in Dunnocks consistent with avian pox. (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.

Figure S1.2. Confirmed 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, d) after the same lesion sloughed off on 25 August 2023.

Figure S1.3. Other causes of lesions seen in birds at the study site. All are clearly distinguishable from the discrete nodular lesions seen in Dunnocks at the site. (a) Generalized proliferative skin lesions affecting the tarsometatarsus, tarsus and digits of a Bullfinch *Pyrrhula pyrrhula*. (b, c) Chaffinch *Fringilla coelebs* consistent with knemidokoptosis and/or *Fringilla papillomavirus* infection (Lawson *et al.* 2018). (d) *Ixodes* sp. ticks on the head of a Great Tit *Parus major*.

Figure S1.4. Maximum likelihood phylogeny showing how the sequence of *Avipoxvirus* (APV) from the current study fits into the various clades of APV. It was based on a maximum likelihood tree of 1000 bootstraps in RAxML (Stamatakis, 2014) using the nomenclature used by Gyuranecz *et al.* (2013). The right hand side of the plot shows the APV phylogeny, with the Canary Pox subclade B1 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.

Data S2 Additional methods.

Table S3.1. 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.

Figure S3.1. (a) 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.