



The Slow Invasion by the Non-native Edible Dormouse *Glis glis* (L., 1766) (Rodentia: Gliridae) in England: Where and How Many Are There after 120 Years?

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Abstract: The edible dormouse *Glis glis* was introduced to Britain in 1902, at Tring in Hertfordshire. It slowly invaded a wider area. The present paper confirms a recent more rapid increase in both distribution and abundance. Twenty-three years of regular population monitoring at a woodland study site, using nestboxes and tagging individuals, shows a consistent numerical increase. The possibility that the presence of nestboxes caused the observed population increase (as happens with some bird species) is discounted. The number of *Glis* culled in woodland trials match our population estimates as do reports of increasing culling in buildings. Using several methods for estimating population density, the current national population size is shown to be at least an order of magnitude larger than a recently-published estimate, which has used historical data and does not accord with our current evidence. In view of the negative impact of *Glis* in both natural and built environments, the mismatch in estimates of their total number affects the seriousness with which the Invasive Non-native Species Secretariat should view the ongoing increase and spread.

Key words: alien species; biological invasion; long-term population dynamics

Introduction

Long life, periodic failure of reproduction, and long hibernation that curtails an extremely short active season, make the life history of the nocturnal edible dormouse (*Glis glis*) – termed *Glis* hereafter – unique among small arboreal rodents (MORRIS & MORRIS 2010). A few were introduced to Britain in 1902 at Tring in the Chilterns area (Hertfordshire) c. 50 km NW of London. Several accounts of increasing distribution have been published, including LEVER (1977) who reviewed location records during the period 1925–1951. This, and later maps of reported distribution, indicated that the core area remained centred on woodlands in the Chilterns. Overall, a slow spread within that area is apparent from

the literature, with occasional isolated (but more widespread) confirmed records from elsewhere. A population in Hockeridge Wood (a typical Chilterns site), was monitored regularly and showed a statistically significant increase from 1996 to 2008 (MORRIS & MORRIS 2010), which has continued since then (TROUT et al. 2021) despite reproductive failure in some years (TROUT et al. 2015).

Substantial damage to forestry interests has been reported (PLATT & ROWE 1964, MORRIS et al. 1977) and significant predation on hole nesting birds (TROUT et al. 2012). *Glis* have also shown a propensity to invade houses and other buildings, causing significant nuisance (MORRIS 2008, TROUT & MOGG 2016). Control by legal culling is increasingly required and is recorded nationally in compliance with

the Berne Convention of 1979 (which protects all species of European dormice). Local authority and private records of *Glis* culls in buildings reveal significant spread. Reports of nuisance and damage are increasing, both within and beyond the Chilterns (TROUT & MOGG 2016).

The British population of *Glis* lives outside the natural European distribution of this species (although within the same limits of latitude and longitude) and may therefore experience different population dynamics. Population densities are reportedly lower in the northern parts of the species' natural range (e.g., 0.8–2/ha and 2/ha in Lithuania, Latvia and northern Poland (PILÄTS et al. 2009, JUSKAITIS et al. 2015) than in central and southern Europe (e.g. 10–50/ha: ROSSOLIMO et al. 2001, KRYŠTUFEK & FLAJŠMAN 2007, JUSKAITIS et al. 2015). BEIBER (1995) demonstrated pre-breeding densities of 19 and 22/ha in July at two sites in mid-Germany. The first attempt to estimate the population density of *Glis* living in English woodland was made in 1989 (HOODLESS & MORRIS 1993), using 'Distance Sampling' (WHITESIDES et al. 1988). Over four nights, counts were made of vocal animals heard along three woodland transects among mature trees, resulting in an estimate of c.1.4/ha (range 0.6–1.8). This was scaled up to estimate the total British population size at about 10,000 animals by taking account of the extent of the total woodland area in the Chilterns where *Glis* was likely to have become established (MORRIS 1993, HARRIS et al. 1995), assuming they had not spread to more than two-thirds of local woodlands or beyond the Chilterns area. Upgrading that national figure from the 1990s, a new estimate was published by MATHEWS et al. (2018), putting the total British *Glis* population at 23,000 (range 9,800–82,000). This assumed a pre-breeding population density of 0.84/ha, taking the mean of data from 30 years ago. Their formal estimate of total population size is surprisingly low, and ignores the statement by MORRIS & MORRIS (2010) that "a four-fold increase in population size has occurred in less than a decade".

The present paper re-assesses both the distribution of *Glis* in Britain and change in its abundance, based upon a variety of sources and approaches. It also addresses concerns about the potential impact of installing nestboxes at our study site.

