

Original Contribution

Evidence of Spread of the Emerging Infectious Disease, Finch Trichomonosis, by Migrating birds

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Abstract: Finch trichomonosis emerged in Great Britain in 2005 and led to epidemic mortality and a significant population decline of greenfinches, *Carduelis chloris* and chaffinches, *Fringilla coelebs*, in the central and western counties of England and Wales in the autumn of 2006. In this article, we show continued epidemic spread of the disease with a pronounced shift in geographical distribution towards eastern England in 2007. This was followed by international spread to southern Fennoscandia where cases were confirmed at multiple sites in the summer of 2008. Sequence data of the ITS1/5.8S/ITS2 ribosomal region and part of the small subunit (SSU) rRNA gene showed no variation between the British and Fennoscandian parasite strains of *Trichomonas gallinae*. Epidemiological and historical ring return data support bird migration as a plausible mechanism for the observed pattern of disease spread, and suggest the chaffinch as the most likely primary vector. This finding is novel since, although intuitive, confirmed disease spread by migratory birds is very rare and, when it has been recognised, this has generally been for diseases caused by viral pathogens. We believe this to be the first documented case of the spread of a protozoal emerging infectious disease by migrating birds.

Keywords: trichomonosis, *Trichomonas gallinae*, *Carduelis chloris*, *Fringilla coelebs*, migration, emerging infectious disease

INTRODUCTION

The international spread of emerging infectious diseases (EIDs) can be facilitated by a variety of means, and much

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attention has been given to anthropogenic factors, such as habitat degradation and urbanisation, international travel, regulated and unregulated trade and species translocation (Daszak et al., 2001; Bradley and Altizer, 2007). Pathogen movement and disease spread also can occur through non-anthropogenic routes, such as long-distance movement of migratory species, and this subject has been particularly topical in recent years following the emergence of H5N1 highly pathogenic avian influenza (Gilbert et al., 2006; Kilpatrick et al., 2006; Gauthier-Clerc et al., 2007; Keawcharoen et al., 2008). For instance, the extent to which waterfowl species infected with highly pathogenic H5N1 avian influenza virus may be capable of long-distance migration has been debated (Olsen et al., 2006). Migrating house finches (*Carpodacus mexicanus*) with asymptomatic infection are thought to have assisted the spread of *Mycoplasma gallisepticum*, the cause of epidemic conjunctivitis in this species, across Eastern North America (Dhondt et al., 1998; Hosseini et al., 2006). Migration is energetically demanding; therefore, birds infected with pathogens may be unable to move long-distances (Weber and Stilianakis, 2007). Perhaps as a consequence, there are few documented examples of pathogen spread through bird migration; furthermore, when these have been recognised, the examples are typically of viruses or bacteria rather than of protozoal parasites.

Trichomonosis, caused by infection with the protozoan *Trichomonas gallinae*, is well known internationally as a cause of morbidity and mortality in columbiform species and birds of prey (Forrester and Foster, 2008). In 2005, trichomonosis was recognised as an EID of wild finches in Great Britain (Pennycott et al., 2005; Lawson et al., 2006) with late summer/autumn seasonal epidemic mortality primarily involving greenfinches *Carduelis chloris* and chaffinches *Fringilla coelebs*. In 2005 and 2006, finch species represented 84% (292/347) of trichomonosis cases examined post mortem; collectively, the greenfinch and chaffinch accounted for 80% (279/347) of these birds, and columbiform species for 11% (37/347). Trichomonosis was also diagnosed in a small number of individuals from other passerine hosts, including the bullfinch *Pyrrhula pyrrhula*, goldfinch *Carduelis carduelis*, brambling *Fringilla montifringilla*, siskin *Carduelis spinus*, house sparrow *Passer domesticus*, yellowhammer *Emberiza citronella*, dunnock *Prunella modularis* and great tit *Parus major*; collectively, all these accounted for only 9% (31/347) of trichomonosis cases (Robinson et al., 2010).

The 2006 trichomonosis epidemic is estimated to have caused a decline of ca. 35% and ca. 20% of the breeding population for greenfinch and chaffinch, respectively in the region of greatest disease incidence (Robinson et al., 2010). Although the disease had been infrequently diagnosed in captive and free-ranging finches previously (Chalmers, 1992; USGS, 2002; Anderson et al., 2009), the outbreak in Britain was the first reported instance of large-scale epidemic mortality due to trichomonosis in passerine species. The origin of *T. gallinae* in British finches is unknown, but sympatric columbiform species are considered the most likely source (Robinson et al., 2010).

Although both greenfinch and chaffinch are widespread across Great Britain, finch mortality due to trichomonosis was initially (i.e. in 2005 and 2006) greatest in western and central counties of England and Wales, whilst the number of incidents observed in eastern England was low (Robinson et al., 2010). In this article, we demonstrate the spread of finch trichomonosis to eastern England in 2007 and then to southern Fennoscandia in 2008. Possible mechanisms for the observed pattern of disease spread are explored.

