

ORIGINAL ARTICLE

Not extinct but thriving—The rediscovery of the horseshoe bat fly *Phthiridium biarticulatum* (Diptera: Nycteribiidae) in the United Kingdom

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Abstract

Bat flies are haematophagous ectoparasites of bats, which have been infrequently studied in the United Kingdom. *Phthiridium biarticulatum* Hermann (Diptera: Nycteribiidae) is one of three species of bat fly that have been recorded in the United Kingdom. It was last recorded in 1959 and is considered extinct. We report the presence of *P. biarticulatum* on Lesser Horseshoe Bats *Rhinolophus hipposideros* (Bechstein) (Chiroptera: Rhinolophidae) at 14 sites across South West England, with a host infestation rate of 17.1% (58/339) of adult bats across 28 surveyed sites with maternity colonies in buildings. Using a species distribution model, we predict range suitability for *P. biarticulatum* across South West England and Wales. Our findings indicate that *P. biarticulatum* is not only present in the United Kingdom but may be common across the Lesser Horseshoe Bat's range, highlighting the need for ongoing monitoring of the Nycteribiidae, a neglected group of parasites, given their potential to vector pathogens.

KEYWORDS

bat flies, bats, Hippoboscidae, Nycteribiidae, species distribution modelling

INTRODUCTION

The fortunes of parasites are tied to those of their hosts, with declines in the host population leading to declines in parasite populations, unless the parasites are able to find new host species. With a plentiful supply of hosts, specialisation may enable a parasite to evolve to overcome host defences (Møller et al., 2005). While some parasites may survive with reduced fitness on sub-optimal hosts (Araujo et al., 2015), this is not possible for highly specialised species. Additional constraints on parasite survival arise when part of the parasite's lifecycle occurs away from the host, where it may be exposed to more extreme environmental conditions and risks being unable to find a new host if the host population becomes locally extinct (Wawman, 2024).

Bat flies (Diptera: Nycteribiidae and Streblidae) are haematophagous ectoparasites of bats. They are part of the superfamily Hippoboscoidea that contains the families Hippoboscidae (flat or louse flies and keds), Glossinidae (Tsetse flies) and the two families of bat flies Streblidae and Nycteribiidae (Gracioli & Dick, 2023). There are about 500 bat fly species in the families Nycteribiidae and Streblidae worldwide (Gracioli & Dick, 2023; Szentiványi et al., 2019) and 16 of the 285 species of Nycteribiidae are known from Europe (Mlynárová et al., 2023).

Bat flies are highly adapted to parasitise bats, with strong claws and spiny bristles to hold on to their hosts. The Streblidae are winged species found in the New World, but the Nycteribiidae are wingless. The eyes of the Nycteribiidae are reduced or absent (Hutson, 1984), and they have developed an unusual resting position with the head

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held backwards across their backs (Hutson, 1972). Rather than laying eggs, female Nycteribiidae give birth to fully mature larvae that are deposited on the walls of bat roosts (Hutson, 1984). Adult Nycteribiidae are present on hosts throughout the year and have been reported feeding on hibernating bats (Hutson, 1984).

Phthiridium biarticulatum Hermann (Diptera: Nycteribiidae) is one of three species of bat fly that has been recorded in the United Kingdom. Across Europe, *P. biarticulatum* has been found on a range of host species (Hutson, 1984; Mlynárová et al., 2023; Szentiványi et al., 2016), but in the United Kingdom is mainly associated with Lesser Horseshoe Bats *Rhinolophus hipposideros* (Bechstein) and Greater Horseshoe Bats *Rhinolophus ferrumequinum* (Schreber) (Chiroptera: Rhinolophidae) (Hutson, 1984). The loss of potential hosts was thought to be the cause of its decline and subsequent extinction in the United Kingdom (Hutson, 1984), where *P. biarticulatum* was last recorded in 1959.

In the United Kingdom, native bat populations are thought to have declined considerably during the twentieth century due to habitat loss, pesticide use, disturbance and the loss of roost sites as old mine workings were blocked off and farm buildings were renovated for housing (Hutson et al., 2001; Mathews et al., 2018). These declines might have caused their ectoparasites to become extinct. *Rhinolophus ferrumequinum* was lost from half of its former range in the United Kingdom and regional populations decreased, and despite a slow increase in the population since 1995, it is still considered rare and endangered (Battersby, 2005; Mathews et al., 2018). *Rhinolophus hipposideros* has also undergone severe declines with a loss of some of its former range, but numbers have been slowly increasing since the 1990s (Battersby, 2005; Mathews et al., 2018).