Materials and Methods

Increase in distribution

Reliable historical information is available on the distribution of *Glis* in England from publications

cited by THOMPSON (1953), CORBET (1971) and MORRIS (1997). TROUT & MOGG (2016) reported the location of *Glis* infestations in buildings collated from local authority records from 2006–2009, with some additional small-scale surveys. We collated unpublished recent national records, derived from 461 different postcodes over a period of 6 years up to 2017, of *Glis* culls in buildings that were carried out under a government licence. However, *Glis* control is almost entirely confined to buildings. Distribution records from woodlands (its principal habitat) are severely lacking. We did not use the National Biological Monitoring (NBM) database, as many early records are unconfirmed; they were not repeated and appeared to result from misidentification of grey squirrels *Sciurus carolinensis*.

Increase in numbers

A wild population was monitored regularly within the 100 ha Hockeridge Wood complex, an Ancient Semi-Natural Woodland (ASNW) comprising mature deciduous trees (c. 50% beech *Fagus sylvatica*), with oak (*Quercus robur*) and various mature softwood species. Wooden nestboxes (n=145) were attached to trees in 1996, covering about 20% of the wood and checked monthly from May until November each year (MORRIS & MORRIS 2010). A further 75 nest boxes were added in 2008 and were inspected until 2019 (TROUT et al. 2015). The 220 nestboxes covered about a third of the wood at a density of c. 6.7/ha. Animals were marked individually using 12 mm by 2 mm diameter microchips ('PIT tags') and, by the end of 2018, the capture database comprised more than 25,000 records representing c. 10,000 individual *Glis*. Each year was designated a breeding or non-breeding year.

The number of individuals handled each year was recorded and the change from the first 5 years to the last 5 years calculated. Early August data was also chosen as a key month because all animals that had emerged from hibernation would be potentially available. No young would be included as they were too small to microchip. Standard errors of the means were used to construct confidence limits, realising that for a mean of five data points (e.g. for breeding years only) these limits were not very accurate. However, the alternative of including data from 15 years ago (from a consistently rising population) required to deliver 10 points is also inappropriate and misleading to indicate the current density.

A calendar of captures was generated covering 24 years and recording the capture history for each microchipped *Glis*. This included when it was first found and when it was known-to-be-alive (KTBA) even if not seen during one or more nestbox checks

or even skipping complete years. The last capture record was taken as the final month of life. The number of adults KTBA in any month provides a population index and the overwinter KTBA figure represents the minimum baseline population.

A fully time-dependent Cormack–Jolly–Seber model was fitted to the complete capture histories, using the program MARK, to calculate capture probabilities for each period. These were then converted into population density estimates (including marked young) for the last five years; the last five breeding years and also specifically for August. Population density figures were extrapolated to estimate the total British population size, using the same 27,000 ha figure of suitable habitat adopted by MATHEWS et al. (2018). However, we divided it into ancient semi-natural woodland ASNW (16,500 ha), which (such as our main study site) provides excellent habitat for *Glis*, and other woodland (10,500 ha). We considered the latter to be subjectively less suitable and reduced the estimates of *Glis* density there by 50%. Thus, the national population estimates are 21,750 x the calculated density per ha.

Nestbox occupation and the impact of introducing nestboxes

NEWTON (1995) reviewed evidence for the impact of adding refuges to woodland sites. He experimentally added nestboxes at 7.5/ha to sites with few, moderate or many natural refuges for hole nesting birds. He found no impact on population density with many natural refuges already. The WEIBE (2011) review agreed. Supporting this, a recent paper by ELIAS & STOLESON (2021) found abundant natural cavities in a deciduous forest led to a lack of nest-box occupancy by northern saw-whet owls. To assess the impact of nestboxes at our study site, four assessments were made using recent data from breeding years. First, to indicate the level of competition for nestboxes, the percentage of 220 nestboxes occupied by adults in mid-August (when most young are born) in the last three breeding years was calculated. Second, numbers of individual tagged adult *Glis* captured in visits during the active season was compared to the number known-to-be-alive (KTBA) in a breeding year to give an indication of their prevalence in boxes. A box plot and whisker analysis using the package ‘R’ (2017) was used to demonstrate the rate of presence of *Glis* in the nestboxes. Third, the proportion of adults found in nestboxes in August during a breeding year, of all those adults KTBA in that August, was calculated. Finally, the overall lifetime recapture rate of adults (survived at least one winter) was explored by calculating the mean annual recapture rate

of animals of increasing age. The hypothesis was that high nestbox use and high recapture values would indicate intense competition for use of nestboxes and thus providing nestboxes would increase the *Glis* carrying capacity of the habitat, whereas low values indicate that individuals used them only intermittently and occupied other refuges among the trees.

