REVIEW

Current and future impacts of nest predation and nest-site competition by invasive eastern grey squirrels *Sciurus carolinensis* on European birds

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ABSTRACT

1. The eastern grey squirrel (hereafter 'grey squirrel') is considered one of the most damaging invasive alien species in Europe, with negative effects on native ecosystems. Despite it being widely perceived as a significant predator of bird eggs and chicks and as a competitor for nest-sites, evaluation of the grey squirrel's impact on European bird populations has been hindered by limited empirical data.

2. The aim was to review the incidence of grey squirrels as nest predators of and nest-site competitors with European birds, and to use this information to identify species at potential risk of negative effects from within the grey squirrel's expanding range in continental Europe.

3. A comprehensive literature review was conducted and data were used alongside additional new data, to assess nest predation and competition by grey squirrels in their current European range. Bird species were grouped by nest-site type, which was used to predict the impact on similar species groups in regions of continental Europe predicted to be colonised by grey squirrels in the current century.

4. Camera-monitoring and field evidence for 12 bird species and 12420 nests in Britain showed that grey squirrels rarely depredated eggs or chicks, affecting just 0.5% of nests. Nest-site competition was also minor, with grey squirrels occupying 0.8% of 122 small tree-

cavities and 14% of 57 larger cavities. At least 69 bird species in continental Europe could be exposed to potential nest predation or competition from expanding grey squirrel populations within the current century, but population-level effects currently appear to be unlikely.

5. Current evidence shows that grey squirrels are unlikely to be significant predators of or competitors with nesting birds in their present or projected range in Europe. However, further studies of more species in different regions would be valuable, particularly in urban and suburban habitats.

Keywords: alien, Europe, IAS, invasive, mammal, nest, woodland

Running head: Impacts of grey squirrels on European birds

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INTRODUCTION

Invasive alien species (IAS) which have been deliberately or accidentally translocated by humans to regions outside of their native range are considered one of the greatest threats to global biodiversity (Vilà et al. 2011, Early et al. 2016). In the novel environment of their introduced range, IAS can have severe negative impacts on indigenous species and ecosystems through predation, resource competition, habitat modification and disease

47 transmission (Lowe et al. 2000, Clavero et al. 2009, Vilà et al. 2011, Welch & Leppanen
48 2017).

49 Predicting which IAS will have serious negative impacts can be hampered by limited
50 information on the species' ecology in its native or introduced ranges (Manchester & Bullock
51 2000, McCreless et al. 2016). This data deficiency can hinder policy-makers in prioritising
52 strategies for the management or eradication of IAS that may become established in new
53 areas (Roy et al. 2014).

54 Some of the most damaging IAS are mammals (Lowe 2000, McCreless et al. 2016), and the
55 eastern grey squirrel *Sciurus carolinensis* (hereafter 'grey squirrel'), native to eastern North
56 America, is considered one of the worst IAS in the world (Lowe 2000, Shuttleworth et al.
57 2016a). Since translocation to parts of Europe (Britain in 1876, Ireland in 1911, Italy in
58 1948), the grey squirrel has had severe negative effects upon local ecosystems, particularly
59 by its replacement of the native red squirrel *Sciurus vulgaris* across much of Britain, Ireland
60 and parts of northern Italy via resource competition and disease transmission (see Bertolino
61 et al. 2014, Shuttleworth et al. 2015, and references therein).

62 Another potential negative impact of invasive grey squirrels is predation of European
63 breeding birds. Although native red squirrels occasionally depredate nests (e.g. Weidinger
64 2009, Maziarz et al. 2019), their replacement could change the predation pressure on
65 European birds that have not evolved to co-exist with grey squirrels (Sage & Sotherton
66 2015). Grey squirrels are known predators of songbird eggs and chicks in their native and
67 introduced range (Moller 1983, Hewson & Fuller 2003), but this was previously thought to
68 have negligible effects on the birds in Britain (Kenward 1983). However, such predation is
69 now considered to be potentially significant for some bird species (Hewson & Fuller 2003,
70 Sage & Sotherton 2015). This shift in perception coincided with substantial declines of many
71 British woodland birds since the 1970s, the causes of which are poorly understood, but may
72 include nest predation by grey squirrels (Fuller et al. 2005).

The risk posed by grey squirrels to British birds (Hewson & Fuller 2003) should also apply to those same species, and their close relatives, in other parts of Europe where the grey squirrel is already established or predicted to colonise (Di Febbraro et al. 2013, Bertolino et al. 2015, Di Febbraro et al. 2019). Birds considered vulnerable include those building 'open' (cup-shaped or domed) nests in trees, shrubs or on the ground, such as finches (Fringillidae) and warblers (Phylloscopidae and Sylviidae), and also cavity-nesting birds that use tree holes or nest-boxes, such as tits (Paridae) and woodpeckers (Picidae; Hewson et al. 2004, Fuller et al. 2005). Grey squirrels may also compete with larger birds, such as tawny owls *Strix aluco* and stock doves *Columba oenas*, for nest sites in tree cavities or nest-boxes (Fuller et al. 2005).