Bat flies have rarely been studied in the United Kingdom. There are few verifiable records of *P. biarticulatum* from the United Kingdom and Ireland. Early records previously accepted as *P. biarticulatum*, or one of its many synonyms, include reports of '*Nycteribia biarticulata* Hermann' from Raglan Castle in Monmouthshire, Wales (no date given) and from Red Hole, Eavestone, near Rippon in Yorkshire in 1885 (Kelsall, 1887), which would appear to be outside the likely historical range, restricted to Wales and Southern England, suggested by later records. *Phthiridium biarticulatum* is listed as one of the species photographed by the entomologist Ethel Katherine Pearce who died in 1940 (Chandler, 2009) but no metadata is provided for the specimen. None of these specimens are available to check the identifications.

The Natural History Museum, London (NHM), has nine *P. biarticulatum* listed in its online catalogue (<https://data.nhm.ac.uk/>, last accessed, 8 January 2026). Five are some of the 18 specimens of *Nycteribia hermanni* Leach [sic] taken from a single *R. hipposideros* in a disused ironworking near Barnstaple, Devon, by Oxley Grabham on 21 October 1898 (Austen, 1906). Further specimens are listed under the synonym *Stylidia biarticulata* (Hermann) [sic] in the catalogue of the Rothschild collection of Nycteribiidae in NHM (Theodor, 1967). All of these NHM museum records are considered correct (after updating the binomials) and have not been examined. All of the NHM records are summarised in Table 1.

In 1959, 195 *R. hipposideros* were checked for ectoparasites, yielding a total of 152 *P. biarticulatum*, and one *P. biarticulatum* was

found on an individual *R. ferrumequinum*, in Gloucestershire (Humphries, 1959). These records from 1959 are the last historical records in the United Kingdom. In the early 1980s, no bat flies were found in a sample of 114 *R. ferrumequinum* and 38 *R. hipposideros* from Wales (Gwynedd and Dyfed) and southern England (Devon, Wiltshire, Dorset, Gloucestershire and Sussex), and it was concluded that the species had declined markedly in the United Kingdom with its hosts (Hutson, 1984). Subsequently, *P. biarticulatum* was declared regionally extinct in the United Kingdom (Falk & Pont, 2017) and is currently listed as '? Extinct' in the UK checklist of Diptera (Chandler, 2025).

Here we report the presence of *P. biarticulatum* on *R. hipposideros* across South West England where it was believed to be extinct. We use a species distribution model (SDM) to predict probability that bats in a given location will be infested with *P. biarticulatum*. We explore the sex ratios of these ectoparasites, aiming to test the hypothesis that skewed ratios observed in some studies may be due to large numbers of males clustering around unmated (teneral) females as seen in some Hippoboscidae found on birds, such as the Swift Louse Fly *Crataerina pallida* (Latreille) (Walker, 2010). We also discuss whether this species was truly extinct and recolonised the region or went undetected due to a lack of recording of these species.

METHODS

Rhinolophus hipposideros were captured at 28 maternity colony sites in buildings across South West England and Wales, during August and September 2024 and 2025 (Figure 1). Adult bats were caught with a hand net, either inside the roost or on emergence. Biometrics (weight, forearm length, sex, breeding status) were taken, and the bats were thoroughly searched for ectoparasites, which were removed with tweezers. All ectoparasites were stored in 70% ethanol in tubes and labelled with the date, location and host ID. Additional bat flies were available from sites outside the main study, via submissions to the UK Hippoboscidae and Nycteribiidae Recording Scheme.

Bat flies were identified using a binocular microscope, with reference to keys for the known species in the United Kingdom (Hutson, 1984) and Europe (Mlynárová et al., 2023). The sex of each fly and whether it was teneral were recorded. An Olympus TG6 camera held over one eyepiece of a Swift S306S stereo microscope was used to photograph specimens.

Voucher specimens of *P. biarticulatum* collected from one of the two sites outside of the main study will be deposited in the Entomology Collection at the Oxford University Museum of Natural History, Oxford, UK.

Species distribution model

We used an SDM framework in R (R Core Team, 2025) to estimate *P. biarticulatum* distribution in Britain. We selected climatic and landscape variables that are likely to affect the distribution of both *P. biarticulatum* and its host species (Table 2).