Independent *Glis* data from other sources

Population density estimates were made based on recent experimental removal trials, culling *Glis* in woodland over 10-day periods. One was from 8 ha within a 75 ha wood, others from a 12 ha triangular wood isolated on 2 sides by open fields. The trial in 2019 lasted 10 consecutive days and, in 2020, there were two 5-day sessions 4 weeks apart in July/August on the same area. Culls were followed by monitoring for any additional animals that were present and before significant immigration might occur. Numbers culled relate to adults only and represent a minimum population density.

The number of requests to two local authorities for help in *Glis* management in buildings during the early 2000s were made available to the authors. The licence returns to Government (provided by pest control companies authorised to remove *Glis* from domestic and industrial properties) were also obtained, including numbers culled and postcode locations. Neither relates to woodland (the principal habitat of edible dormice) nor does it include numbers culled unofficially by property owners who did not report their actions.

During three years (2013–2015), *Glis* were removed from buildings at an estate of 62 detached houses near High Wycombe, providing information on the numbers of *Glis* culled within an area of 15 ha. This does not offer a strictly comparable estimate of population density but does demonstrate local abundance in the built environment.

Results

Evidence of the increasing distribution of edible dormice

Since the introduction of *Glis* in 1902, the population has clearly expanded its range. THOMPSON (1953) mapped 22 locations within seven 10x10 km grid squares between 1911 and 1950. CORBET (1971) indicated that *Glis* were present in nine grid squares. LEVER (1977), JONES-WALTERS (1991), MORRIS (1997) AND TROUT & MOGG (2016) provided later information suggestive of increasing numbers and spread into 13 grid squares. Records of *Glis* in the Chilterns remain broadly bounded by the M25, M40

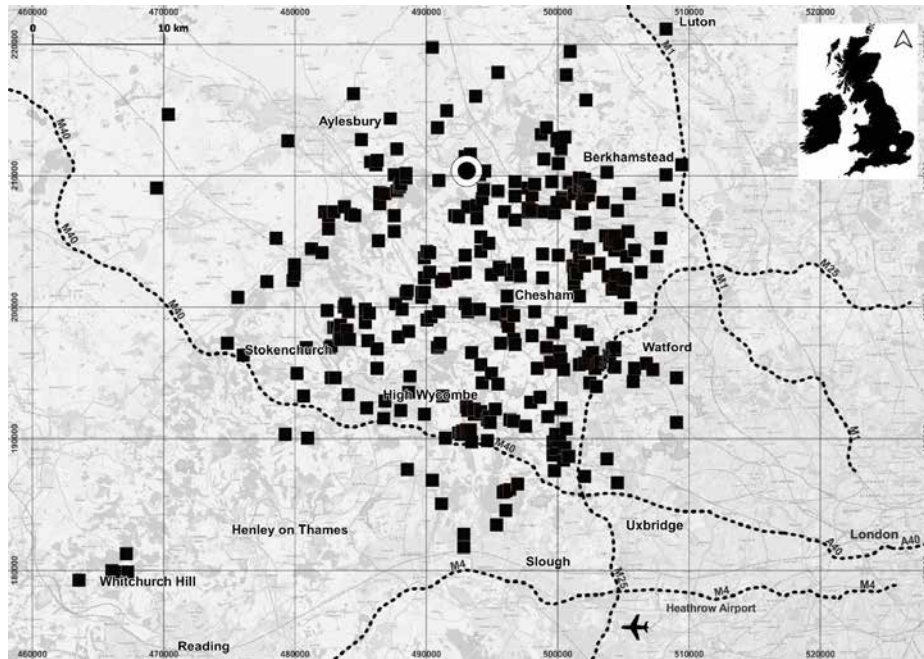


Fig. 1. Distribution of cull records in 2017 of edible dormice within the general area of the Chilterns, excluding records from more than 50km from the original release site (circled) at Tring. Scale grid = 10 km.

Table 1. Numbers of individuals handled each year.