METHODS

Spatial Distribution of the Epidemic in Britain

Pattern of Garden Bird Mortality Reports

In 2005, a nationwide system for the investigation of causes of garden bird morbidity and mortality in Britain was created (the Garden Bird Health *initiative*, GBHi) (Robinson et al., 2010). Reports of garden bird mortality were received opportunistically from members of the public via the Royal Society for the Protection of Birds (RSPB), or directly to each of the veterinary diagnostic centres, and systematically from approximately 750 identified, constantly observed, sites across Britain through the British Trust for Ornithology's Garden BirdWatch (BTO GBW) scheme (Cannon et al., 2005). BTO GBW participants provided weekly reports on whether or not they observed sick or dead birds in their garden throughout the study period. Post-mortem examinations were performed on 1,238 garden bird carcasses of 45 species, including 797 finch species, submitted from a subset of incidents from both sources of mortality reports between the 1st January 1st 2006 and the 31st December 2007. Our case definition

for incidents of finch trichomonosis is detailed in (Robinson et al., 2010). In brief, finch trichomonosis was confirmed if one or more dead finches from a mortality incident had characteristic necrotic ingluvitis lesions in combination with the detection of motile trichomonads directly or following culture and/or nested PCR amplification of part of the *T. gallinae* SSU rRNA gene. A finch trichomonosis incident was defined as a mortality incident which occurred between the 1st April and the 30th September and which involved two or more dead finches (greenfinch or chaffinch), or one or more sick finch(es) with typical signs of disease (fluffed-up plumage, lethargy and dysphagia), or if trichomonosis was confirmed post mortem within this time period. This 6-month interval was selected to minimise the likelihood of confounding these data with finch mortality due to salmonellosis, outbreaks of which occur during the winter months and which also result in non-specific signs of malaise in finches (Pennycott et al., 2002; Lawson et al., 2010).

In order to evaluate the geographical distribution of the epidemic in Britain in 2007, data from the opportunistic and systematic reporting schemes were independently examined using techniques extrapolated from Robinson et al. (2010), which controlled for temporal and spatial reporting biases.

Ring Return Data

The BTO operates the British and Irish Ringing Scheme under which volunteers annually ring ca. 800,000 birds a year (Coiffait et al., 2009). Of these ringed birds, ca. 15,000 are subsequently reported each year (15% of which are outside the British Isles), either dead or alive away from the original site of ringing. For all such records, the date and place of finding are reported and, for many of the birds found dead, a putative cause of death is given based on the circumstances of finding (e.g. bird fluffed up and lethargic before death consistent with disease, carcass found in close proximity to window consistent with trauma, evidence of cat kill consistent with predation). To quantify large-scale spatial and temporal variations in greenfinch mortality, the species most frequently affected by trichomonosis, we examined records of a total of 2,206 recoveries of marked greenfinches found dead between the 1st June and the 30th November for the period from 1996 to 2007 (inclusive). We used this period within each year as it relates to the period of peak trichomonosis-related mortality. As we were mostly interested in longitudinal spread from the main area

of the initial outbreak (western Britain), we excluded records of birds that were found dead north of 55°N (approximately the latitude of Newcastle-upon-Tyne).

Ring return records were classified according to the standardised reporting codes of the EURING code exchange scheme (Speek et al., 2001) based on the information submitted by the recorder. Post-mortem examinations were not performed on the ring return records, and this dataset is independent of the disease surveillance undertaken by the GBHi. For the temporal analysis, we aggregated these codes into five causes of death: predation, disease, ‘natural causes’ (mostly birds that looked emaciated with no obvious trauma and so presumed starved, but some are likely to have been in poor body condition as a result of disease), ‘collision’ (mostly with road traffic or windows) and ‘unknown’. To compare among categories, we standardised the number of reports each year by the mean number of annual reports for each category during the period 1996–2005 before the epidemic. For the spatial analysis, we considered all reports of diseased finches ($n = 69$), those reported as dying due to ‘natural causes’ ($n = 17$) and those for which cause of death was unknown, i.e. there was no obvious sign of trauma or other reason for mortality ($n = 853$).

Surveillance for Garden Bird Disease in Fennoscandia

Disease investigation of unusual mortality events in free-ranging wildlife in Fennoscandia is performed by governmental organisations and a comprehensive general surveillance program covering the entire region has been in place since the 1960s. In Finland, Norway and Sweden, reports of wild bird morbidity and mortality are received from members of the public and licensed bird ringers on an *ad hoc* basis. Collectively, approximately 27,000 wild bird post-mortem examinations of circa 50 species have been performed since 1992 with no confirmed cases of finch trichomonosis. There was no change in the intensity of surveillance, or in the range of species targeted, in response to the emergence of finch trichomonosis in Great Britain. In Norway, carcasses are also submitted by inspectors belonging to the Norwegian Food Safety Authority. In Finland, disease events are also reported by those participating in the winter bird census, organised by the Finnish Museum of Natural History, which monitors over two hundred winter feeding places for birds (Väisänen and Koskimies, 1991).