TABLE 1 Records of UK museum specimens of *Phthiridium biarticulatum*, showing the synonyms they are listed under, with dates, locations, host species and sources of information.

Listed as	Date	Location	Host	Number of bat flies	Source	Notes
<i>Phthiridium biarticulatum</i>	21 October 1898	Barnstaple, Devon 51.1° N, 4.1° W	<i>R. hipposideros</i>	5	Austen (1906), GBIF (2023) NHMUK012808505 ♂ NHMUK012808506 ♀ NHMUK012808507 ♂ NHMUK012808508 NHMUK012808505 ♀	5 of 18 mentioned by Austen
<i>Stylidia biarticulata</i>	12 June 1906	Wells Cathedral, Somerset	<i>R. ferrumequinum</i>	2♂, 1♀	Theodor (1967)	
<i>Stylidia biarticulata</i>	19 June 1906	Wells Cathedral, Somerset	<i>R. hipposideros</i>	1♂	Theodor (1967)	
<i>Stylidia biarticulata</i>	12 May 1912	Braunton, Devon	<i>R. ferrumequinum</i>	1♂, 2♀	Theodor (1967)	
<i>Stylidia biarticulata</i>	1 January 1914	Longton, Staffordshire	<i>R. hipposideros</i>	2♂	Theodor (1967)	
<i>Stylidia biarticulata</i>	1921	Bristol	<i>Rhinolophus</i> sp.	1♂	(Theodor, 1967)	
<i>Stylidia biarticulata</i>	18 August 1921	Lympsham, Cheddar, Somerset	<i>R. hipposideros</i>	1♀	Theodor (1967)	
<i>Stylidia biarticulata</i>	25 October 1921	Lympsham, Cheddar, Somerset	<i>R. hipposideros</i>	1♀	Theodor (1967)	
<i>Stylidia biarticulata</i>	December 1922	Dundry, Somerset	<i>R. hipposideros</i>	1♂	Theodor (1967)	
<i>Phthiridium biarticulatum</i>	23 October 1933	Lympsham, Cheddar, Somerset	<i>Rhinolophus</i> sp.	1♀	GBIF (2023) NHMUK0128511	3 bats of same species each had one Nycteribiid
<i>Stylidia biarticulata</i>	4 January 1942	Redd's Cavern, Burrington Combe, Somerset	<i>R. hipposideros</i>	2♂, 3♀	Theodor (1967)	
<i>Phthiridium biarticulatum</i>	1 January 1954	Box Common Caves, Nailsworth, Gloucestershire 51.6° N, 2.2° W	<i>R. hipposideros</i>	1	GBIF (2023) NHMUK0128510	
<i>Stylidia biarticulata</i>	23 October 1954	Box Common Caves, Nailsworth, Gloucestershire	<i>R. hipposideros</i>	1♀	Theodor (1967)	
<i>Phthiridium biarticulatum</i>	4 March 1956	Box Caves, Nailsworth, Gloucestershire	<i>R. hipposideros</i>	2	GBIF (2023) NHMUK0128512 ♂ NHMUK0128513 ♀	

Note: Where possible records from other sources have been paired with the Natural History Museum, London, accession numbers, but none of the specimens have been re-examined.

Using individual adult hosts as the sampling unit, we recorded *P. biarticulatum* presence/absence on individual bats (absent = 0, present = 1) and fitted a generalised additive model (GAM) with a binomial error distribution in the *mgcv* package (Wood, 2004). Presence of *P. biarticulatum* was the dependent variable; environmental and landscape variables were the predictors. We included latitude and longitude as a smooth term (Duchon spline, $k = 25$) to account for spatial non-independence of sites and specified a random effect for 'roost site' to account for repeated sampling of bats in the same roosts. We also included Julian day of the year the bat was sampled. We checked model residuals with the *DHARMA* package (Hartig et al., 2024) and checked for multicollinearity and concurvity with the *performance* package (Lüdtke et al., 2021).

We estimated variable importance by hierarchical partitioning in the *gam.hp* package (Lai et al., 2024), and model predictive power by calculating area under the receiver operating characteristic curve (AUC) through 5-fold cross-validation. We then used the final model built with all data to predict *P. biarticulatum* occurrence across Britain. We created a binary (presence/absence) map using the minimum training presence threshold.