Time period	Min/max	Mean (Standard Error)	Increase
First 5 years 1996–2000	49 / 157	97 (SE 22.3)	
Last 5 years 2014–2018	235 / 1,571	999 (SE 257)	X 10
First 5 breeding years	96 / 177	131 (SE 13.8)	
Last 5 breeding years	1,373 / 2,048	1,709 (SE 98.6)	X 13
First 5 non-breeding years	48 / 112	71 (SE 12.1)	
Last 5 non-breeding years	268 / 551	309 (SE 61.3)	X 4.3

and M1 motorways (although these were constructed 50–70 years after the initial release) and the chalk scarp slope in the west representing a sharp change in habitat to open farmland. Fig. 1 shows 331 cull locations in 20 grid squares recorded by licensed pest control companies in 2017, suggesting that *Glis* is now more widespread and having infilled apparent gaps in the earlier maps. Fig. 1 also shows at least one significant new satellite population (in the built environment) to the southwest near Reading. There are additional recent verified records of breeding populations beyond the Chilterns area, including eastwards in Essex, in Ascot (southeast Berkshire) and Denham and Hanwell towards London. Some

are more than 50 km from Tring, beyond Fig. 1, indicating a widening presence across the countryside and into the peri-urban area of London.

Evidence of population increase

From nestbox monitoring. Our 23 years of monitoring microchipped *Glis* in Hockeridge Wood (1996–2018) revealed an increase in numbers of individuals handled (Table 1). In 1996–2000, compared to 2014–2018, the numbers increased by a factor of 10, except in the non-breeding years, when many adults were absent from the nestboxes. The mean number of overwintering individuals KTBA increased sevenfold from 67 (SE 19) in the five years 1996–2000 to 471 (SE 84) in the five years 2014–2018. The number of individual PIT tags recorded in adults each year (Fig. 2) shows a significant rise ($R^2 > 0.9$) during the two decades of study, in both breeding and non-breeding years. In the first 5 years using only data from August (before any young were marked), an average of 18.6 (SE 2.8) individual adults were found compared with 100.8 (SE 14.8) in the last 5 years.

Cormack–Jolly–Seber recapture models. These indicate that the average estimated population density in the active months increased sixfold between the first and last ten years of data, (Table 2). Using data from August only (before young were tagged), the mean estimated adult population rose sixfold from 88 individuals to 551.

Nestbox occupation. In Hockeridge Wood, the proportion of occupied nestboxes in mid-August

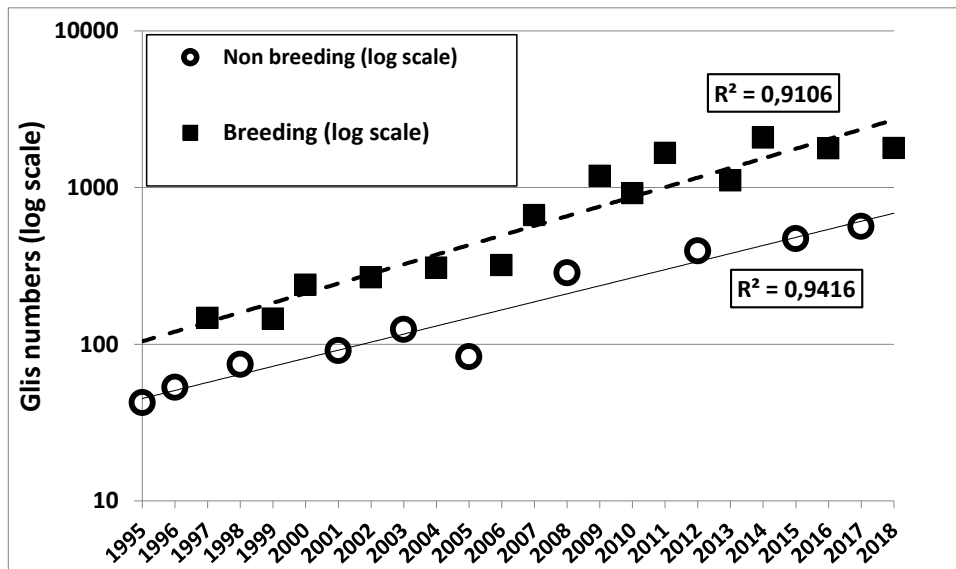


Fig 2. Annual numbers of individual microchipped *Glis* recorded in Hockeridge wood site, separated for breeding and non-breeding years. (No microchips were available in 2004–2006).

Table 2. Population estimates generated by the Cormack–Jolly–Seber model for the first 10 years and last 10 years at Hockeridge wood, based upon numbers of *Glis* that were tagged and recaptured per 20ha.