Where nest-site availability is a limitation on cavity-nesting bird densities and diversity, as in most of the heavily modified forests of Europe, extensive competition that further limits the resource may have population-level effects if too many pairs of birds are prevented from breeding (Newton 1998). In many bird species, predation of eggs and chicks is typically the major cause of breeding failure, and populations can generally absorb very high losses. The loss of individual breeding attempts is generally insignificant for birds at the population level, as many species can have repeated breeding attempts. However, increased levels of predation from novel invasive species can be additive to typical losses from other causes, potentially leading to population declines (see Newton 1998 for a thorough review).

Despite concerns over competition and predation by invasive grey squirrels, limited data has prevented rigorous assessment of their impact on European bird populations (Gurnell et al. 2016). Newson et al. (2010) used indirect evidence from England to show negative associations between grey squirrel abundance and nest failure rates in several bird species, including the common blackbird *Turdus merula* and green woodpecker *Picus viridis*. However, lack of direct evidence of nest predators meant these relationships could not be linked explicitly to attacks by grey squirrels.

Identifying nest predators has long been problematic, as predation is rarely witnessed, and interpretation has relied on field signs of damage to the nest, eggs or chicks. The many potential predators, including birds, mammals and snakes, means that field signs can be ambiguous, particularly for open-nesting birds (Groom 1993, Larivière 1999).

These limitations have increasingly been overcome by automated cameras installed at nests to record predation events (Cox et al. 2012), which has greatly expanded the understanding of predation by revealing the variety of predators and their modes of attack (e.g. Weidinger 2009, Maziarz et al. 2019). Sage and Sotherton (2015) reviewed camera studies of nest predation by tree squirrels from Europe and North America, reporting a generally low incidence, particularly for grey squirrels. However, only two studies came from within the grey squirrel's European range, and both reported no attacks on two species of songbird (Stevens et al. 2008, Mallord et al. 2012).

Further nest-camera studies from Britain have yet to be reviewed, despite featuring songbirds for which the grey squirrel has been proposed as a potentially significant nest predator, including the hawfinch *Coccothraustes coccothraustes* (Kirby et al. 2018) and the wood warbler *Phylloscopus sibilatrix* (Bellamy et al. 2018). These studies provide important new information of additional species and larger samples.

Aside from open-nesters, previous reviews of grey squirrel impacts on European birds have largely overlooked cavity-nesting birds, such as tits. Several studies in Britain have reported characteristic field signs of gnawed, enlarged entrances of tree cavities or nest-boxes, which could only be caused by depredating grey squirrels (Perrins 1965, Dunn 1977, Hewson et al. 2004, Shuttleworth et al. 2016b). Such studies could indicate the incidence of grey squirrel predation of small cavity-nesting birds. For larger birds, such as the tawny owl, no study has quantified cavity competition from grey squirrels, despite widespread anecdotes and the potentially obvious field signs of animals or den material inside cavities (Hewson & Fuller 2003, Shuttleworth et al. 2016b).

This review aims to be more comprehensive than any previously attempted in quantifying grey squirrel competition and predation of bird nests in Europe, by considering open- and cavity-nesting species, and also including some previously unpublished data. Additionally, I undertake the first review of bird communities in regions of continental Europe predicted to be colonised by grey squirrels within the current century. The range expansion of grey squirrels in Italy (Bertolino et al. 2015), and potentially across much of continental Europe (Di Febbraro et al. 2013, 2016), could have widespread implications for European bird populations, and I use information from the grey squirrel's current range to identify birds vulnerable to negative impacts in regions of range expansion. The results can inform future management to minimise any such effects, to safeguard bird species of conservation importance.

METHODS

Nest predation

For open-nesting birds, a search of the Web of Science citation indexing service was made for studies using nest cameras, as these were considered to provide the most reliable evidence of predators for this group. Searches followed the guidelines given by Pullin and Stewart (2006), and used the keywords in the following search term: bird AND camera* AND nest AND (predation OR predator). Returns were filtered for areas within the grey squirrel's European range within Britain and Ireland during the corresponding period of each study (Gurnell 1987, The Mammal Society 2018), or within the Italian range (Bertolino et al. 2015). Only wooded and surburban/urban habitats were considered, where grey squirrels are most abundant (Merrick et al. 2016). Information extracted from studies included the bird species, habitat, position of nests within the wooded strata (ground, shrub layer, tree canopy), number of nests and associated predation events or overall breeding failures, and how many failures involved grey squirrels.

For cavity-nesting birds, another literature search for grey squirrel predation of this group used keywords in the search term: bird AND nest AND predation AND (cavity OR hole OR nest box). As with open-nesting birds, results were filtered for woodland and suburban/urban habitats in the grey squirrel's European range. To limit publication bias, further information was extracted from available PhD theses on relevant woodland birds. Predation of cavity nests attributed to grey squirrels was only included if the authors specified direct observation or distinctive field signs (gnaw marks around an enlarged cavity entrance; Perrins 1965), or if direct contact with authors confirmed this.