Post-mortem examinations on finch carcasses submitted from multiple sites of mortality in each of these three countries were performed at central governmental laboratories. Trichomonosis was diagnosed on the basis of characteristic lesions of necrotic ingluvitis along with the presence of trichomonad protozoa in wet preparations or in trichomonad culture from lesions (Neimanis et al., 2010).

Molecular Comparison of *T. gallinae* Isolates from British and Fennoscandian Finches

DNA was extracted from archived frozen ingluvitis lesions or positive parasite cultures from Fennoscandian finches found dead in 2008, using standard techniques (Table 1). PCR amplification and sequencing of part of the ITS1/5.8S/ITS2 ribosomal region and SSU rRNA gene was performed using the primers and cycling conditions described by Robinson et al. (2010). Amplicons were sequenced and the sequence data were compared with those obtained previously from *T. gallinae* isolated from British greenfinches found dead in 2005–2006 (Robinson et al., 2010).

Assessment of Bird Migration as a Mode of Parasite Spread

We examined recoveries of birds which had been ringed in Britain and re-encountered on mainland Europe in the

period 1980–2008. We limited ring recovery data to greenfinch, chaffinch, wood pigeon *Columba palumbus* and collared dove *Streptopelia decaocto* as these were the species in which trichomonosis was most frequently confirmed in Britain and determined the extent of migration of each species between Britain and Fennoscandia. Available data for species less frequently affected by trichomonosis, particularly goldfinch *Carduelis carduelis* and house sparrow *Passer domesticus*, were also reviewed.

RESULTS

Spatial Distribution of the Epidemic in Britain

Pattern of Garden Bird Mortality Reports

Post-mortem examinations were performed on 1,228 garden bird carcasses during 2006 and 2007; overall, the categories for cause of death were 64.2% ($n = 788$) significant infectious disease (\pm trauma or predation), predation alone 5.5% ($n = 68$), trauma alone 17.4% ($n = 214$), other causes in 1.3% ($n = 16$) and was undetermined in the remaining birds 11.6% ($n = 142$). In Britain, a total of 1,054 finch trichomonosis incidents were recorded between the 1st April 2006 and the 30th September 2006, and 1,505 finch trichomonosis incidents were recorded between the 1st April 2007 and the 30th September 2007 through the opportunistic reporting scheme according to our pre-defined criteria (Fig. 1).

Table 1. Details of the trichomonosis cases in Fennoscandia 2008 from which DNA was extracted for PCR amplification and sequencing

Case number	Species	Date found	Location	PCR and sequence of ITS1/5.8S/ITS2 ribosomal region	PCR and sequence of SSU rRNA gene
Finland 1	Greenfinch	Oct 10	Turku, Finland	Yes	No
Finland 2	Greenfinch	Nov 5	Turku, Finland	Yes	Yes
Norway 1	Greenfinch	Aug 22	Hedmark, Norway	Yes	No
Norway 2	Greenfinch	Sep 4	Akershus, Norway	Yes	Yes
Norway 3	Greenfinch	Sep 4	Akershus, Norway	Yes	No
Norway 4	Greenfinch	Sep 25	Oslo, Norway	Yes	Yes
Norway 5	Greenfinch	Oct 22	Vestfold, Norway	Yes	Yes
Sweden 1	Greenfinch	Aug 3	Västervåla, Sweden	Yes	No
Sweden 2	Greenfinch	Aug 3	Västervåla, Sweden	No	Yes
Sweden 3	Chaffinch	Aug 14	Surahammar, Sweden	No	Yes
Sweden 4	Greenfinch	Oct 6	Nyhem, Sweden	Yes	No
Sweden 5	Greenfinch	Oct 22	Bjursås, Sweden	Yes	Yes
Sweden 6	Greenfinch	Oct 28	Nyköping, Sweden	Yes	No