Average, including juveniles	Average C–J–S population estimate	Lower estimate	Upper estimate	<i>Glis</i> population density/ha	Lower 95% estimate/ha	Upper 95% estimate/ha
First 10 years 1996–2005	156	82	471	7.8	4.1	23.5
Last 10 years 2009–2018	945	675	1,389	47.2	34	69

(when the sexes occupy separate boxes) was 56%, 55% and 62% in the last 3 breeding years 2014, 2016, 2018; i.e. just under half were not occupied. In addition, the overall occupation rate 2009–2018 was 29%. The proportion of adults handled in the early August 2009–2018 (when many females are pregnant or lactating) was 21.9% (SE 3.7) of all the adults KTBA. Thus, c. 80% (70–90%) of adults KTBA were not in a nestbox on the day of inspection. Examination by a box and whisker analysis showed marked adults (that had survived at least one hibernation) of any age up to 14 had a median value recapture rate of less than one in ten nestbox inspections and no third-quartile data exceeded one in 5.

Woodland culls. Table 3 shows the cull data from trials in 2010, 2019 and 2020 Table 3. In 2010 the preliminary (non-lethal) experimental ‘cull’ in Hockeridge Wood resulted in <100 individual marked adults caught and released alive and more were caught in the same area later that year (BROOKS & TROUT, 2012), despite there being no vacancies created that might have encouraged immigration. In 2019 (a non-breeding year) the lethal cull and a non-lethal follow-up accounted for <200 *Glis*. In 2020 (a breeding year), the cull in the same wood resulted in

<300 adult *Glis* accounted for. The post cull numbers do not appear to result from immigrants immediately responding to the vacuum caused by the culls since only two of 115 microchipped *Glis* handled in the immediately adjacent section of Hockeridge Wood in 2019 were among those culled in 2020.

Reports from the built environment. Local District Council records of *Glis* control operations show 14–50 per killed per year between 1945 and 1951 (LEVER 1977). TROUT & MOGG (2017) show cull returns from the early 2000s, including the locations, and Figure 3 shows the rising trend ($R^2 \approx 0.7$) in requests for control in Wycombe and Chilterns Districts 1998–2007.

Licensee reports to Government (‘Defra’) 2011–2018 also indicate a significantly increasing trend in numbers culled in breeding years ($R^2=0.89$). Defra issued fewer than 100 licences to cull *Glis* in 2008, resulting in 423 being killed, a mean of 4.2 per location. Nine years later, 453 licences were issued and 2,541 animals were culled in 2017 (mean 5.6 per location). This represents 4.5 times as many sites and 33% higher cull rate/site within a decade. Both 2008 and 2017 were non-breeding years. Unreported infestations controlled by householders, together with

Table 3. The number of adult *Glis* captured in woodland culls and their derived population density estimates.

Place	Wood size (ha)	Duration of cull (days)	Year	Number culled (+ additional adults found soon afterwards)	Apparent population density culled/ha	Apparent population density if additional animals taken into account
Small wood	8	10 (in July)	2010	124 (+12) N.B. all released	15.5	17.5
Other wood cull #1	12	10 (in July)	2019	169 (+62 found 4 weeks later)	14.1	19.8
Other Wood cull #2	12	2 x 5-days July/August	2020	270 (+36 found 2 weeks later)	22.5	25.5

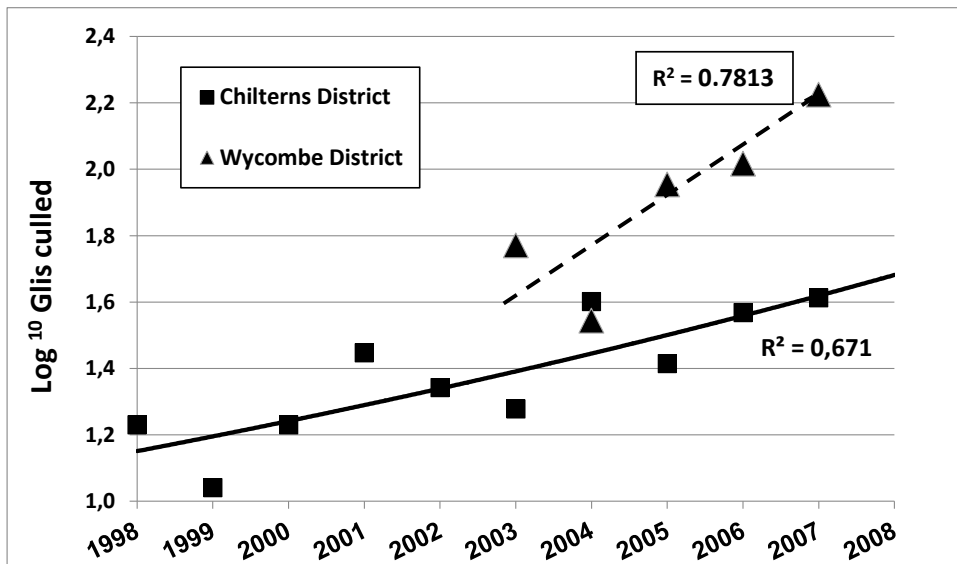


Fig. 3. Requests to local authorities to cull *Glis*. R² value is exponential trendline.