Nest-site competition

Grey squirrel competition with European cavity-nesting birds for potential nest-sites was reviewed with another literature search, using keyword combinations in the search terms: nest AND squirrel AND (woodpecker OR tit OR stock dove OR owl). These woodland species are abundant and well monitored within the grey squirrel's British range, and are representative of different sizes and types of nest cavity, so can act as effective proxies for other woodland species in their respective cavity-nesting guild. Grey squirrel occupation of tree cavities and nest-boxes was based on the reported presence of grey squirrels and/or den material inside (leaves, twigs etc.).

Previously unpublished data for nest-site competition were available from nest-boxes provided for tawny owls and stock doves at Monks Wood, a 160 ha deciduous woodland in Cambridgeshire, eastern England (52°11' N, 0°50' E). Monks Wood's tree canopy is dominated by common ash *Fraxinus excelsior* and English oak *Quercus robur* originating from regrowth after clear-felling around 1920. Grey squirrels are commonly encountered at Monks Wood (personal observations), where there is no management to control numbers, although density estimates were unavailable. The large wooden nest-boxes were fixed to

mature trees throughout the entire wood at a height of 3-4 m, and measured approximately 25 x 25 x 75 cm tall with an entrance of 25 x 20 cm.

Fifteen nest-boxes were monitored in 2012, 19 in 2013, 12 in 2018 and 11 in 2019, representing all available nest-boxes in those years. Distances between boxes ranged from 67 m to 406 m, with a mean of 249 m. Previous studies (Redpath 1995) indicate that Monks Wood can hold at least 11 breeding territories of tawny owls, meaning that each territory could theoretically include at least one nest-box, depending on territory boundaries. One or two nest-box inspections took place between April and July each year, during the breeding period of tawny owls and stock doves (du Feu 2003, Joys & Crick 2004). During nest inspections, presence of grey squirrels or recent den material (uncompressed green leaves and/or pliable twigs) denoted that the nest-box was unavailable to birds during that year's breeding season. Den material in nest-boxes was compressed by birds or removed by a researcher between breeding seasons, making nest-boxes available to birds or squirrels each spring.

Quantitative analyses of predation and competition

For each study identified in the literature reviews, and the unpublished data, the overall number of nest-sites and associated incidences of predation or competition were calculated over the reported time period. Individual nest-boxes monitored over multiple years were treated as independent in each year, due to potential mortality and turnover of individuals between breeding seasons.

Rates of grey squirrel predation were treated as minima, acknowledging the possibility of events where distinctive field signs were not detected. Rates of competition were treated as maxima, due to the possibility of birds with long breeding seasons (particularly stock doves) using a nest-box before or after grey squirrels in the same year. Grey squirrels were

assumed to be present in all studies within the species' European range, as they are common in wooded and suburban habitats (Newson et al. 2010, Merrick et al. 2016).

Bird species identified in the studies were assigned to one of four groups according to their typical nest site, based on information in Snow et al. (1998). The four were groups were: 1) open-nesters on the ground or in low bushes ≤1 m above the ground; 2) open-nesters in the shrub or canopy layers located >1 m from ground; 3) small cavity-nesters using tree holes or nest-boxes with an entrance diameter ≤7 cm; and 4) large-cavity nesters using tree holes or nest-boxes with an entrance diameter >7 cm.

Evaluation of potential future impacts of grey squirrels on European birds

Bird communities in regions of southern Europe at risk from colonisation by grey squirrels within the current century were identified in a final literature search in Web of Science, using the keywords and search term: bird AND community AND (forest OR urban OR park) AND (Italy OR Switzerland OR France). Studies were selected that listed the bird species of forest and urban or suburban habitat in regions predicted for grey squirrels by the year 2095 in northern Italy, south-east France and southern Switzerland (Bertolino et al. 2008).

Additional information was sourced by examining bird species' ranges from the European Breeding Bird Atlas (Hagemeijer & Blair 1997) in the region of grey squirrel occupation and expansion. This was used to identify nocturnal or crepuscular bird species in particular, which may not be well represented in standard surveys. Selected species were limited to those utilising forest, urban or suburban habitats and nesting in or among trees and shrubs (rather than in or on buildings), where grey squirrels forage. Large open-nesting birds, including large corvids and raptors, were excluded as they are unlikely to be displaced or depredated by grey squirrels. Remaining species were assigned to the same four groupings of nesting site as for predation and competition studies (ground, shrub/canopy, small cavity, large cavity). These groupings were used to identify those bird species vulnerable to future

negative impacts of grey squirrels, based on information for the corresponding groups in the predation and competition studies.

RESULTS

Nest predation

The literature search and filtering of studies of camera-monitored nests yielded five results from Britain (Table 1), comprising 222 unique nests of three species of open-nesting bird in broadleaved woodland or suburban habitats. This total excluded two studies of wood warblers (Mallord et al. 2016, Maziarz et al. 2018) that contributed to a third (Bellamy et al. 2018), so only the latter was considered in analyses.

Grey squirrel predation rates for a further nine species of cavity-nesting bird were available from 15 studies in Britain, comprising 12198 nests, although 77% of these were from one study (Table 1). Most studies of cavity-nesters (60%) involved birds breeding only in natural tree-holes, but the majority of nests (85%) were in nest-box studies.

