1 **REVIEW**

2 Recent history, current status, conservation and management of native 3 mammalian carnivore species in Great Britain

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ABSTRACT

1. After historical declines in population sizes and ranges, we compare and contrast the recent history and contemporary variation in the status of Great Britain's eight native mammalian carnivore species from the 1960s to 2017.
2. Wildcat *Felis silvestris* conservation status is unfavourable and is masked by hybridisation with domestic cats *Felis catus*. Red foxes *Vulpes vulpes* remain widespread but are currently declining. European otter *Lutra lutra*, European pine marten *Martes martes* and European polecat *Mustela putorius* populations are characterised by rapid recovery. Otters have almost completely recolonised Great Britain, polecats have expanded their range throughout southern Britain from refugia in Wales and pine martens have expanded their range from the Scottish Highlands. European badgers *Meles meles* have generally increased in population density. Status assessments of stoats *Mustela erminea* and weasels *Mustela nivalis* are data-deficient but available evidence suggests that stoats may have increased while weasels may have declined.
3. Anthropogenic processes influencing carnivore status include legal protections, habitat quality, reintroductions, predator control, pollutants, hybridisation and diseases and associated control practices. Population effects of pollutants, such as anticoagulant rodenticides, remain poorly characterised. The widespread interface with domestic and feral cats makes the wildcat's situation precarious. Recent declines in rabbit *Oryctolagus cuniculus* populations are a concern, given that several carnivore species depend on them as food.
4. We conclude that, with the exception of the wildcat, the status of Great Britain's mammalian carnivores has markedly improved since the 1960s. Better

understanding of the social aspects of interactions between humans and expanding predator populations is needed if conflict is to be avoided and long-term co-existence with people is to be possible.

Keywords: carnivores, hybridisation, monitoring, pollutants, predator control

Running head: Carnivores in Great Britain

INTRODUCTION

Eight species of terrestrial mammalian carnivore are native to, and extant in, Great Britain (defined here as England, Scotland, Wales and their islands): wildcat *Felis silvestris*, red fox *Vulpes vulpes*, European otter *Lutra lutra*, European badger *Meles meles*, European pine marten *Martes martes*, stoat *Mustela erminea*, weasel *Mustela nivalis* and European polecat *Mustela putorius*. Since their arrival 5000–20000 years ago (Montgomery et al. 2014), they have had mixed fortunes, depending in part on whether they were reviled as vermin, used for sport, valued for fur, appreciated as rodent-catchers, or combinations thereof during their shared histories with humans (Lovegrove 2007). Langley and Yalden (1977) illustrated the eighteenth and nineteenth century declines of what they termed Britain's 'rarer carnivores' (wildcat, pine marten and polecat), which they attributed largely to intensive predator control by gamekeepers, leading to persistence only in refugia where control was least intensive. Otter and badger populations were also greatly reduced but did not experience such pronounced range contractions (Cresswell et al. 1989, Jefferies 1989), despite local pressures from digging (Cresswell et al. 1989) or hunting (Jefferies 1989). By the twentieth century, only fox, stoat and weasel appeared unaffected by control (Tapper 1992). The advent of World War I, cessation of sporting activities and the loss of a generation of gamekeepers led to a reduction in predator control (Langley & Yalden 1977). Contemporaneous reports suggest that the most affected species showed signs of recovery almost immediately (Lovegrove 2007). By the 1970s, there was evidence that the wildcat, pine marten and polecat were beginning to recolonise their former ranges (Langley & Yalden 1977). Otters, however, were experiencing catastrophic decline

78 (Jefferies 1989), later ascribed primarily to exposure to organochlorine pesticides
79 (Chanin & Jefferies 1978).

80 Since the 1970s, legal, social and practical developments have altered the anthropogenic
81 pressures faced by Britain's carnivores. Management practices have changed, with bans
82 on certain traps and toxicants, and greater reliance on rearing and releasing pheasants
83 *Phasianus colchicus*, as opposed to fostering wild gamebirds (Tapper 1992). Legal
84 protections have been put in place internationally (e.g. the European Union's Habitats
85 Directive 1992) and nationally for conservation (e.g. Wildlife & Countryside Act 1981)
86 and on animal welfare grounds (e.g. Protection of Badgers Act 1992). Land use change
87 (Swetnam 2007) and agricultural intensification have been associated with biodiversity
88 loss (Robinson & Sutherland 2002). The mechanisms and implications of exposure to
89 some contaminants are now better understood (Shore & Rattner 2001), advances in
90 genetics have revealed the extent of hybridisation between wild and domestic species
91 (Driscoll et al. 2007, Costa et al. 2013), and developments in epidemiology have
92 enhanced knowledge of carnivores as disease reservoirs (Delahay et al. 2009).

93 A century after the rarest of Britain's carnivores reached their nadir and forty years
94 after the publication of the paper by Langley and Yalden (1977), it is timely to compare
95 and contrast the status of the eight species. We have gathered literature from the 1960s
96 to 2018 and include the latest population estimates. We review processes that affect
97 carnivores, positively and negatively. Although two non-native carnivore species, feral
98 ferret *Mustela furo* and American mink *Neovison vison*, have become established in Great
99 Britain, they are not considered here, other than as an influence on native species.