unreported deaths by non-target poisoning from legitimate rodent control operations, cats etc. will have resulted in additional but unquantified deaths.

In a housing estate near High Wycombe of 15 hectares, 41 houses out of 62 (66%) were reported as infested over a 3-year period, with up to 145 *Glis* being removed from a single house in one year. In the years 2013–2015, a total of 452, 380 and 468 were killed during the active season representing c. 9–11 per infested house.

Edible dormouse density estimates

1. Direct calculations from the recapture database. The average density of adults handled in August during the last five breeding years was 7.2/ha (SE 1.4), higher than the average at 5.4 (SE 0.7) for the last 5 years that included non-breeding years. The calculated overwinter population density for those KTBA in 2014–2018 averaged 21.6/ha (SE=3.9). The estimated average density of adults KTBA in August for the last 5 years was 14.8/ha (SE=2) and for the last five breeding years 18.7 (SE=5). In 2018,

the highest number KTBA during the year, including marked juveniles, was 741, equivalent to 22.5/ha. The average annual density of unique microchips recorded during the last 5 years 2014–2018 was 39.7./ha (SE=10) and 52/ha (SE=3.3) for the last five breeding years.

2. The Cormack–Jolly–Seber modelled population density estimates based on recaptures provide various indices of increasing abundance. For the last 5 years and the last 5 breeding years, the number of *Glis* averaged 41/ha (95% Confidence Limits=29–60) and 45/ha (95% CL=35–59) respectively. Using data only from August over the past 5 years the model estimates averaged 27.5/ha (95% CL=19–43). The figure for the last 5 breeding years was 48/ha (95% CL=28–87). In non-breeding years the average density was 20.1 adults/ha in August (95% confidence limits 17–25), still equivalent to 2,000 per square kilometre.

3. Independent estimates from woodland culls. LEVER (1977) reported 80 *Glis* removed from woodland from a 4ha section of a large wood (equivalent

Table 4. Estimated UK *Glis* population; our analyses rounded to the nearest 5000.

Data set	Estimated UK total	Lower estimate	Upper estimate
MATHEWS et al. (2018)	23,000	9,800	82,000
Annual unique last 5 yrs	865,000	425,000	1,305,000
Annual unique last 5 Br yrs	1,125,000	985,000	1,270,000
Overwinter KTBA 5 yrs	470,000	300,000	640,000
C–J–S Model last 5 yrs	890,000	635,000	1,295,000
C–J–S Model last 5 Br yrs	960,000	770,000	1,280,000
Adult cull in wood	340,000		370,000 incl. survivors
Adult cull in wood 2019	305,000		430,000 incl. survivors
Adult cull in wood 2020	490,000		555,000 incl. survivors
Cull in housing estate	630,000		
August adult data only			
C–J–S Model last 5 yrs	600,000	405,000	940,000
C–J–S Model last 5 Br yrs	1,045,000	610,000	1,890,000
Individuals last 5 yrs	120,000	85,000	150,000
Individuals last 5 Br yrs	160,000	100,000	215,000
KTBA last 5 yrs	320,000	240,000	405,000
KTBA last 5 Br yrs	405,000	200,000	620,000

to 20/ha) in 1963 with 20 more removed in the following year. Our cull density data are broadly similar, Table 3. If the additional animals culled in 2020 were not immigrants, but simply had not been captured earlier, the population density was, including final survivors, likely to be c.40/ha.

4. Numbers of *Glis* culled in the built environment. Culls from houses do not normally provide a density figure, simply a total removed from one or more buildings. However, a population density estimate is possible from the High Wycombe study. The culls represented 30/ha, 25/ha and 31/ha. The year 2015 was non-breeding. TROUT & MOGG (2016) reported many houses required repeat culling operations within the same season implying rapid immigration by *Glis* into a ‘vacated’ preferred built refuge habitat (with no food source within).