The total 12 species of bird with data for grey squirrel nest predation belonged to three of the four categories of nesting site (see Methods), including open-nesting songbirds on the ground, songbirds in the shrub layer or tree canopy, and songbirds and woodpeckers using small cavities or nest-boxes (Table 1). The latter group also included the ring-necked parakeet *Psittacula krameri*, itself an IAS in Europe (Butler et al. 2013). All studies were within the contemporary British range of grey squirrels, which were stated or considered to be present at each site, and possibly common, due to their ubiquity and often high density in wooded and suburban habitats (Gurnell 1987, The Mammal Society 2018). The only partial exception was the national analysis of woodpeckers by Glue and Boswell (1994), which included a small minority of data from outside of the grey squirrel's contemporary range in Britain, although the vast majority of data was from within the range.

Grey squirrels were recorded as nest predators of between six and eight (50-67%) of the 12 bird species (Table 1; the imprecision was due to incomplete reporting in some multi-species studies). Grey squirrels depredated nests in all wooded strata (the ground, shrub layer and tree canopy), affecting 1.4% of open nests compared to 0.4% of cavity nests. For all nest types, the incidence of predation attributed to grey squirrels was very low, affecting between 0 and 5.6% of nests in individual studies, or 0.5% of nests in all studies. As a percentage of nest failures, grey squirrels accounted for between 0 and 26% of losses in each study, or 2.2% overall.

Studies with the highest incidence of predation by grey squirrels involved cavity-nesting blue tits *Cyanistes caeruleus* and great tits *Parus major* using nest-boxes in woodland, ring-necked parakeets in urban habitats, and ground-nesting wood warblers (Table 1). There were no records of grey squirrel predation of the open-nesting spotted flycatcher *Muscicapa striata* or hawfinch (though the sample size was small for the latter, Table 1), nor of the cavity-nesting lesser spotted woodpecker *Dryobates minor* or willow tit *Poecile montana*. However, Parry and Broughton (in press) suspected grey squirrel predation of 11% of 128 willow tit nests in north-west England, but this could not be confirmed (omitted from Table 1).

Ideally, daily nest predation rates attributable to grey squirrels would have been calculated from the duration of nest exposure, using the Mayfield (1975) method, to avoid bias toward successful nests or those found later in the breeding cycle. However, no study contained sufficient detail to be able to reconstruct this information, as the relevant exposure duration and timing of failures caused by squirrels were not reported. Nevertheless, 17 of 25 studies specified that most nests (mean 85%, range 35-100%) had been found and monitored from early in the breeding cycle, by the egg stage, i.e. during nest-building, egg-laying or incubation (Table 1). As such, recorded exposure to predation was of relatively long duration in most studies, and so recording bias would have been reasonably limited for those studies with a higher percentage of nests found early, and completely absent for those cavity-nesting species where the full breeding cycle was recorded.

Nest-site competition

In the literature search and in additional data for nest-site competition, grey squirrel occupation of large nest-boxes provided for tawny owls and stock doves in Britain ranged from 5.3% to 25% per year, and was 14% over all four years (Table 2). Despite this, between 25% and 68% of nest-boxes remained empty each year, or 40% overall. In smaller cavities, grey squirrels were present in 1.9% of tree-holes originally excavated by green woodpeckers or great spotted woodpeckers *Dendrocopos major* (Table 2). However, there was no evidence of grey squirrels occupying tree cavities considered suitable for nesting tits (Table 2).

Potential future impacts on European birds

For regions of continental Europe predicted to be occupied by grey squirrels in the current century, inventories of bird communities were available from northern Italy (predominantly Piedmont and Lombardy) and southern Switzerland (Lugano), but no studies were found for south-east France (Table 3).

A total of 57 species were identified in six studies of birds in forest habitats, and 48 species were identified in five studies of urban or suburban habitats. Combining all habitats, with a further seven species from the European Breeding Bird Atlas, gave a total of 69 bird species in the four nest-site groupings (Table 4). Most of these species were open-nesters in the shrub/canopy layer (44%) or small cavity-nesters (30%), with some species nesting on/near the ground (19%) or in large cavities (7%).

Eleven of the 14 species present in studies of nest predation and competition conducted in Britain were also recorded among the 69 species in the continental bird communities, including birds in each of the four groups of nest-site location (Table 4). Studies in Britain

(Table 1) indicated that, as open-nesters, most (62%) species in the continental bird communities were at greater risk of attack by colonising grey squirrels, compared to the fewer cavity-nesters, although the general risk was low.

Regarding nest-site competition, 81% of cavity-nesting species present in regions of continental Europe were songbirds, woodpeckers and the ring-necked parakeet, which all breed in small tree-holes or in nest-boxes (Table 4). The results from Britain (Table 2) suggested that these species would be at negligible risk of competition from grey squirrels. However, the results indicated that the five species that nest in larger cavities in continental Europe may be at a relatively greater risk of competition from grey squirrels, which occupied 14% of potential nest-sites in Britain (Tables 2 & 4).