Sex ratio analysis

After excluding all hosts from which only one bat fly was collected, and checking for the distribution of model residuals, a generalised

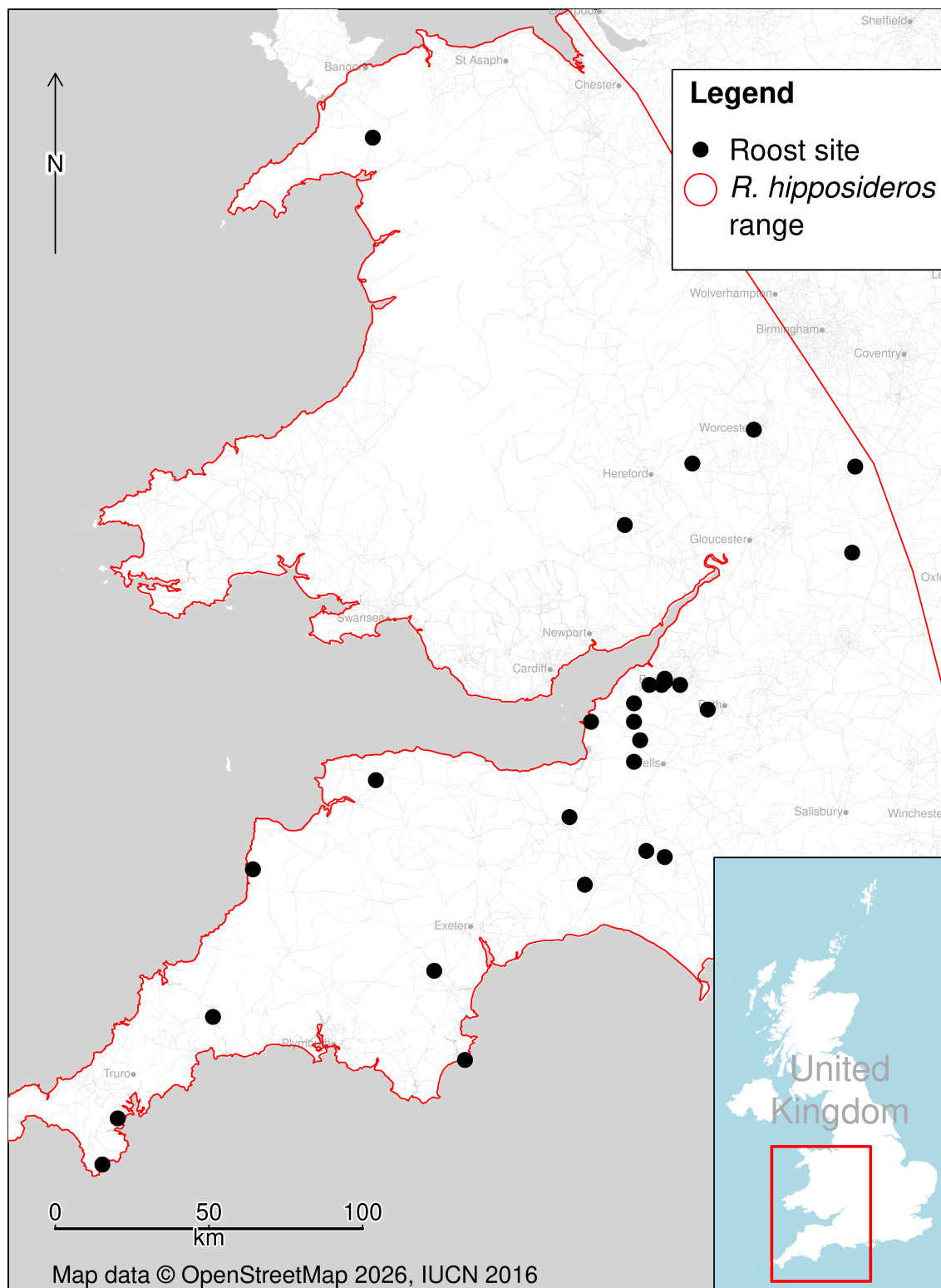


FIGURE 1 *Rhinolophus hipposideros* roost sites sampled in 2024 and 2025, showing the known range of *R. hipposideros* in Britain (IUCN, 2026).

linear model was used to model the proportion of female flies against Julian day, using the default Gaussian distribution. The full model specification and R code for this model are available in the [Supporting Information](#).