Estimating the size of the national population of *Glis*

Extrapolation of the various density figures from our monitoring studies allows multiple estimates of the size of the national *Glis* population. It is based on the same total area of suitable habitat in the Chilterns of 270km² (27,000ha) used by MATHEWS et al. (2018), but we divided it into ASNW and other woodland which we judged, without evidence, carried 50% fewer *Glis* per ha. Our overall estimates would be even higher if we had assumed the same density figure for all woods. Their and our estimates are shown in Table 4. The number of animals handled each year suggests a national population of 500,000–850,000

and up to 1.1 million in breeding years. The modelling indicates a national population of just under 900,000. Based on the number of individual PIT tagged individuals reported per year in breeding and non-breeding years, a UK *Glis* population of 500,000 to over 1 million is possible. Even restricting the data to the single month of August, when we know this is only a proportion of those known are alive, the number of adults captured suggests a figure of 120,000–600,000. In addition, numbers occur in an unknown proportion of houses and mature gardens. The estimates from culled animals in woodland indicate 300,000–500,000 and those that remained uncaptured lift this to 350,000–550,000.

Discussion

Our data come from three independent sources: cull records from the built environment, which indicate the distribution; nestbox monitoring and woodland culls. A potential criticism of our woodland study data is that (as demonstrated for some bird species) nestboxes may have artificially increased the suitability of the habitat for *Glis*. Our nestbox placement was at c. 6.7/ha, below the additional 7.5/ha used by NEWTON (1994) in his experimental study of nestbox use by birds. He found that additional nestboxes had no impact on bird numbers where many alternative refuges already existed. The Wiebe (2011) review concurred. Likewise, ELIAS & STOLESON (2021) found when a population of owls

had sufficient natural cavities that they rarely used nestboxes. The daytime occupancy rate of nestboxes by the adult nocturnal *Glis* has remained low in recent years, with less than two thirds of them being used, even in August in a breeding year. We find most adult *Glis* in nestboxes only once or twice a year and our evidence is that the animals did not rely on nestboxes for daytime refuge. The low level of recaptures from four analyses indicates that intense competition for nestboxes was not occurring in our study wood, individuals did not rely on them as daytime refuges because there were many alternatives. We conclude, as the above authors concluded, that nestboxes over two decades have not influenced competition for refuges nor provided evidence of enhancing *Glis* presence to create an exceptionally high and unrepresentative local population density.

Distribution and numbers

The area of known *Glis* locations, centred on the Chilterns Area of Outstanding Natural Beauty (but extending beyond it) is particularly rich in woodland, with c. 110 km² of Ancient Semi Natural Woodland and 70 km² of other woodland available; with houses, gardens and parkland contributing another 100 km². The wide dispersion of control events reported to Defra suggests that it is unlikely *Glis* are absent from any significant woodlands in the Chilterns area. There is also the confirmed occurrence of isolated breeding populations elsewhere to consider and the probability of further spread west of the M40 and into suburban London now that *Glis* are being culled east of the M25 motorway.

One consequence of increasing numbers is a greater probability of people catching *Glis* alive in their house, then releasing them elsewhere, instead of killing them. This contributes to their further spread and we know that it is already happening, despite being illegal. It is evident that *Glis* now occurs well beyond the Chilterns, with uncertainty as to the number and extent of new populations that may have become established. Following the original introduction at Tring in 1902, it was more than 20 years before reports emerged in local newspapers, implying that new populations (perhaps at relatively low density) had established in nearby villages but remained unreported. The same may also be true now at the edge of our mapped range.

Population modelling and actual numbers both indicate that the *Glis* population at our study site increased greatly in two decades, in parallel with the numbers of requests for assistance and the number of *Glis* culled as reported to local authorities and

Defra. Whilst several of the reported data sets may be challenged in detail (e.g. varying degrees of effort applied to reporting or in culling, small sample sizes affect confidence limits) it is evident that a considerable population increase has occurred in recent years.

As expected, our modelling estimates and the numbers of individuals captured in a year are highest for breeding years and the adult breeding population density at Hockeridge Wood varies from 40–50/ha. Whilst only 5–7 adults/ha were handled in early August, the number KTBA that month was 15–19/ha. The number of tagged adults recorded each year indicates densities average 21/ha overwinter and up to 52/ha in summer if young are included. Our short duration culls in woodland indicate a pre-breeding density of 20–40/ha. The 25–31/ha removed during three successive years from a housing estate included reinfestations. All our figures are, despite the different ways of estimating them, consistent with each other and similar to densities of 10–50/ha reported in central and southern Europe (ROSSOLIMO et al. 2001, KRYŠTUFEK & FLAJŠMAN 2007, KRYŠTUFEK 2010).