DISCUSSION

Grey squirrels as nest predators in Europe

This review is the most comprehensive to date of the negative impacts of grey squirrels on European birds. The review is also the first assessment of the implications for birds of grey squirrel range expansion in continental Europe during the current century. Despite widespread perception of the grey squirrel as a significant predator of bird eggs and chicks (Hewson & Fuller 2003, Sage & Sotherton 2015), this was not supported by the empirical evidence. All of the information came from Britain, where grey squirrels are long-established and common (Newson et al. 2010, Shuttleworth et al. 2016a), but many studies did not record any nest predation by grey squirrels, and where predation was confirmed the incidence was low, or very low.

Previous assessments of grey squirrels' impacts on European birds have largely overlooked predation of cavity-nesting songbirds, despite studies reporting characteristic field signs that could only be attributed to this species. These studies, reviewed here, show that grey

329 squirrels do sometimes attack the nests of songbirds and woodpeckers breeding in tree
330 holes or nest-boxes, and may expend some effort in gnawing through the entrance to do so
331 (Hinsley et al. 1999, Broughton et al. 2011). This effort, and greater seclusion of eggs and
332 chicks, may explain why cavity nests were depredated less frequently than open nests.

333 The results of the review agreed with those from North America, which were assessed by
334 Sage and Sotherton (2015), where fewer than 1.8% of camera-monitored bird nests were
335 attacked by grey squirrels. Therefore, the substantial evidence from nest studies of a wide
336 range of birds throughout its native and introduced range indicates that the grey squirrel is
337 not a significant nest predator. Some opportunistic predation of eggs and chicks does occur,
338 as in other squirrel species in their native or introduced ranges (see Sage & Sotherton 2015
339 and Zarco et al. 2018), which may vary with habitat and individual behaviour, but this
340 appears to be insignificant for birds at the population level, at least in the regions studied to
341 date.

342 One limitation of the predation results is that some inherent bias was inevitable due to many
343 nests, particularly those of open-nesters, only being found and monitored once the breeding
344 attempt was well underway. This would underestimate grey squirrel predation of eggs,
345 particularly during the laying stage when the incomplete clutch is generally unattended.
346 However, a large proportion of nests were indeed monitored from the beginning, or soon
347 after the beginning, of the nesting cycle. There was no obvious indication of studies with
348 longer periods of monitoring recording higher nest predation by grey squirrels, and so
349 significant bias related to differences in nest exposure seems unlikely.

350 The results for grey squirrels contradict the indirect studies from Britain that reported some
351 negative relationships between grey squirrel abundance and bird population metrics.
352 Newson et al. (2010) found lower population growth for five woodland birds, including the
353 green woodpecker, with increasing abundance of grey squirrels. Similarly, Amar et al. (2006)
354 found a negative relationship between grey squirrel abundance and that of lesser spotted

355 woodpeckers and hawfinches. Bonnington et al. (2014a) reported that grey squirrel
356 abundance was associated with a slightly reduced abundance of open-nesting bird species,
357 which interacted with tree cover. However, when Sage and Sotherton (2015) experimentally
358 reduced the abundance of grey squirrels, this had a limited effect on woodland bird
359 communities. The present literature review showed that grey squirrels very rarely
360 depredated nests of woodland birds such as woodpeckers or hawfinches, though the small
361 sample size for the latter means it should probably be taken as indicative rather than
362 definitive. Nevertheless, it seems possible that more significant variables affecting nest
363 predation could correlate with grey squirrel abundance, but these may be more difficult to
364 detect and analyse.

365 The review found relatively few predation studies from urban or suburban habitats, and
366 these showed contrasting patterns. Grey squirrels were not recorded at any open nests of
367 spotted flycatchers in British gardens (Stevens et al. 2008), but they accounted for 26% of
368 nest failures (but only 4.7% of all nests) in the cavity-nesting ring-necked parakeet around
369 the London conurbation (Butler et al. 2013). It is unclear whether this difference reflects prey
370 naiveté in the parakeet (itself a relatively recent IAS) to a novel predator in Britain, or
371 whether there were local differences between studies in the abundance or behaviour of grey
372 squirrels.

373 In other British cities, Groom (1993) and Bonnington et al. (2015) considered grey squirrels
374 to be insignificant predators of the open nests of common blackbirds and song thrushes
375 *Turdus philomelos*, although cameras were not used. Additionally, Bonnington et al. (2013)
376 found negligible indirect effects of grey squirrel presence on the breeding success of
377 common blackbirds. Hanmer et al. (2016) used cameras to monitor eggs in artificial nests,
378 mimicking those of thrushes, and found that grey squirrels accounted for only 11% of
379 attacks. Hanmer et al. (2016) also found increased predation by grey squirrels where
380 supplementary food (peanuts) was provided for birds in local gardens, which may have
381 attracted grey squirrels to the vicinity of nests. The widespread supplementary feeding of

garden birds in Britain (Davies et al. 2009) and other parts of Europe (e.g. Tryjanowski et al. 2015, Pierret & Jiguet 2018) may inflate the abundance of grey squirrels and the associated risk of nest predation in urban areas (Bonnington et al. 2014b). However, the evidence from British cities suggests this risk is generally low.