100

METHODS

We searched Scopus, Google Scholar and Google using scientific and common names (wildcat, [red] fox, [European] otter, [European] badger, [European] pine marten, stoat, weasel, [European] polecat) and the keywords 'Britain', 'England', 'Scotland' or 'Wales' and 'distribution', 'density' and 'monitoring'. Publications until 5 October 2018 comprising systematic surveys of distribution and abundance were catalogued. Further publications were added from their citations. *Ad hoc* records were not included because of the difficulty of distinguishing hybrids (wildcats and polecats) and because our objective was to assess status using large-scale accounts.

Distribution data were digitised (QGIS Development Team 2009) and scaled to hectads. Range expansion, if any, was modelled following Preuss et al. (2014). Only surveys using comparable approaches, i.e. nationwide surveys using carcass collection and verifiable sightings, were included. Central points of the 1960-1975 core ranges (Langley & Yalden 1977) were used as the starting point from which later expansion was measured. For wildcats the starting point was Scotland, for pine martens it was northern Scotland, and polecats it was central Wales. Range change was measured between starting points and range margins in each decade. Distances from central points were measured to the centre of each hectad in which presence was confirmed in later surveys. Outliers unlikely to be part of a contiguous population were removed. Range margins were estimated by fitting a gamma distribution to distance to central point data, using the 95^{th} quantile to represent the location of the range edge. This approach was preferred as it is less sensitive to sampling variation (Preuss et al. 2014). The slope of the regression with time was taken as the rate of expansion.

POPULATION CHANGE AND CURRENT STATUS

Wildcat *Felis silvestris*

The wildcat's range diminished earlier than those of pine marten or polecat. In 1915 wildcats were limited to the Scottish Highlands, showing the most restricted distribution of Langley and Yalden's (1977) rarer carnivores. By the 1970s, wildcats could be loosely grouped into two populations: a south-western population in the southern Highlands, Argyll and Bute; and a north to north-eastern population stretching from the north-central Highlands to the Grampians (Langley & Yalden 1977). Three distribution surveys using carcass collection, live trapping and sightings were undertaken between the 1980s and 2010s (Fig. 1). An intensive camera-trapping survey was also carried out by Kilshaw et al. (2016) to assess wildcat occupancy with habitat covariates. It is difficult to assess changes in wildcat distribution, or to model range expansion, owing to the presence of, and changes in reporting of, hybrids (Fig. 1). Our model of wildcat range change was inconclusive (expansion rate 0.2 km per year over 30 years, 95% confidence interval: -4.4 to 4.9, Appendix S1b). In the 1980s, wildcats were distributed throughout northern and central Scotland and there was an increase in records in the east of the country and an expansion of range north-east into Caithness, compared to the 1970s (Easterbee et al. 1991). The two population groupings (Langley & Yalden 1977) were less evident. Davis and Gray (2010) divided records into 'possible' (44%) and 'probable' (56%) wildcat sightings, using pelage characteristics (Kitchener et al. 2005). 'Probable' wildcat records were more common north of the Highland boundary line than 'possible' wildcat records, which appeared more frequently in the south and east of Scotland. Wildcat distribution is currently assumed to be that of the 'probable' records (Scottish Natural Heritage 2013). Kilshaw et al. (2016) reported that

149 the probability of wildcat occupancy is highest in the central and eastern Highlands, the
150 edges of the Cairngorms, along the west coast and in a few areas in the far north. The
151 Scottish Wildcat Action project has not received any records verified as wildcats from
152 the northern Highlands since 2015 (R. Campbell, unpublished data). It is also believed
153 that there are no wildcats south of central Scotland (Kilshaw et al. 2016). The latest
154 population estimate for wildcats is 200 (95% confidence interval: 30 – 430; Mathews et
155 al. 2018; Appendix S2). However, the reliability of this estimate is considered to be low
156 and estimates vary depending on how strict a definition of wildcat is used.

157 **Red fox *Vulpes vulpes***

158 Red foxes are present throughout mainland Great Britain, Anglesey, Isle of Wight and
159 Skye (Harris et al. 1995, Webbon et al. 2004). It is likely that the species' value in sport
160 hunting meant that foxes were protected to some degree from systematic control and
161 this prevented the historic declines seen in other carnivores (Tapper 1992). Foxes
162 feature in numerous surveys, including the Game and Wildlife Conservation Trust's
163 (GWCT) National Gamebag Census (NGC; Aebischer et al. 2011) and the British Trust for
164 Ornithology's (BTO) Breeding Birds Survey (BBS). The NGC provides a long-term index
165 of individuals killed per unit area as part of game management and NGC records of foxes
166 killed on game estates suggest a population increase in Britain from the 1960s, followed
167 by stabilisation from the 1990s to 2009 (Fig. 2; Aebischer et al. 2011). Data from the
168 BBS over a similar time period partly corroborate this; however, recent data indicate a
169 45% decline in the numbers of foxes seen on BBS sites in England (-41% throughout the
170 United Kingdom) from 1996-2016, particularly after *c.* 2008 (BTO 2018, Harris et al.
171 2018). There are no other data to corroborate this decline and causes are not
172 understood, though timing is coincident with significant declines in BBS records of

rabbits *Oryctolagus cuniculus* in England (-44%), Scotland (-82%) and Wales (-48%; Harris et al. 2018).