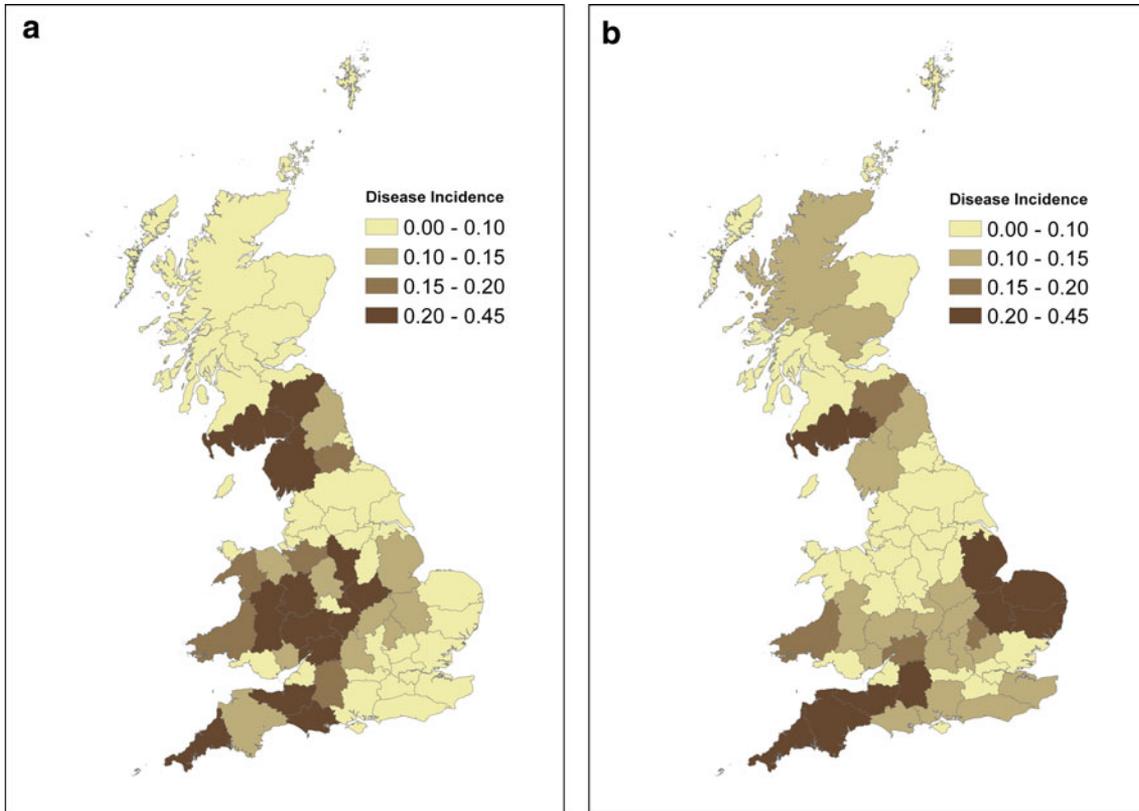


Figure 1. Relative frequency of finch trichomonosis (incidents per thousand households) during the periods (a) the 1st April and the 30th September 2006 and (b) the 1st April and the 30th September 2007.

In total, 125 greenfinches were examined post mortem between the 1st April and the 30th September in 2006, and 126 for the same period in 2007. Infectious disease was considered to be the cause of death for 78% (97/125) of those greenfinches examined in 2006 and 86% (108/126) in 2007; trichomonosis accounted for 93% (90/97) and 99% (107/108) of these infectious disease diagnoses during the same years, respectively.

The seasonal peak for finch trichomonosis incidents each year was in the autumn (peak August–October); however, the spatial distribution of the outbreak varied between years. Both the opportunistic and systematic surveillance schemes independently supported the eastward spread of the epidemic in 2007. In 2006, areas of epidemic finch mortality due to trichomonosis reported through the opportunistic survey occurred primarily in Wales and the western counties of England; in 2007, high numbers of finch trichomonosis incidents were reported from eastern England. This eastward spread was confirmed by the systematic survey with a mean longitude for reports in 2006 of 2.64°W (quartile range 1.70°W–3.11°W) and 1.97°W in 2007 (quartile range 0.93°W–2.80°W, $t_{72} = 1.99$, $P = 0.05$).

Ring Return Data

The numbers of ringed greenfinches reported dead during 2006 and 2007 (336 and 348, respectively) were substantially higher than the number reported dead in any of the previous 10 years (mean per year 130, range 107–157). The proportion of individuals recorded as having died as a result of disease was also larger, 7% of all the recoveries in 2006/07 compared to a mean of 1.6% (range 0–2.3%) in the previous 10 years (Fig. 2). The number of birds reported as having died from natural or unknown causes showed a smaller increase reflecting the fact that some birds dying of disease will not have been identified as such, and the fact that diseased individuals are more likely to succumb to starvation or other mortality causes. In contrast, the number of birds reported as having died through collision impacts showed no change.