Nest-site competition between grey squirrels and birds

The review indicated that nest-site competition with grey squirrels was negligible for songbirds and woodpeckers using small cavities. Although the typical dimensions of woodpecker cavities overlap with those of den sites attractive to grey squirrels (Sanderson 1975, Broughton et al. 2015), the cavities used by tits are probably too small for grey squirrels (Broughton et al. 2015, Shuttleworth et al. 2016b).

Competition for larger nest-boxes provided for tawny owls and stock doves was potentially more significant, and grey squirrels occupied up to 25% of available nest sites annually. This occupation by grey squirrels may have prevented some birds from nesting, although the presence of vacant boxes each year suggested that nesting sites were not limiting. However, not all nest-boxes may have been available to owls due to territoriality, and so it is possible that some pairs may have been prevented from nesting if a grey squirrel occupied a nest-box and alternative natural sites were lacking.

Although all information for larger cavities came from a single woodland in England, this was considered representative of many woodlands in managed landscapes, with few large natural cavities available as alternatives to nest-boxes (personal observations) due to the century-old tree trunks being too young to develop many hollows (Ranius et al. 2009). As such, competition between birds and grey squirrels was unlikely to be under-estimated through an abundance of available nest-sites.

406 This result is supported by Newson et al. (2010), who found only positive correlations in
407 English woodland between the abundance of grey squirrels and the population growth rates
408 of two potential competitors, the stock dove and western jackdaw *Coloeus monedula*.
409 Nevertheless, as with nest predation of urban birds, further direct evidence from a wider
410 range of species and habitats would be useful in further understanding the impact of grey
411 squirrels on birds that nest in large cavities. The same bird species may differ in its
412 population size and habitat use between different geographical regions, such as Britain and
413 areas of continental Europe (Wesołowski & Fuller 2012), although large tree cavities are
414 consistently used by stock doves, western jackdaws and tawny owls throughout their range
415 (Snow et al. 1998). On the basis of current evidence, therefore, nest-site competition from
416 grey squirrels seems unlikely to have had any population-level effect on birds in British
417 woodland, and may not do so elsewhere, but this requires confirmation.

418

419 **Potential impacts of grey squirrel range expansion in continental Europe**

420 This review suggests that bird communities in regions of continental Europe where the grey
421 squirrel is predicted to expand over coming decades are generally at little risk of increased
422 nest predation or competition. Grey squirrel predation of the nests of native European bird
423 species did not exceed an overall 5.6% in any study conducted in Britain, and many species
424 experienced no squirrel predation at all; this included some birds that had been suggested
425 as being particularly vulnerable, such as the lesser spotted woodpecker, hawfinch and
426 spotted flycatcher (Fuller et al. 2005, Newson et al. 2010).

427 The non-native ring-necked parakeet suffered one of the highest rates of grey squirrel
428 predation in Britain (4.7% of nests, Butler et al. 2013). This parakeet is also present as an
429 IAS in urban areas of northern Italy (Grandi et al. 2018), where similar predation may occur,
430 although this may not be considered to be a negative conservation impact.

Few European bird species are likely to compete with grey squirrels for nest-sites in larger cavities, and the results from Britain suggest that any competition would be minor in its effects. While grey squirrels may occupy up to four den sites per hectare (Shuttleworth et al. 2016b), any conflict could be offset by the squirrel's abandoned dreys (nests) in the tree canopy creating additional nest-sites for some bird species, such as the tawny owl and Eurasian kestrel *Falco tinnunculus* (Redpath 1995, Village 2010). Abandoned dreys may also provide nest-sites for other species of conservation interest, such as the long-eared owl *Asio otus* (Glue 1977).

The black woodpecker *Dryocopus martius* was identified in the literature review as at risk of potential competition with grey squirrels. This bird has a keystone role throughout much of Central Europe, as it excavates relatively large tree cavities for nesting, which are later used by many other species, including red squirrels, tawny owls and stock doves (Johnsson et al. 1993, Kosiński & Walczak 2019). However, neither the black woodpecker nor any close relatives occur in Britain or Ireland, and so no information was available to assess negative impacts of grey squirrels, which may find black woodpecker cavities particularly attractive due to their large dimensions. The time and energy expended in excavating these cavities, which may take weeks or even years (Kosiński & Walczak 2019), mean that displacement by grey squirrels could be significant for black woodpeckers, as well as for other cavity-users.

Besides birds, such as the black woodpecker, continued expansion of the grey squirrel's range in Europe will also bring it into contact with more mammal populations. Experience from Britain and Ireland indicates that severe negative impacts are likely for the red squirrel. Other mammals affected may include bats and dormice (e.g. *Dryomis nitedula*, *Eliomys quercinus*) that also occupy tree cavities, and which may be vulnerable to competition and displacement. However, there is some evidence to suggest that the presence of the European pine marten *Martes martes* may suppress the abundance and spread of invasive grey squirrels (Sheehy et al. 2018). The widespread presence of pine martens in continental Europe, and possibly also beech martens *Martes foina*, could have a similar limiting effect on

458 the spread of the grey squirrel across the region. Ecological studies of bird and mammal
459 species before and during contact with grey squirrels are essential if we are to understand
460 the conservation implications of these interactions.