Previous causes of fox declines include hunting pressure (Tapper 1992) and localised outbreaks of mange caused by *Sarcoptes scabiei* (Soulsbury et al. 2007). Some of these declines have been offset by spread into areas or habitats where foxes were previously scarce (Baker et al. 2006), such as Norfolk (Tapper 1992) and urban spaces (Scott et al. 2014). A survey of England and Wales found that in the 2010s foxes were recorded in ~90% of 65 cities, where they had been scarce or absent in the 1980s (Scott et al. 2014). Although urban foxes are increasing, they still comprise a small proportion of the total population. Webbon et al. (2004) estimated the total rural fox population in Britain to be 225000, whereas the estimate for urban foxes was 33000 in 1995 (Harris et al. 1995). The latest estimate of the total fox population is 357000 (95% confidence interval: 104000 - 646000; Mathews et al. 2018; Appendix S2).

European otter *Lutra lutra*

As an apparent competitor with humans for fish, the European otter has long been viewed as a pest. Otter hunting began in the Middle Ages (Lovegrove 2007). Historical records indicated a slow decline in numbers from the late eighteenth century onwards, caused by predator control, sport hunting with hounds and pollution (Jefferies 1989). Otters rarely scavenge and have large territories, making them less likely than other carnivores to enter baited traps (Jefferies 1989). While local extinctions occurred in some catchments, regional extinctions were initially avoided (Harris et al. 1995).

By the late 1950s, hunt records indicated that otters were experiencing sudden and rapid decline, with the most severe reductions in southern England (Jefferies 1989).

196 Various potential drivers were considered, including habitat destruction, disturbance,
197 introduction of American mink, the associated spread of canine distemper virus,
198 hunting pressure and the possibility of increased mortality arising from the severe
199 winter weather of 1962-3 (Chanin & Jefferies 1978). The timing and sudden onset of the
200 decline, simultaneous to that observed in predatory birds, suggested that
201 organochlorine pesticides, principally dieldrin, were likely to be responsible for
202 increased mortality (Chanin & Jefferies 1978). Dieldrin, introduced in the 1950s as a
203 sheep dip and seed dressing, was detected in 81% of otters examined between 1963
204 and 1973 (Mason et al. 1986). Voluntary restrictions were placed on dieldrin use in the
205 1960s and 1970s, followed by mandatory bans in the 1980s (Macdonald 1983).

206 National otter surveys began in the 1970s (Fig. 3, Appendix S3), when otters were
207 recorded at only 6% of sites in England (Lenton et al. 1980), 20% in Wales (Crawford et
208 al. 1979) and 57% in Scotland (Green & Green 1980). By the 1980s, European otters
209 were present at 10% of sites in England (Strachan et al. 1990), 38% in Wales (Andrews
210 & Crawford 1986) and 65% in Scotland (Green & Green 1987). Reintroductions were
211 carried out in East Anglia, Hertfordshire and the upper Thames in the 1980s and early
212 1990s (Jefferies et al. 1986, Harris et al. 1995, Roche et al. 1995). Surveys in the 1990s
213 recorded otters present at 23% of sites in England (Strachan & Jefferies 1996), 53% in
214 Wales (Andrews et al. 1993) and 88% in Scotland (Green & Green 1997). By the 2000s,
215 European otters were recorded at 36% of sites in England (Crawford 2003), 72% in
216 Wales (Jones & Jones 2004) and 92% in Scotland (Strachan 2007). The most recent
217 surveys found European otters at 59% of the original sites surveyed in England
218 (Crawford 2010) and, when accompanied by spot checks in areas not covered by the
219 original surveys, these data show that only Kent and East Sussex are yet to be

220 substantially recolonised (Fig. 3). Otters are considered to be at carrying capacity in
221 south-west England and the Wye Valley, with evidence of otter presence at over 80% of
222 sites (Crawford 2010). The 2009-10 survey in Wales indicated otter presence at 90% of
223 sites (Strachan 2015). The contemporaneous survey in Scotland indicated that there
224 may have been a decline in occupancy since the previous decade, with detection at 78-
225 80% of sites surveyed (Findlay et al. 2015). However, there was some uncertainty as to
226 whether this was a real decline or a result of inclement weather during surveying and
227 reduced detectability (Findlay et al. 2015). Otters are now widespread throughout both
228 Wales and Scotland (Fig. 3). In England, Crawford (2010) estimated that otter
229 distribution had expanded at approximately 3.6 km per year, and this trend is expected
230 to lead to complete recolonisation of England, and therefore Great Britain, by 2030
231 (Crawford 2010).

232 Dieldrin is still detectable in otters (Chadwick 2007) but is not considered likely to
233 affect populations at the observed trace levels (Crawford 2010). The presence of
234 invasive American mink, which became widespread during the otters' absence, has not
235 impeded otter recolonisation, probably because otters cause shifts in mink behaviour
236 (Harrington et al. 2009). The latest population estimate for otters in Britain is 11000,
237 although the reliability of this estimate is considered to be very low (Mathews et al.
238 2018; Appendix S2).

239 **European badger *Meles meles***

240 European badger populations declined during the nineteenth century to the extent that
241 the species were considered uncommon (Cresswell et al. 1989). Declines were due to a
242 combination of control by gamekeepers, sett disturbance and badger baiting (Wilson et
243 al. 1997). The extent of pressure varied regionally. For example, in East Anglia, intensive

activity by gamekeepers reduced numbers to a tenth of those in neighbouring counties (Harris 1993).