RESULTS

A total of 339 adult bats were examined for ectoparasites at 28 roosts. In total, 148 bat flies were collected from 58 individual bats at 12 sites

TABLE 2 Environmental and climatic predictors included in the species distribution model (SDM) used to predict the habitat suitability for the bat fly *Phthiridium biarticulatum*, showing their contribution to the model.

Variable	Statistic	Source	Importance (%)
Arable/horticulture	% cover	Rowland et al. (2025)	0.81
Broadleaf woodland	% cover	Rowland et al. (2025)	1.50
Julian day of year	-	-	0.61
Mean annual rainfall	2020–2024 mean	Met Office (2025)	0.71
Roost site	-	-	47.1
Urban/suburban	% cover	Rowland et al. (2025)	1.18
Winter minimum temperature (°C)	2020–2024 mean	Met Office (2025)	4.64
Location x, y coordinates	-	-	43.46

across South West England and Wales (Figure 2). Host infestation rate was 17.1% (58/339) and bat flies were found at 42.9% of sites (12/28), but as only a sample of bats at each site were checked for ectoparasites, it is not possible to say that sites where no flies were found were free from infestation. In addition, two bat flies were received by the Hippoboscidae and Nycteribiidae Recording Scheme from sites in South West England, bringing the total sites at which *P. biarticulatum* was found to 14. The number of bat flies ranged from 1 to 19 (mean = 2.46 flies) per infested host. All bat flies were identified as *P. biarticulatum*. Photographs of some bat flies can be seen in Figure 3.

Species distribution model

The SDM had an independent AUC of 0.8987, indicating high predictive power. The smooth terms for x, y and roost site contributed most to the model (Table 2). Amongst the parametric terms, minimum winter temperature was the most important. Predicted probability of occurrence is highest in Cornwall and Devon (Figure 4), mirroring the spatial distribution of infestation rate seen in the raw data (Figure 2).

Sex ratio analysis

Sex ratios of bat flies on individual adult hosts were rarely equal, with some bats having up to five bat flies of a single sex, but overall the mean proportion of female bat flies was 0.51 (median 0.50, $n = 58$). After removing records from all hosts where only one bat fly was collected, the mean became 0.55 (median 0.50, $n = 28$). A slight increase in the proportion of females was observed over the course of the season, but this was not statistically significant (see [Supporting Information](#) for full results).

Only two teneral bat flies were collected, both male, so it was not possible to test the hypothesis that the unequal sex ratios on some individual hosts were because excess males were attracted to newly emerged females.

DISCUSSION

Phthiridium biarticulatum was found on 17.1% of adult *R. hipposideros* bats, and at 12 of the 28 roost sites checked in Wales and South West England. In addition, two *P. biarticulatum* were received from other sites in the South West that were not part of the main study. This shows that *P. biarticulatum* is not extinct in the United Kingdom and suggests that it is widespread across the South West region. It may be that *P. biarticulatum* was never extinct in the United Kingdom or that it was and it has been reintroduced.

We found a strong spatial effect in *P. biarticulatum* distribution that was not explained by environmental variables. It is not clear if this is due to a historic decline and ongoing recovery, or due to other factors not accounted for in the modelling. Further sampling in South Wales would be useful to test model predictions and improve the predicted distribution map. Sampling in different roost types (e.g., underground roosts and hibernation sites) and at different times of year may also help identify limiting factors and explain the observed distribution.

Earlier limited sampling makes it impossible to conclude whether *P. biarticulatum* was truly extinct in the United Kingdom. There are no records in the iRecord database for *P. biarticulatum* (https://irecord.org.uk/species-details?xu=on&taxa_taxon_list_id=13074, last accessed, 30 December 2025). However, there are only two records of bat flies from the United Kingdom, two of *Nycteribia kolenatii* Theodor & Moscona, one of which is unverified, and none of *Basilia nana* Theodor & Moscona. There are also no records of *P. biarticulatum* on the iNaturalist website (<https://www.inaturalist.org/>, last accessed, 30 December 2025) from anywhere in the world, and only 104 worldwide, of which six are from the United Kingdom (NHM specimens) on the GBIF website (https://www.gbif.org/occurrence/search?offset=0&taxon_key=1638184, last accessed, 7 January 2026). This suggests that as a group, these species are rarely recorded, likely due to limited sampling effort. The sample size of 114 *R. ferrumequinum* and 38 *R. hipposideros* in South West England and Wales in the early 1980s (Hutson, 1984) may not have been sufficient to detect *P. biarticulatum* if the bat fly had undergone a period of decline with its host.