Consistency encourages confidence around the various estimates given here, but our information on *Glis* population density and estimates of the total population size conflict profoundly with figures given in the *Review of the Population and Conservation Status of British Mammals* by MATHEWS et al. (2018), proposing a national total of 23,000 animals (range 10,000–82,000). All our analyses suggest that this significantly underestimates the true situation and our estimates for the total population are 10–20 times greater. Even estimates based only on adults in August are at least at 6 times greater, (though the KTBA data for that month indicates the true figure to be over twice that estimate) and even in non-breeding years our annual estimates are ten times larger.

It is important to consider how such a large discrepancy has arisen. MATHEWS et al. (2018) estimated the total British population of *Glis* based on the Mammal Society's *Red Data Book* (MORRIS 1993), extended by HARRIS et al. (1995). Both of those sources relied on the original population density estimate made by HOODLESS & MORRIS in 1989, based on counting *Glis* calls along about 500 m of sampling transect. It was assumed that 100% of each sex were vocalising although the actual proportion was unknown at the time (and still remains unresolved 30 years later). Nor was it established what proportion of the population would be vocalising during the period during each transect sample. Furthermore, it was also not appreciated at that time

that *Glis* fails to breed in some years, and this would make a profound difference if 1989 was a non-breeding year. Subsequent research across Europe has revealed that reproductive failure in *Glis* is associated with failure of autumnal production of beech mast (MORRIS & MORRIS 2010, TROUT et al. 2015, HOELZL et al. 2015, RUF & BIEBER 2020). When that occurs, a significant proportion of older animals are not recorded in nestboxes but they are still alive. Apparently, many do not appear in spring or they quickly return underground and do not form part of the active population that summer (TROUT et al. 2015, RUF & BIEBER 2020). According to PACKHAM et al. (2008), beech mast was not abundant in 1989 so in retrospect, we would now expect *Glis* numbers monitored, and apparent population density, to have been low that year as in Fig. 2. Thus, the estimated national population then of 10,000 *Glis*, is likely to have been an underestimate, as are all subsequent estimates derived from it.

Nevertheless, MATHEWS et al. (2018) updated the figure of >1/ha published by HOODLESS & MORRIS (1993), and using the median value of 13 years (1995–2008) of a possibly exponentially rising number (Fig. 2) based on MORRIS & MORRIS (2010). However, our continued monitoring of the same wood shows that numbers continued to increase.

Our capture-mark-recapture population model estimates the current population density to be between 35 and 48 *Glis*/ha in good habitat. Paradoxically, the paucity of recaptures especially in non-breeding years may have created an upward bias because the model is based on recaptures.

The numbers of *Glis* culled in ten-day trials in woodland provide an independent measure of likely minimum population densities, ranging from 20–40/ha. Extrapolation generates a country-wide estimate of 250,000 – 450,000 animals as the national population, rising to 370,000–550,000 if we include the post-cull monitoring data. These figures, like the other results presented here, are an order of magnitude greater than suggested by MATHEWS et al (2018). A further challenge to their estimate is posed by the 2,431 *Glis* officially removed under licence in 2017 (a non-breeding year). If their national estimate was correct, those culled animals from 453 properties would represent 10% of the entire UK population. Similarly, the c. 450 *Glis* culled per year from a single estate of 62 houses sited on only 15 hectares is equivalent to 2% of the proposed national population. We are aware of two reports of 300 being taken from single properties. These indisputable numbers cannot be reconciled with a UK pre-breeding population of 9,800–82,000 *Glis* and we contend that our

analyses offer a more realistic assessment.

We conclude that the pre-breeding population density of *Glis* in England now more closely matches the situation reported historically in Germany and southern Europe. However, *Glis* is an invasive species in England and the species is spreading more widely from the single reintroduction point after 120 years. Climate change, influencing both tree flowering and especially increased winter rainfall during their long hibernation underground may influence the future population trajectory. The aim of the official Invasive Species Strategy (DEFRA 2015) is to minimise the risk posed by such non-native species and reduce their negative impacts. Our estimate for the total British population of *Glis*, as well as its increasing distribution, suggest that the presence of this species needs to be taken more seriously than hitherto and the economic and biological cost of edible dormice is not fully appreciated. With increasing numbers and continuing spread there are significant implications for the likely cost and complexity of control measures, without which *Glis* will become an increasing household nuisance, cause more economic damage and have a greater adverse impact on other biota.

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