By the 1970s, badgers were more common in south-west and central England, and central and north Wales (Appendix S3), but remained unrecorded in parts of East Anglia and northern Scotland (Neal 1972). In the 1980s, badger distribution expanded and the population was estimated to be 250000 in Great Britain, although gaps remained in London, East Anglia, Lincolnshire, Lancashire and northern Scotland (Cresswell et al. 1990). By 1994-97, the number of badger social groups in Britain had increased by 24%, although colonisation of new areas was minimal (Wilson et al. 1997).

In 2006-09, surveys of mainland Scotland indicated that badger main sett numbers had increased since the 1990s, though differences in methodology made direct comparisons difficult (Rainey et al. 2009). In England and Wales, numbers of badger social groups increased by 88% (equivalent to 2.6% per annum) between 1985-88 and 2011-13 (Judge et al. 2014). The magnitude of changes in sett density varied by region, due to a combination of landscape and local effects. England saw a 103% increase, whereas in Wales densities remained stable (Judge et al. 2014). Combining results from Scotland (Rainey et al. 2009), with Judge et al. (2014), leads to an estimate of 81000 (95% confidence interval: 75400–86600) badger social groups in Britain by 2013. Judge et al. (2017) combined their earlier sett survey with analysis of social group size variation, to derive a population estimate of 485000 individual badgers in England and Wales. Even allowing for methodological differences, evidence suggests that badger populations increased substantially in England and Wales between the 1980s and 2011-13 (Cresswell et al. 1990, Judge et al. 2017).

European pine marten *Martes martes*

When the European pine marten population reached its nadir in *c*. 1915, its range was restricted to the north-west of the Scottish Highlands and small, isolated areas of northern England and north Wales (Langley & Yalden 1977). By 1975, there was some spread eastwards into the Scottish Grampians, while the Welsh population was not thought to have expanded and English records were limited to sporadic sightings in Yorkshire and the Lake District (Langley & Yalden 1977).

By the 1980s in Scotland, the main populations were still confined to north of the Great Glen, though pine marten occurrence was nearly continuous throughout the central and western Highlands (Velander 1983). As the prevailing view was that this northern population was too remote to recolonise southern Scotland, a reintroduction took place in Galloway Forest, southwest Scotland in 1980 and 1981 (Shaw & Livingstone 1992). In the 1990s, pine martens expanded south of the Highlands into Argyll and Bute, Stirling and Perth and Kinross. By 2013, they had been recorded throughout much of central and eastern Scotland, on Skye and Mull and beyond the release sites in Galloway (Fig. 4; Croose et al. 2013, 2014). Our model of range expansion estimates that between 1975 and 2015 the Scottish pine marten population expanded at a rate of 1.7 km per year (95% confidence interval: 0.8-2.7 km, Appendix S1b). Despite repeated surveys during the 1980s and 1990s (Appendix S3), evidence of pine marten presence in England and Wales remained limited, suggesting that at best only a few low-density populations remained. There is occasional evidence of pine martens from Shropshire and Hampshire, potentially the result of covert releases. Recent evidence in Northumberland indicates that European pine martens are expanding south through the Borders, recolonising parts of northern England (Vincent Wildlife Trust [VWT],

291 unpublished data). Between 2015 and 2017, 51 pine martens were translocated from
292 Scotland to Wales in order to reinforce populations there; this has proven successful
293 with high survival and breeding in the wild (VWT, unpublished data). The latest
294 population estimate for pine martens is 3700 (95% confidence interval: 1600 - 8900;
295 Mathews et al. 2018; Appendix S2).

296 **Stoat (ermine) *Mustela erminea***

297 There are no national surveys for the stoat and so data are from the GWCT's NGC. Stoats
298 are thought to be common and widespread throughout Great Britain, including on the
299 Isle of Wight and the Scottish islands of Shetland, Islay, Jura, Mull, Skye, Raasay and Bute
300 (McDonald & King 2008a). In 2010 stoats were sighted for the first time on Mainland,
301 Orkney and an eradication programme is underway there in an attempt to protect
302 ground-nesting birds, Orkney voles *Microtus arvalis orcadensis* and the predatory birds
303 that eat them (Fraser et al. 2015). In spite of intensive predator control in the
304 nineteenth century, stoat numbers did not exhibit the declines seen amongst the larger
305 mustelids (Tapper 1992). This is likely to be due to the stoat's high productivity,
306 reducing potential for culling to cause decline, and its mobility, facilitating immigration
307 into areas where numbers are reduced (McDonald & Harris 2002).