461

462 **CONCLUSIONS**

463 Overall, the present review found no evidence of substantial nest predation by or competition
464 with grey squirrels for a range of bird species in Britain, and no support for a hypothesis of
465 widespread negative impacts from an expanding distribution of grey squirrels in continental
466 Europe. These results give a positive outlook, but have some caveats of limited information
467 for some species, groups and habitats. Published information is lacking completely for some
468 regions (Ireland, Italy), so further field studies would be valuable. In particular, nest camera
469 studies and monitoring of large-cavity nest-sites in Italy could confirm the extrapolations from
470 the British results. Monitoring nests from as early as possible in the breeding cycle
471 (preferably from nest-building) and calculation of exposure periods and daily predation rates
472 attributable to grey squirrels would increase the robustness of such results.

473 Nevertheless, the results from Britain extend and reinforce earlier correlative studies that
474 found no significant negative relationships between grey squirrel abundance and the
475 numbers, population growth or territory selection of most woodland and suburban bird
476 species examined (Hewson et al. 2004, Amar et al. 2006, Newson et al. 2010, Bonnington et
477 al. 2015). For the small number of species where a negative impact was identified, a direct
478 relationship has not been supported by field studies of predation or competition, suggesting
479 other co-variables in operation. Unforeseen local impacts of grey squirrels on birds cannot
480 be ruled out, although the current cumulative evidence suggests that population-level effects
481 are improbable.

482

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716 Table 1. Documented predation by the grey squirrel of bird nests in Britain, detected using nest-cameras for open-nesting species and by
717 diagnostic field signs for cavity-nesting species. The data from two studies denoted by * were included in the study marked **. % nests found by
718 egg stage refers to the percentage of nests in each study that were found early in the breeding cycle, during nest-building, egg-laying or
719 incubation.

Species	Nests	Nest type	Habitat	Stratum	Mean nest height (m)	Failed nests	Predated nests	% nests predated by grey squirrels	% nests found by egg stage	Study duration (years)	Area	Source
Phylloscopus sibilatrix	73	Open	Woodland	Ground	0	35	32	0.0	55	3	Wales	Mallord et al. 2012*
Phylloscopus sibilatrix	66	Open	Woodland	Ground	0	34	34	3.0	100	2	England	Maziarz et al. 2018*
Phylloscopus sibilatrix	144	Open	Woodland	Ground	0	95	95	2.1	?	5	England/ Wales	Bellamy et al. 2018**
Muscicapa striata	63	Open	Suburban/ Woodland	Shrub	3.4	20	20	0.0	74	2	England	Stevens et al. 2008
Coccothraustes coccothraustes	15	Open	Woodland	Shrub/ Canopy	>4	5	3	0.0	?	4	England/ Wales	Kirby et al. 2018
Poecile montana	56	Small tree-cavity	Woodland	Shrub	?	17	11	0.0	?	2	England	Lewis et al. 2009
Poecile montana	81	Small tree-cavity	Woodland	Shrub	2.2	21	18	0.0	?	4	England	Stewart 2010
Poecile montana	68	Small tree-cavity	Woodland	Shrub	2	36	19	0.0	100	18	England	Rustell 2015

Poecile montana	39	Small nest-box	Woodland	Shrub	1.5	2	0	0.0	100	9	England	Last & Burgess 2015
Poecile palustris	124	Small tree-cavity	Woodland	Shrub/ Canopy	3	19	13	1.6	81	7	England	Broughton et al. 2011
Poecile palustris	10	Small tree-cavity	Woodland	Shrub	0.7	2	1	0.0	100	1	England	Broughton et al. 2015
Poecile palustris	29	Small tree cavity/nest-box	Woodland	Shrub/ Canopy	2.3	8	7	0.0	100	1	England	Carpenter 2008
Dryobates minor	27	Small tree-cavity	Woodland	Canopy		11	3	0.0	70	3	England	Charman et al. 2012
Dryobates minor	37	Small tree-cavity	Woodland	Canopy		9	4	0.0	53	4	England/ Wales	Smith & Smith 2018
Dryobates minor	61	Small tree-cavity	Woodland	Shrub/ Canopy	5.4	6	2	0.0	?	51	Britain	Glue & Boswell 1994
Dendrocopos major	224	Small tree-cavity	Woodland	Shrub/ Canopy	11	13	6	0.0	35	4	England	Broughton et al. 2015
Dendrocopos major	594	Small tree-cavity	Woodland	Shrub/ Canopy		16	0	0.0	?	22	England	Smith 2006
Dendrocopos major	346	Small tree-cavity	Woodland	Shrub/ Canopy	5.3	31	13	0.3	?	51	Britain	Glue & Boswell 1994
Picus viridis	132	Small tree-cavity	Woodland	Shrub/	4.6	11	3	1.5	?	51	Britain	Glue & Boswell 1994