In the 10 years before the outbreak of epidemic mortality in 2006, reports of dead ringed greenfinches were more or less evenly distributed across England with respect to longitude (Fig. 3). In 2006, 60% of recoveries came from a region spanning 3.5°W (mid-Wales) to 1°W (Portsmouth

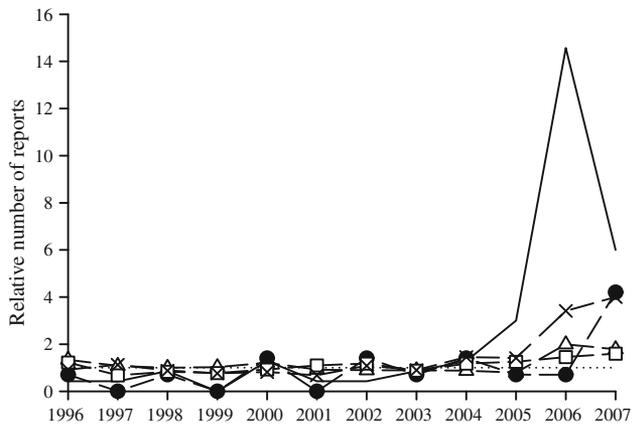


Figure 2. Number of ringed greenfinches reported in each year ascribed to particular mortality causes: disease (solid line, $n = 69$), predation (dashed line with triangles, $n = 525$), collision (dashed line with squares, $n = 522$), 'natural causes' (dashed line with circles, $n = 17$) or unknown cause (dashed line with crosses, $n = 853$). Number of mortality reports expressed relative to the mean number reported annually during 1996–2005 (dotted line).

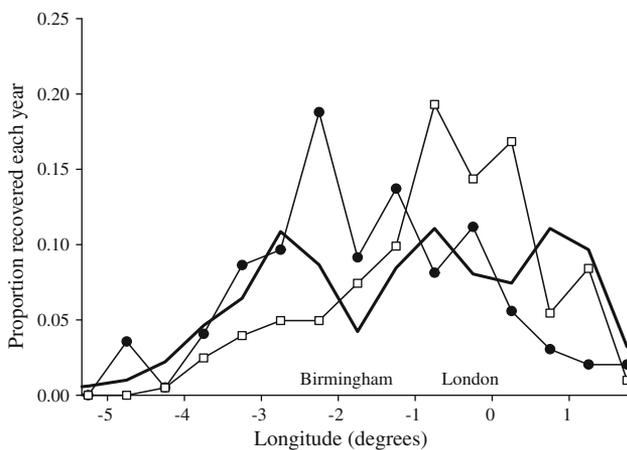


Figure 3. Number of dead ringed greenfinches reported in each 30-min longitude band during 1996–2005 (line), 2006 (circles) and 2007 (squares).

and Nottingham), whereas in 2007, 66% of recoveries came from a region spanning 1.5°W (Southampton and Sheffield) to 1°E (east London) (Fig. 3). The median longitude of recoveries shifted significantly eastwards from 1.75°W in 2006 to 0.75°W in 2007 (Wilcoxon rank-sum test $z = 6.37$, $P < 0.0001$).

Surveillance for Garden Bird Disease in Fennoscandia

Finch mortality incidents were first reported in Fennoscandia in the municipality of Surahammar, Sweden

($59^{\circ} 43' \text{ N}$, $16^{\circ} 06' \text{ E}$) in mid-June of 2008 (Fig. 4) with the index case of finch trichomonosis confirmed in a greenfinch found dead on the 21st July 2008 (Neimanis et al., 2010). In Norway, mortality incidents consistent with finch trichomonosis were first reported in the eastern municipality of Hvaler ($59^{\circ} 05' \text{ N}$, $10^{\circ} 55' \text{ E}$) in late July, with the index case confirmed in a greenfinch found dead on the 9th August 2008. The majority of subsequent finch mortality reports in Norway and Sweden occurred in the month of August. In Finland, finch mortality consistent with trichomonosis was first reported in Kaarina ($60^{\circ} 24' \text{ N}$, $22^{\circ} 22' \text{ E}$) from the mid-August with the index case confirmed in a greenfinch found dead on the 15th October 2008. Most reports of such incidents of finch mortality were received during this month. As in Britain, reported finch trichomonosis incidents in Fennoscandia were almost always associated with bird-feeding stations within private gardens (Neimanis et al., 2010).

Molecular Comparison of *T. gallinae* from British and Fennoscandian Finches

PCR amplification and sequencing of part of the ITS1/5.8S/ITS2 ribosomal region of *T. gallinae* from 11 Fennoscandian cases (7 locations) (Table 1) identified a consensus sequence of 214 nucleotides for all PCR products, and they also were identical to the sequence obtained from *T. gallinae* isolates from 46 British finches (Genbank accession no. GQ150752 for greenfinch and GQ150753 for chaffinch) (Robinson et al., 2010; Lawson, unpublished data). NCBI BLAST identified 100% sequence identity with 100% query coverage with multiple other reports of *T. gallinae*, but no other organism, confirming the species identification. Nested PCR amplification and sequencing of part of the SSU rRNA gene from seven Fennoscandian cases (seven locations) (Table 1) identified a consensus sequence of 149 nucleotides, with 100% identity to that obtained from British finches (Genbank accession no. GQ214405) and those of multiple other *T. gallinae* isolates on Genbank.