308 Stoat numbers were severely reduced by myxomatosis in rabbits (Sumption &
309 Flowerdew 1985). One game estate in Suffolk reported a tenfold reduction in the
310 numbers of stoats killed in the years after the initial outbreak (Tapper 1992). Stoats
311 were, and remain, extremely reliant on rabbits (McDonald et al. 2000) and the loss of
312 this important food source was believed to have impaired productivity and survival
313 (Sumption & Flowerdew 1985). The NGC shows that indices of the numbers of stoats
314 killed per unit area on game estates increased steadily from the 1960s (Fig. 5; Aebischer

et al. 2011), alongside rabbit recovery, though the NGC reported another dip in stoats killed in the 1980s (Aebischer et al. 2011). In a comparative study of stoat and weasel diets between the 1960s and 1990s, McDonald et al. (2000) concluded that there was little evidence that reductions in prey were causing this downturn, some of which may have been attributable instead to changes in trapping effort affecting the NGC (McDonald & Harris 1999). Since then, there has been a steady increase in stoats killed on game estates from the 1990s to 2009 (Fig. 5). The impact on stoats of the recent apparent reductions in rabbit numbers is unknown. The latest population estimate for stoats is 438000 (Mathews et al. 2018), unchanged from that of Harris et al. (1995), indicating the sparsity of data. Both of these estimates are considered to have low reliability (Appendix S2).

Weasel (common weasel, least weasel) *Mustela nivalis*

Weasel population trends are also from the GWCT's NGC. Weasels are relatively prolific breeders and, similar to stoats, did not appear to experience nineteenth century declines (Tapper 1992). They are also thought to be common and widespread throughout mainland Great Britain (McDonald & King 2008b). In contrast to stoats, weasel abundance increased during and after myxomatosis, likely a result of reduced rabbit grazing, increased rough grassland and increased abundance of field voles *Microtus agrestis* (Jefferies & Pendlebury 1968), which are frequent prey of weasels (McDonald et al. 2000).

The NGC reveals a decline in indices of weasels killed per unit area on game estates from the 1960s onwards (Fig. 5). Models of weasel populations suggest that this decline is unlikely to be the result of trapping by gamekeepers as, similar to stoat, the weasel's high productivity and mobility buffer populations against intense culling (McDonald &

339 Harris 2002). Weasel productivity is particularly sensitive to prey abundance (King
340 1980) and populations fluctuate with vole abundance (Tapper 1979). It is therefore
341 possible that there has been a negative effect of rabbit recovery on field vole
342 populations and, consequently, weasels (Sumption & Flowerdew 1985). Weasel indices
343 from the NGC started to increase again from the 1990s but are still below those
344 recorded in the 1960s (Fig. 5). The latest population estimate for weasels is 450000
345 (Mathews et al. 2018). In common with stoats, this estimate is the same as that of Harris
346 et al (1995), indicating the paucity of data for these species (Appendix S2).

347 **European polecat *Mustela putorius***

348 Having reached their nadir in *c.* 1915, European polecat populations began to recover
349 following the alleviation of predator control during the early twentieth century, the
350 banning of gin traps in 1958, and the recovery of rabbit populations after the
351 myxomatosis epizootic of the mid-twentieth century (Langley & Yalden 1977). Rabbits
352 are also important prey for polecats (Birks & Kitchener 1999) and, although rabbits
353 were previously abundant, they were catastrophically reduced as the disease swept
354 across the country (Sumption & Flowerdew 1985). Rabbit numbers began to recover by
355 the 1960s and by the 2000s were approaching pre-myxomatosis levels (Aebischer et al.
356 2011), although more recently rabbits have experienced significant declines (see the
357 Red Fox section). Reports suggest that polecats were already expanding their range by
358 the 1960s but rabbit and polecat recovery are likely to be closely linked (Sumption &
359 Flowerdew 1985).

360 National polecat surveys have taken place between the 1980s and 2010s (Appendix S3).
361 From the 1990s, surveys attempted to distinguish between polecats and hybrid polecat-
362 ferrets, based on a pelage classification system (Birks & Kitchener 1999). Classifications

of carcasses in this way and, more recently, using molecular genetic techniques, suggest that polecat-ferrets are more prevalent at the edge of the polecat's range (Costa et al. 2013).

In the 1980s, polecats occupied most of Wales and the border counties of Shropshire and Worcestershire (Tapper 1992). By the 1990s, polecats were present in all counties on the English side of the Welsh border (Birks & Kitchener 1999). The 2000s were characterised by increased density of records in Derbyshire, Buckinghamshire, Berkshire, Wiltshire, Dorset and Hampshire (Birks 2008). Unofficial releases led to polecats becoming established in Cumbria, Argyll and Perthshire, well outside of the core range, though the pelage characteristics of some of these animals suggested they were from captive stock (Birks 2008). By 2015, polecats had recolonised most of central and southern England (Fig. 6) and remained widespread in Wales and the West Midlands (Croose 2016). The most noticeable gaps in current distribution are in northern England and Scotland, potentially due to difficulties in dispersing around conurbations. Overall, the polecat's range expanded eastwards at 4.9 km per year between 1975 and 2015 (95% confidence interval: 2.6-7.1 km, Fig. 6, Appendix S1b). This is faster than the pine marten's expansion, which is not unexpected; polecats have faster reproductive ability and greater flexibility in habitat requirements than pine martens (Birks 2015, 2017). The latest population estimate for polecats is 83300 (95% confidence interval: 68000 - 99000; Mathews et al. 2018; Appendix S2).