				Canopy								
Cyanistes caeruleus, Periparus ater, Parus major, Poecile palustris	9372	Small nest-box	Woodland	Shrub	2	2025		0.2	100	29	England	Dunn 1977
Cyanistes caeruleus	132	Small nest-box	Woodland	Shrub	1	42		0.0	100	4	England	Broughton et al. 2015
Parus major	19	Small nest-box	Woodland	Shrub	1	7		0.0	100	4	England	Broughton et al. 2015
Cyanistes caeruleus, Parus major	421	Small nest-box	Woodland	Shrub	2.3	157	134	2.6	100	10	England	Flegg & Cox 1975
Cyanistes caeruleus, Parus major	320	Small nest-box	Woodland	Shrub	2.5	94	39	5.6	100	5	England	Hinsley et al. 1999
Psittacula krameri	106	Small tree cavity/nest-box	Suburban	Shrub/ Canopy	8.3	19	5	4.7	73	3	England	Butler et al. 2013

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721 Table 2. Documented potential competition for nest sites between grey squirrels and cavity-nesting birds in England. Potential competition was
722 quantified by the incidence of cavity occupation by grey squirrels in suitable nest sites for birds, and also the availability of vacant cavities.

Species	Nest sites	Nest type	Habitat	Stratum	Mean height (m)	Grey squirrel occupation overall %	Vacant overall %	Study duration (years)	Area	Source
Columba oenas, Strix aluco	57	Large nest-box	Woodland	Shrub/ Canopy	3.5	14.0	40.2	4	England	own data
Cyanistes caeruleus, Parus major, Poecile palustris	70	Small tree-cavity	Woodland	Shrub	0.7	0	68.6	1	England	Broughton et al. 2015
Dendrocopos major, Picus viridis	52	Small tree-cavity	Woodland	Shrub/ Canopy	11	1.9	86.5	4	England	Broughton et al. 2015

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732 Table 3. Studies from southern/central Europe documenting breeding bird communities
733 (excluding large open-nesting species) in the regions predicted to be colonised by grey
734 squirrels in the current century (Bertolino et al. 2008).

Community	Species	habitat	Region	Source
All species	41	rural forest	North Italy	Popy et al. 2010
Strix aluco	1	rural forest	North/central Italy	Capizzi 2000
Strix aluco	1	urban park	North Italy	Sacchi et al. 2004
All species	29	rural forest	North Italy	Caprio et al. 2009
All species	36	suburban parkland	North/central Italy	Sorace & Visentin 2007
All species	28	rural forest	North Italy	Laiolo et al. 2004a
All species	13	rural forest	North Italy	Laiolo et al. 2004b
All species	38	rural/urban	North Italy	Bani et al. 2009
Psittacula krameri	1	urban	North Italy	Grandi et al 2018
All species	11	urban/suburban	North/central Italy	Sorace & Gustin 2010
All species	30	urban	South Switzerland	Fontana et al. 2011

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747 Table 4. Birds (excluding large open-nesting species) breeding in the region of
748 southern/central Europe predicted to be colonised by grey squirrels in the current century
749 (Bertolino et al. 2008), derived from studies in Table 3 and distribution maps from the
750 European Breeding Bird Atlas. Birds are grouped by nest type (open-nester or cavity-nester:
751 tree cavity or nest-box) and by nest situation in the vegetation strata (on the ground or in low
752 shrubs <1 m high, or in the taller shrub/canopy layer), or in a small (<7 cm diameter
753 entrance) or large (>7 cm diameter entrance) cavity.

Open-nester		Cavity-nester	
Ground/shrub	Shrub/canopy	Small cavity	Large cavity
Anthus trivialis	*Acanthis flammea*	*Aegolius funereus*	*Coloeus monedula*
Caprimulgus europaeus	*Aegithalos caudatus*	*Certhia brachydactyla*	*Columba livia*
Erithacus rubecula	*Asio otus*	*Cyanistes caeruleus*	*Dryocopus martius*
Hippolais polyglotta	*Carduelis carduelis*	*Dendrocopos major*	*Falco tinnunculus*
Luscinia megarhynchos	*Chloris chloris*	*Dryobates minor*	*Strix aluco*
Phylloscopus bonelli	*Coccothraustes coccothraustes*	*Jynx torquilla*	
Phylloscopus collybita	*Columba palumbus*	*Lophophanes cristatus*	
Phylloscopus sibilatrix	*Cuculus canorus*	*Otus scops*	
Phylloscopus trochilus	*Fringilla coelebs*	*Parus major*	
Scolopax rusticola	*Garrulus glandarius*	*Passer hispaniolensis*	
Sylvia atricapilla	*Hippolais polyglotta*	*Passer italiae*	
Sylvia borin	*Lanius collurio*	*Passer montanus*	
Sylvia curruca	*Linaria cannabina*	*Periparus ater*	
	Loxia curvirostra	*Phoenicurus phoenicurus*	
	Muscicapa striata	*Picus viridis*	
	Oriolus oriolus	*Poecile montana*	
	Phoenicurus ochruros	*Poecile palustris*	
	Pica pica	*Psittacula krameri*	
	Prunella modularis	*Sitta europaea*	
	Pyrrhula pyrrhula	*Sturnus vulgaris*	
	Regulus ignicapilla	*Upupa epops*	
	Regulus regulus		
	Serinus serinus		
	Spinus spinus		
	Streptopelia decaocto		
	Streptopelia turtur		
	Troglodytes troglodytes		
	Turdus merula		
	Turdus philomelos		
	Turdus viscivorus		

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