Assessment of Bird Migration as a Mode of Disease Spread

Both of the finch species which appear to be the most susceptible to trichomonosis, the greenfinch and the chaffinch, are partial migrants (Fig. 5). The majority of greenfinches that breed in Norway (but not Sweden, which winter further south) spend the winter in Britain, the

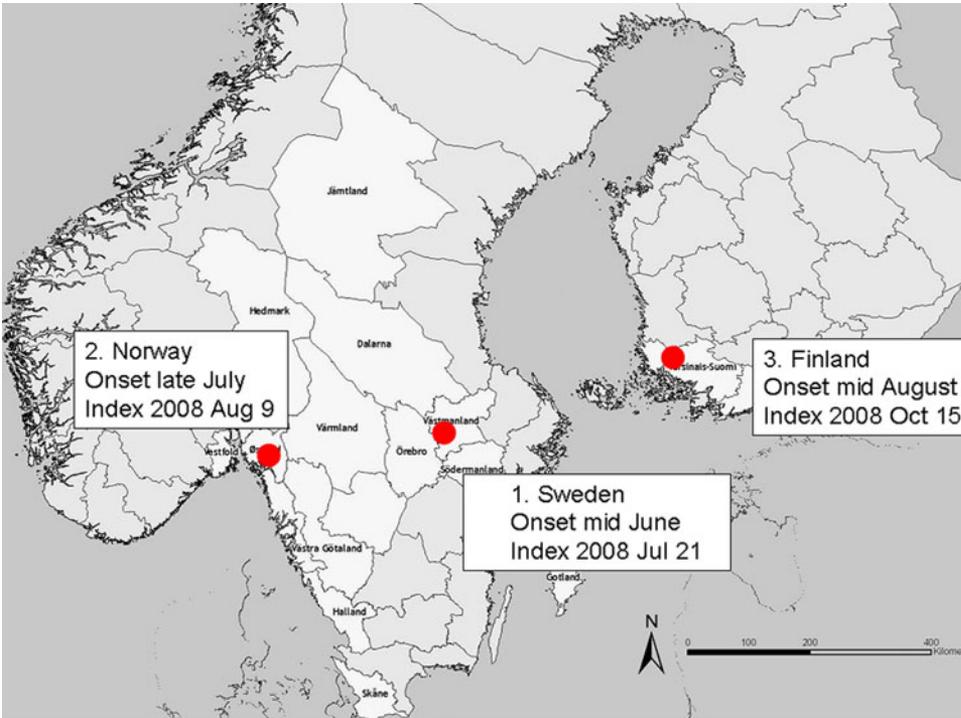


Figure 4. Emergence of finch trichomonosis in Fennoscandian finches. Red dot marks location of index case in Sweden, Norway and Finland. Counties and Provinces marked in white represent areas with reported outbreaks of finch mortality in 2008. Figure modified from Neimanis et al. (2010). (Color figure online).