ANTHROPOGENIC PROCESSES AFFECTING CARNIVORE STATUS

Legislation

There are various legal protections for carnivores in Great Britain (Fig. 7, Appendix S4). Protections that ban direct control and disturbance are likely to aid species recovery where these pressures were a cause of population decline. Range expansions and population increases have occurred for some species (notably otters, badgers, pine martens and polecats) following the introduction of legal protection. However, legal protection is less effective where non-compliance is high, or where other factors beyond the legal mandate are limiting populations. Hybrid animals create a particular legal difficulty, as hybrids are not usually protected, even when sympatric 'pure' wild types are (Trouwborst 2014). 'Pure' animals may be confused with hybrids by hunters, leading to inadvertent killing. While badger recovery in Great Britain has been coincident with legislation, badger populations elsewhere have not increased following legal protection. For example, badger populations in Northern Ireland appear to be constrained by climate, habitat, farming practices or food availability, rather than by persecution (Reid et al. 2012).

Habitat quantity, quality and connectivity

Habitat loss and fragmentation are major contributing factors to biodiversity loss and can be more significant for habitat specialists (otters and pine martens) than for generalists that are better able to exploit modified landscapes (foxes, stoats and weasels; Bright 1993, Crawford 2010). Habitat fragmentation may increase intra-guild predation among carnivores, as has been observed between foxes and pine martens (Lindström et al. 1995). To counter habitat loss, a series of international and national regulations aimed at protecting habitat extent and quality have been implemented over the last six decades, including the European Union's Habitats Directive and Water Framework Directive. The result has been a wide-ranging protected area network that

410 includes Special Areas of Conservation, Ramsar wetlands, national parks, and Sites or
411 Areas of Special Scientific Interest. Existing habitats have been enriched via the creation
412 and maintenance of den sites for otters and pine martens (Chanin 2003, Croose et al.
413 2016) and the promotion of wildcat-friendly forestry management in wildcat priority
414 areas (Scottish Natural Heritage 2013). More generally, afforestation since the 1950s,
415 notably in Scotland, has provided additional, if not ideal, habitat for pine martens (e.g.
416 Croose et al. 2013, 2014). Even with the protected area network, a lack of connectivity,
417 through fragmentation or via natural or anthropogenic barriers, may prevent dispersal.
418 Many monitoring tools rely on collecting road casualty carcasses, testament that these
419 species are vulnerable to road mortality (Appendix S3). Roads, urban areas and large
420 continuous tracts of other unfavourable habitat may act as physical barriers to
421 recolonisation. Genetic studies on badgers and wildcats suggest that while large roads
422 can have a significant impact on gene flow, they are not impermeable, as animals can
423 utilise crossing points (Frantz et al. 2010, Hartmann et al. 2013). Recolonisation of areas
424 that require crossing of landscape barriers may therefore be possible, but the rate of
425 expansion is likely to depend upon barrier size and landscape configuration.

426 Agricultural intensification and its consequences for biodiversity are well documented
427 (e.g. Tattersall & Manley 2003). Agri-environment schemes aimed at mitigating the
428 effects of agricultural intensification have been implemented since the 1980s, the most
429 recent being the Environmental Stewardship scheme, which was introduced in 2005.
430 Although Environmental Stewardship has been criticised for its limited benefits and
431 high costs (Kleijn et al. 2011), studies show that it can lead to increases in small
432 mammal abundance (Broughton et al. 2014), potentially benefitting their predators
433 (Johnson & Baker 2003, Askew et al. 2007).

Translocations, releases and escapes

Range expansion and density increase have, in some carnivore species, been assisted by human intervention. Formal conservation translocations have been carried out for otters and pine martens. These may use captive-bred stock, such as for otters (Jefferies et al. 1986) and possible future wildcat releases (Scottish Natural Heritage 2013), or translocations from the wild, such as for pine martens (Shaw & Livingstone 1992, VWT unpublished data). Rehabilitated animals are also released from wildlife rescue centres (Kelly et al. 2010, Mullineaux 2014). Furthermore, unofficial or accidental releases have occurred; examples include polecat releases in Cumbria and Argyll (Birks & Kitchener 1999, Fig. 6) and the arrival of stoats on Orkney (Fraser et al. 2015). Other unofficial releases have been smaller in scale, e.g. there are sporadic records of pine martens in England, where presumably individuals have escaped or been released from fur farms or wildlife collections (Birks & Messenger 2010, Jordan et al. 2012). The extent of, and survival rates of animals from, unofficial releases are unknown, but releases of sufficient scale can sometimes aid expansion. Polecat populations derived from such releases are thriving in Cumbria but apparently dwindling in Argyll (Fig. 6, VWT unpublished data).

Direct control

Nineteenth century declines in carnivore populations are testimony to the impact of intensive control measures, as are the resurgences of some species once control diminished (Langley & Yalden 1977). While managing predators remains central to game management, the intensity of control (with localised exceptions) is unlikely ever to return to pre-1915 levels (Tapper 1992). While some British carnivores are protected from unlicensed predator control, the trapping or shooting of foxes, stoats and weasels is not regulated in practice, other than to prevent cruelty. Land managers