FIGURE 2 Map showing the locations of all sites and infestation rate (percentage of infested bats) of *Rhinolophus hipposideros* by *Phthiridium biarticulatum* in South West England and Wales.

It is possible that the main hosts of *P. biarticulatum* may have reintroduced the bat fly to the United Kingdom if it had indeed gone extinct. While *R. hipposideros* is a sedentary species (Schofield et al., 2022) and *R. ferrumequinum* usually only makes short seasonal

movements (Ransome, 2023), levels of genetic differentiation between British and French populations of these species are relatively low, indicating that some individuals disperse across the Channel (Dool et al., 2013). *Phthiridium biarticulatum* has been found on other

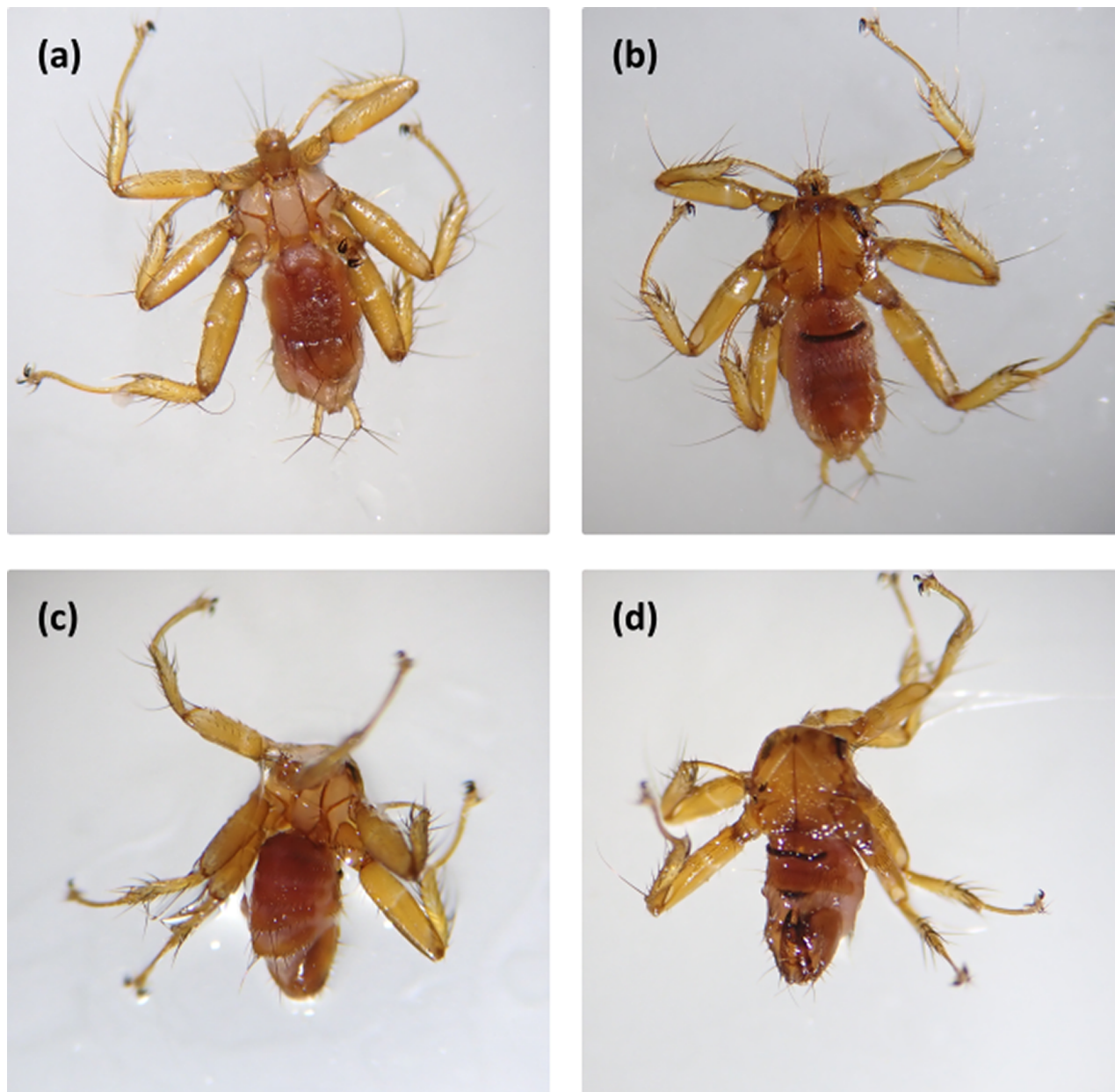


FIGURE 3 Specimens of *Phthiridium biarticulatum* collected for this study. (a) Female dorsal habitus. (b) Female ventral habitus. (c) Male dorsal habitus. (d) Male ventral habitus.