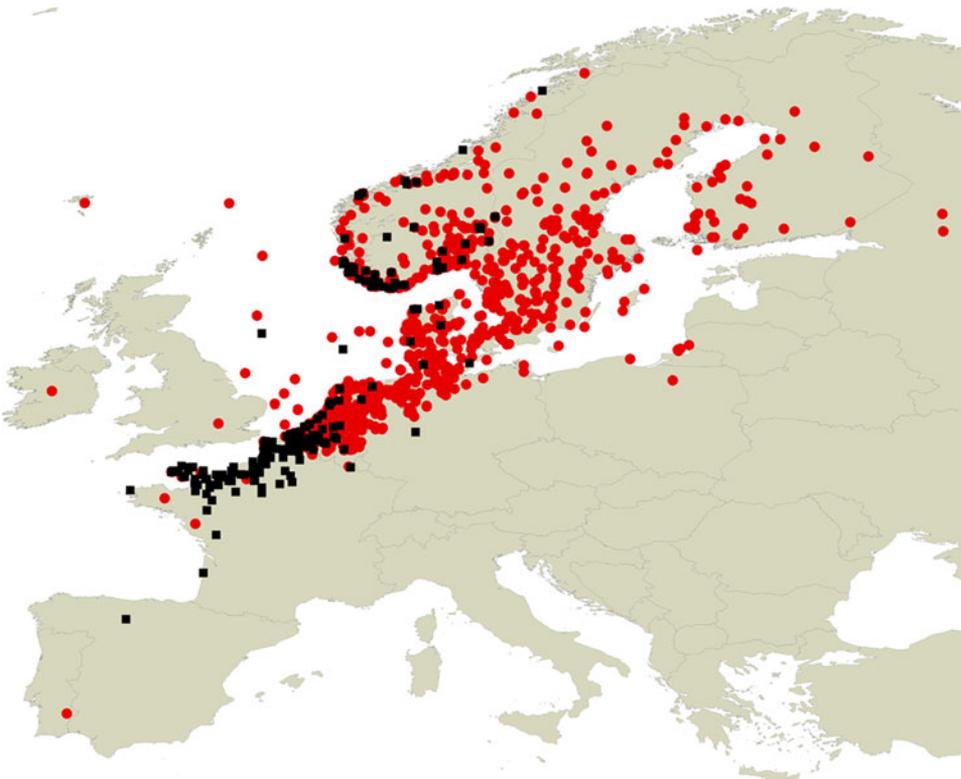


Figure 5. Locations abroad of birds marked or found in Britain. Greenfinch (black squares) and Chaffinch (red circles). Each point indicates the marking or finding of a bird that was found (or marked) in Britain; individuals appear only once on the map. (Color figure online).

Netherlands or northern France, whereas chaffinches from a much broader area of Fennoscandia overwinter in (or migrate through) Britain (Cramp and Perrins, 1994; Wernham et al. 2002). The number of individuals that

augment the resident British greenfinch and chaffinch resident populations is poorly known; however, migrants are thought to account for a small proportion (~1–2%) of the overwintering greenfinch population but a considerable

proportion (~30–50%) of the overwintering chaffinch population (Newton, 1972; Lack, 1986; Main, 1999).

Other finches and columbids are known to be susceptible to *T. gallinae* infection. Of these, the goldfinch migrates south-west from Britain and the Netherlands, to spend the winter in western France and Iberia, and the house sparrow shows a remarkable degree of site fidelity, with only three foreign recoveries representing exceptional movements (from ca. 530,000 British and Irish ringed birds, Wernham et al., 2002). Although collared doves naturally colonised Britain in the 1950s from south-eastern Europe, they are generally sedentary (12 foreign recoveries from ca. 34,000 birds ringed), with exchanges of birds only with the near continent. Similarly, although wood pigeons are quite mobile within Britain, few exchanges with continental Europe are known despite ca. 45,000 birds having been ringed in Britain.

DISCUSSION

Identification and Description of the Epidemic

In Great Britain, trichomonosis, due to *T. gallinae* infection, first emerged in greenfinches and chaffinches in 2005, leading to epidemic mortality in 2006 and 2007. The present study found an eastward shift in spatial distribution between these years, which was supported both through garden bird mortality and ring return data. We did not observe a similar increase in mortality due to other factors; thus, a simple change in reporting behaviour is unlikely to be the cause of the changed number of submissions and birds found dead. Indeed, this increase is counter to the background trend of declining rates of ring recovery in British birds (Robinson et al., 2009).

Outbreaks of greenfinch and chaffinch mortality in Fennoscandia were first identified at multiple sites in the summer of 2008 (Neimanis et al., 2010). Pathological investigations, including amplification and sequencing of the ITS1/5.8S/ITS2 ribosomal region, which have been used to establish the identity of *T. gallinae* (Felleisen, 1997; Gaspar da Silva et al., 2007; Gerhold et al., 2008), confirmed the causative agent as *T. gallinae*. Analyses of ITS1/5.8S/ITS2 ribosomal region and SSU rRNA sequences indicated that *T. gallinae* isolates from Fennoscandia had 100% sequence identity with those isolated from British finches. Recent studies have demonstrated genetic heterogeneity in *T. gallinae* isolated from wild and captive birds of multiple species in some geographical regions (Austria and

U.S.A.) using sequence analysis of the ITS1/5.8S/ITS2 ribosomal region and the SSU rRNA (Gerhold et al., 2008; Grabensteiner et al., 2010). No isolates from British or Fennoscandian birds were included in the previous studies, however; the extent of genetic heterogeneity for these loci in *T. gallinae* infecting these wild columbid populations is still unknown. Whilst the temporal and spatial patterns of disease occurrence indicates the disease spread from Britain to southern Fennoscandia, further molecular analyses, such as random-amplified polymorphic DNA studies, are required to confirm that the strain of *T. gallinae* infecting finches in Fennoscandia is the same as that found in finches in Britain.

Before the cases reported here, finch trichomonosis had not previously been recognised in Fennoscandia despite established, long-term schemes for the investigation of wildlife mortality; therefore, the condition is considered to be a newly emergent disease in this region. There was no record of an increase in the number of columbiform trichomonosis disease incidents in Fennoscandia either before or concurrent with the emergence of finch trichomonosis, nor was there a history of unusual reports of trichomonosis in captive avian collections (poultry, aviary or zoological collections).