458 applying control must comply with welfare regulations and ensure that control is
459 sufficiently discriminatory to avoid taking legally protected species. Wildcats
460 (Macdonald et al. 2010), otters (Crawford 2010), pine martens (Strachan et al. 1996)
461 and polecats (Packer & Birks 1999) are legally protected from unlicensed control, but
462 are sometimes caught in traps, nets or snares set for other species. The potential for
463 unintentional capture may be greatest in areas that are newly recolonised, as practices
464 that were previously unproblematic may need to be adapted. For species with low
465 reproductive rates, such as pine martens, any additional mortality might impede
466 recovery. The current extent of any intentional or unintentional killing of protected
467 carnivores is unclear. Collaboration between carnivore conservationists and managers
468 of game estates and fisheries is required to find workable solutions for reducing
469 conflicts with expanding carnivore populations. Mitigation methods include electric
470 fencing to prevent carnivores gaining access to pheasant pens (Balharry & Macdonald
471 1996), exclusion barriers for spring traps (Short & Reynolds 2001) and diversionary
472 feeding and translocations. There is little evidence of the uptake or efficacy of such
473 mitigation methods in practice (Balharry & Macdonald 1996, Thirgood et al. 2000,
474 Graham et al. 2005).

475 **Environmental pollutants**

476 Predators are at particular risk from bioaccumulating and biomagnifying pollutants.
477 Carnivores may be exposed to insecticides, herbicides, fungicides and biocides used for
478 agricultural purposes, a wide range of industrial organic contaminants, toxic metals, and
479 human and veterinary pharmaceuticals (Shore and Rattner 2001, Harrington &
480 Macdonald 2002, Shore et al. 2014). There are relatively few data on current exposure
481 of British carnivores to most of these (Appendix S5).

Although dieldrin is most commonly cited as the cause of otter decline, polychlorinated biphenyls (PCBs) may also have contributed by impairing reproduction in individuals not poisoned by dieldrin (Mason & Wren 2001). The combined effect of dieldrin and PCBs on otters may have been analogous to how dieldrin (acute mortality) and dichlorodiphenyltrichloroethane (DDT; eggshell thinning leading to reproductive failure) caused catastrophic declines in predatory birds (Ratcliffe 1980, Newton 1986). Otters in Britain are also frequently exposed to polybrominated diphenyl ethers (PBDEs; Pountney et al. 2015), which are structurally similar to PCBs and may have a cumulative effect with PCBs (Hallgren & Darnerud 2002), though there is no evidence that exposure of otters in Britain to PCBs and PBDEs is impairing their reproductive output (Pountney et al. 2015).

Second generation anticoagulant rodenticides (SGARs) are widely used to manage rodent populations (Dawson et al. 2003). SGARs disrupt the blood-clotting mechanism (Watt et al. 2005) leading to fatal haemorrhaging. Evidence of sub-lethal effects caused by exposure is uncertain (Van den Brink et al. 2018). Predators are exposed secondarily by consuming contaminated target prey (rats *Rattus norvegicus,* mice *Mus domesticus*) and non-target prey (mice *Apodemus* spp., voles; Tosh et al. 2012, van den Brink et al. 2018). SGAR residues have been detected in most British mammalian carnivores (Appendix S5) and rates of exposure in polecats have increased over the last 20 years (Sainsbury et al. 2018). While mortality caused by rodenticide does occur in mammalian carnivores in Britain (Appendix S5), the extent of this mortality, and whether it affects populations, remains unknown.

Hybridisation

In Britain, hybridisation occurs between wildcats and domestic cats (Driscoll et al. 2007) and between polecats and feral ferrets (Costa et al. 2013). There is also evidence of limited historical hybridisation between European pine martens and American martens *Martes americana* that had presumably escaped from fur farms (Kyle et al. 2003). Hybridisation between wildcats and domestic cats occurs throughout the wildcat's range (Macdonald et al. 2010). Domestic cat DNA is commonly, if not universally, present in Scottish wildcats (Driscoll et al. 2007, Senn & Ogden 2015, Senn et al. 2018), which have experienced the highest levels of introgression among wildcats in Europe (Hertwig et al. 2009). Classifications of wild-living cats using combinations of skull morphology, pelage and genetic techniques suggest that, depending on the definition used, between 40% and 90% of wild-living cats in Scotland do not qualify as 'true' wildcats (Kitchener et al. 2005). Hybrids occupy similar habitat to wildcats, masking potential range expansion, impeding population estimation and perpetuating introgression (Kilshaw et al. 2016). Currently, a 'trap, neuter, vaccinate and return' programme for farm and feral cats is underway in five priority wildcat areas in the Scottish Highlands, with the aim of reducing hybridisation (Scottish Wildcat Action 2018). In comparison to the wildcat, polecat-ferret hybridisation appears less problematic. Analysis by Costa et al. (2013) of polecats collected during the 1990s and 2000s found that 31% of wild polecats were hybrids, with the highest frequency of hybrids at the eastern edges of the polecat's range. First-generation hybrids were not detected, suggesting that the incidence of hybridisation may have been greater in the past (Costa et al. 2013).

Disease and associated interventions

528 Disease, both naturally occurring and in association with human intervention, can
529 reduce carnivore populations directly. For example, in 1994-1995, sarcoptic mange
530 reduced fox numbers in Bristol by over 95% (Soulsbury et al. 2007). Carnivore
531 populations may also be affected indirectly by disease if it alters the abundance of prey
532 or other sympatric species, as evidenced by changes in stoat and weasel abundance
533 associated with myxomatosis in rabbits (Aebischer et al. 2011). Recent and current
534 effects of rabbit calicivirus on rabbit populations in Britain, and the potential impact on
535 dependent carnivores, is unquantified, although it is possible that rabbit diseases and
536 the associated declines may be contributing to coincident reductions in fox numbers
537 (Harris et al. 2018).