bat species (Chiroptera: Vespertilionidae) that are present in the United Kingdom: the Greater Mouse-eared Bat *Myotis myotis* (Borkhausen), Common Pipistrelle *Pipistrellus pipistrellus* (Schreber) and Brown Long-eared Bat *Plecotus auritus* L. (Hutson, 1984), and on a total of 16 different host species in Europe (Mlynárová et al., 2023; Sándor et al., 2024; Szentiványi et al., 2016). Several species of bat may share a roost which can allow ectoparasites to move to less preferred host species (Sándor et al., 2024). These species may have helped to sustain a population of *P. biarticulatum* that went unnoticed in previous decades.

Our SDM predicted suitable bioclimatic and landcover conditions across South West England and Wales. In current climatic conditions,

the record from Red Hole, Eavestone, near Rippon in Yorkshire in 1885 appears unlikely. The presence of *P. biarticulatum* in the warmer, southern part of the United Kingdom suggests that it may be near the limit of its range in the United Kingdom, but that it may, with climate change, have the potential to expand its range as other related species in the superfamily Hippoboscoidea have done (Kurina et al., 2019; Mihalca et al., 2019; Oboňa et al., 2022, 2025; Wawman, 2024, 2025). However, as a parasite, its range is tied to those of suitable host species, and as bat flies are wingless, they will need to be carried to new areas by their hosts, both of which are predicted to increase their range in Britain under climate change projections (Fialas et al., 2025; Foxley et al., 2025). The infestation rate of 17.1%