Role of Bird Migration in Disease Spread

British breeding populations of columbid and finch species (except goldfinch and linnet *Carduelis cannabina*) migrate relatively short distances in the non-breeding season, typically only moving within the British Isles (Wernham et al., 2002). In 2006, the areas with the greatest numbers of reports of finch trichomonosis were the central and western British counties. Whilst a marked seasonal peak occurred in the number of finch trichomonosis incidents in the late summer and early autumn of 2006, post-mortem examinations showed that the disease continued to occur throughout the winter months (B. Lawson, unpublished data), confirming that the parasite persisted in the British finch population over winter. Within Britain, the greenfinch population is semi-migratory with partial movement towards the south-west in the autumn and an eastward return the following spring (Main, 1996). Consequently, an eastward shift in the distribution of the British finch trichomonosis epidemic from 2006 to 2007 might have been assisted by the spring movement of greenfinches from western to eastern Britain.

Although the greenfinch was the species most frequently found to have died of trichomonosis in both

Britain and Fennoscandia, relatively few greenfinches migrate between Fennoscandia (primarily Norway) and Britain. Fennoscandian breeding greenfinches tend to overwinter in the Low countries (i.e. Belgium, the Netherlands and Luxembourg) (Bakken et al., 2006). Also, there is little overlap between the breeding area of overwintering British greenfinches in Fennoscandia (western Norway) and the areas in southern Fennoscandia where finch trichomonosis first emerged (see Figs 4, 5). In contrast, chaffinches migrate in relatively large numbers from breeding grounds throughout southern Fennoscandia to overwinter in Britain. In both Britain and Fennoscandia, the chaffinch was the second most frequently diagnosed species with trichomonosis. Ring return data indicate that the interchange of chaffinches between Britain and Fennoscandia most commonly involves birds from eastern England, to where trichomonosis spread in 2007.

Trichomonas gallinae is a labile protozoan which is rapidly killed by desiccation and does not remain viable for a prolonged period after the death of its avian host (Kocan and Herman 1971; Erwin et al., 2000). Whilst no resistant cystic form is known and environmental persistence is thought to be short, pseudocyst formation by *T. gallinae* has been demonstrated; the role that this form plays in the parasite's life cycle and whether it might facilitate short environmental persistence is undetermined (Tasca and De Carli, 2003; Forrester and Foster, 2008). It is not amenable to long-distance mechanical transfer by abiotic means, in contrast to some viruses (e.g. Nemeth et al., 2009; Yamamoto et al., 2009). There have been no recent reported trichomonosis cases in host species within captive environments (e.g. poultry or zoological collections) in Britain or in Fennoscandia, and so inadvertent parasite translocation between these regions through anthropogenically mediated animal movement also seems unlikely. Thus, given both the temporal and spatial trends in the spread of the epidemic, we hypothesise that finch trichomonosis spread from Britain to Fennoscandia with migratory chaffinches as the most likely primary vector.

Trichomonas gallinae infection is well known and common in columbiform species, in which infection may be subclinical, or be a cause of morbidity and mortality (Bondurant and Honigberg, 1994). Our current understanding of the host reservoir for finch trichomonosis, however, is limited, and the extent to which the parasite might be spread by clinically healthy finches or by columbiform species is unknown. In particular, the extent to which greenfinches or chaffinches with subclinical or mild

clinical infection are capable of long-distance movement, resulting in the spread of the parasite through migration, requires further investigation.

The situation in Fennoscandia in 2008, with sporadic small numbers of finch trichomonosis disease outbreaks, was similar to the situation seen in Britain in 2005 when finch trichomonosis was first detected there. While it is believed that chaffinches migrate directly from Britain to Fennoscandia across the North Sea in the spring, ring return data show that the return, autumn, migration route involves birds flying through Denmark, Germany, the Netherlands and Belgium, before crossing the English Channel (Norman, 2002). Consistent with our chaffinch vector hypothesis, Peters et al. (2009) reported the emergence of finch trichomonosis in northern Germany in April 2009.

Both the chaffinch and the greenfinch are widespread throughout Europe, with a large degree of mixing of individuals between Fennoscandia and elsewhere as birds undertake their seasonal migrations; consequently, it is likely that the disease will now spread to other European countries. In Britain, the emergence of finch trichomonosis led to declines in the greenfinch population level by up to 35% in the first year of emergence alone, with apparent spill-over into a wide range of sympatric small passerine species (Robinson et al., 2010). We, therefore, recommend vigilance for finch trichomonosis and its impact on finch and other bird species throughout Europe.

CONCLUSIONS

Data from surveillance, ring returns and parasite DNA sequencing support the hypothesis that *Trichomonas gallinae* spread from Britain (most probably from eastern England) to the Fennoscandian finch population via migrating infected chaffinches. Disease spread throughout Europe and to other species is now likely. Continued disease surveillance and population monitoring are required to determine the impact of this EID on populations of wild birds throughout Europe.

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