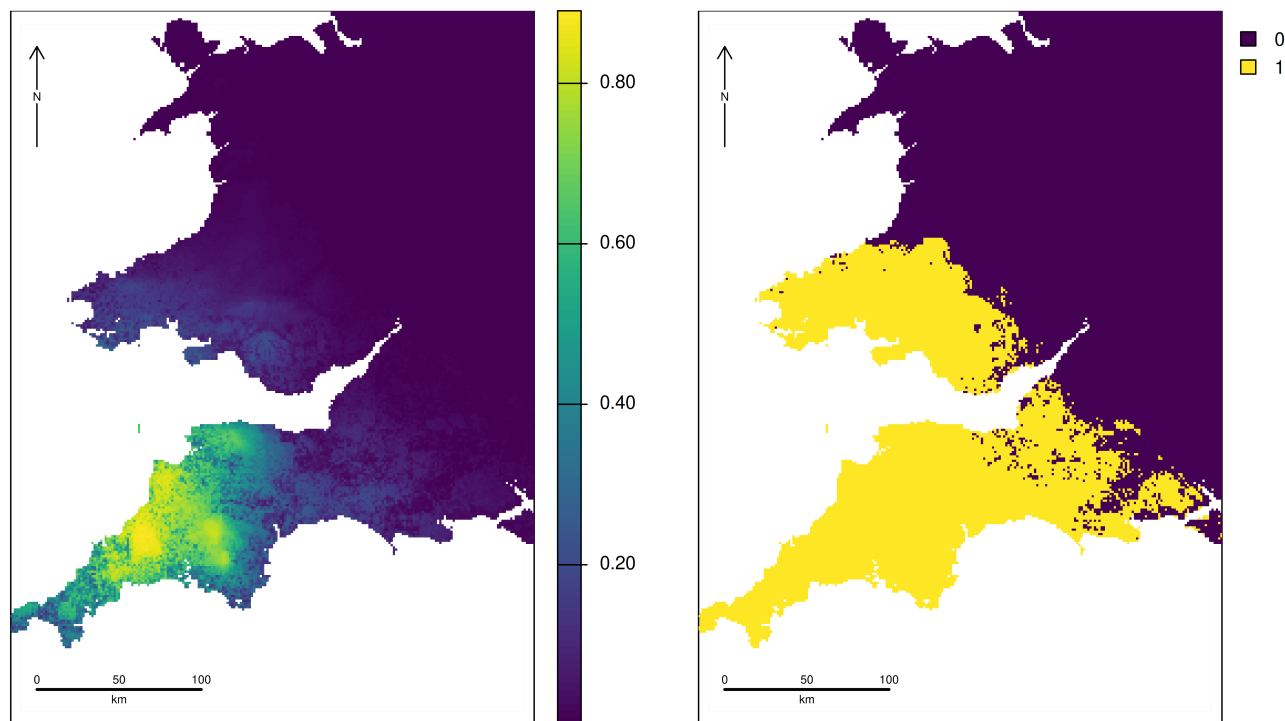


FIGURE 4 Predictions from species distribution model, showing probability of infestation with *Phthiridium biarticulatum* for lesser horseshoe bats in Britain (left) and predicted presence/absence of *P. biarticulatum* (right). Binary map created using minimum training presence threshold.

recorded in our study is lower than that of the only comparable historical study for the same region. In Gloucestershire, in 1959, 195 *R. hipposideros* were checked for ectoparasites, yielding a total of 152 *P. biarticulatum* with an infestation rate of 33.8% (66/195) (Humphries, 1959). The lower infestation rate seen in our study could be a sign of an ectoparasite population recovering from extinction or near extinction, or may be due to other factors, such as climate change, pollution or pesticide use.

Although sex ratios of the flies varied between 100% male and 100% female, overall there were equal numbers of each sex and there was no statistically significant seasonal variation. Sex-specific longevity, which is often seen in ectoparasitic arthropods, often leads to a change in the proportions of each sex as the season progresses, with females predominating towards the end of the season, despite equal numbers emerging (Marshall, 1981). However, in bat flies the seasonal effect is not always found and there may be an excess of females throughout the season (Marshall, 1971), or equal numbers of males and females, with no seasonal trend in the United Kingdom (Hutson, 1984). In the present study it is likely that the survey window was not long enough to detect seasonal changes, especially as it took place at multiple sites that may have different conditions. Density dependent sex ratios were reported in a study of *N. kolenatii* with a much larger sample size ($n = 796$ bat flies) (Szentiványi et al., 2017).

Bats can carry a wide range of microbes (Dhivahar et al., 2023) and their parasites, such as ticks, can harbour a range of zoonotic pathogens (Lv et al., 2018). There has been limited research into the pathogens carried by bat flies, but *Bartonella* sp. (Billeter et al., 2012; Szentiványi et al., 2020) and the flavivirus Dengue virus (Abundes-Gallegos

et al., 2018) have been found in other species. There are reports that some bat flies will occasionally bite humans (Dick & Patterson, 2007), though the risk of disease transmission is unknown.

We only collected bat flies from *R. hipposideros*. To further understand the ecology of *P. biarticulatum* in the United Kingdom, it will be necessary to sample other potential host species across a wider area. As a haematophagous ectoparasite, *P. biarticulatum* has the potential to vector pathogens, but there is a lack of research into the pathogens present in this species and in other bat flies in the United Kingdom. *Phthiridium biarticulatum* may form part of an enzootic cycle between several bat species and other parasites. Combining knowledge of the pathogens present in bat flies with species' ecology will be essential in assessing the risk that *P. biarticulatum* poses to bat, human and other animal health from zoonotic infections.

AUTHOR CONTRIBUTIONS

Denise C. Wawman: Conceptualization; methodology; data curation; investigation; validation; formal analysis; visualization; writing – original draft; writing – review and editing. **Thomas Foxley:** Conceptualization; methodology; data curation; investigation; validation; formal analysis; visualization; writing – review and editing. **Emma Stone:** Conceptualization; writing – review and editing; supervision; funding acquisition. **Orly Razgour:** Writing – review and editing; supervision; conceptualization; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo (Foxley et al., 2026) at <https://doi.org/10.5281/zenodo.18889050>.

ETHICS STATEMENT

The project was approved by the University of Bath Animal Welfare Ethical Review Body (review number NL2302-1) and all work was carried out following best practice guidance (Collins, 2023; Shapiro et al., 2024). The bats were handled under licence from Natural England (2023-66784-SCI-SCI, 2024-69604-SCI-SCI) and Natural Resources Wales (S094417/1).

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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. Computer code and results of sex ratio analysis.

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