538 Other indirect consequences may arise from human intervention to control the risk of
539 transmission of zoonoses or diseases of livestock. Wild species may become persistent
540 reservoirs for zoonotic disease (Hassell et al. 2017) and this can lead to control efforts,
541 such as for managing bovine tuberculosis (bTB) in badgers (Wilson et al. 2011). Bovine
542 tuberculosis is enzootic in a large part of the badger population in England and Wales,
543 and badgers are implicated in the spread of the infection to cattle (Delahay et al. 2013).
544 Methods used to control bTB differ between the countries of Great Britain. Scotland,
545 officially free of bTB since September 2009, has no proactive policy for managing the
546 disease in wild animals, the Welsh government has pursued a badger vaccination
547 strategy since 2012 (Welsh Government 2012) and in England proactive, large-scale
548 badger culling is one of a range of policies aimed at eradicating bTB (DEFRA 2011).
549 From 2013 to 2017 inclusive, 34103 badgers were killed as part of licensed culls in
550 England (Giesler & Ares 2018) and 32601 badgers were killed in 2018 (DEFRA &
551 Natural England 2018). Culling aims to reduce badger populations by around 70% in

552 licensed areas and draws on evidence derived from the Randomised Badger Culling
553 Trial (Bourne et al. 2007). This Trial showed that reduced badger numbers resulted in
554 increased fox numbers in cull areas (Trewby et al. 2008), indicating that there may be
555 broader implications for carnivore community structures emerging from badger culling.

556 **CONCLUSIONS**

557 Our aim was to compare and contrast the current status of Britain's mammalian
558 carnivores and the anthropogenic processes that affect their populations. Overall, the
559 outlook for British carnivores is more positive than in the account of decline drawn by
560 Langley and Yalden (1977). Two of their three 'rarer carnivores' (pine marten and
561 polecat) have staged remarkable recoveries, while the third (wildcat) continues to be
562 threatened by hybridisation. Meanwhile, akin to pine martens and polecats, the
563 formerly rare and restricted otter has recovered much of its former range and is
564 increasing in density. Of the nationally distributed species, badgers have increased in
565 population density but are subject to increasingly widespread, intensive culling; foxes
566 have increased but appear to be in a current period of decline; and stoats and weasels
567 remain data-deficient. The recent apparent declines in rabbit records are a cause for
568 concern, given the number of native carnivores that depend on them as food. Since the
569 1970s there have been significant advances in our understanding of the anthropogenic
570 processes that affect carnivore populations. If humans are to coexist with more
571 abundant carnivores, in more places and in greater diversity, greater emphasis will
572 need to be placed on the social aspects of these processes, whether concerning best-
573 practice use of rodenticides, selective predator control practices, minimisation of
574 hybridisation or management of disease risk.

575

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582

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919

Figures

Fig. 1. Wildcat *Felis silvestris* distribution in Scotland from 1960 to 2008. Data are from Langley and Yalden (1977), Easterbee et al. (1991), Daniels et al. (1998), Davis and Gray (2010). Black circles indicate presence. All presence points were scaled to hectads. On the 2000s map, black circles indicate 'probable' wildcats, grey triangles indicate 'possible' wildcats (Davis & Gray 2010). 1992-93 dates are the dates of Daniels et al.'s (1998) live trapping.

Fig. 2. National Gamebag Census index for red fox *Vulpes vulpes* in Great Britain from 1961 to 2009. Gamebags are indices of the numbers killed per unit area on game estates. Index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Reproduced by permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).

Fig. 3. European otter *Lutra lutra* distribution in Great Britain from 1977 to 2012. Maps recreated from National Otter Surveys of England (Lenton et al. 1980, Strachan et al. 1990, Strachan & Jefferies 1996, Crawford 2003, Crawford 2010), Scotland (Green, & Green 1980, Green & Green 1987, Green & Green 1997, Strachan 2007, Findlay et al. 2015) and Wales (Crawford et al. 1979, Andrews & Crawford 1986, Andrews et al. 1993, Jones & Jones 2004, Strachan 2015) using data provided by Environment Agency (2018), Scottish Natural Heritage, Natural Resources Wales and Joint Nature Conservation Committee (2018). Black circles indicate presence. Grey circles indicate surveyed areas where otters were recorded as absent. Blank areas do not indicate absence. 1980s Scotland survey did not include the Western Isles, Northern Isles or the Scottish Highlands (Green & Green 1987). In England, surveys were carried out in alternate 50 x 50 km squares until the most recent survey (Crawford 2010).

Fig. 4. European pine marten *Martes martes* distribution in Great Britain from1960 to 2018. Data from Langley and Yalden (1977), Velander (1983), Bright and Harris (1994), McDonald et al. (1994), Balharry et al. (1996), Strachan et al. (1996), Birks and Messenger (2010), Croose et al. (2013, 2014) and VWT (unpublished data). Black circles indicate presence. All presence points were scaled to hectads. Only verified records in Birks and Messenger (2010) were included. No surveys were carried out in Scotland in the 2000s, and the 2010s Scotland surveys included only central and southern Scotland (Croose 2013, 2014).

Fig. 5. National Gamebag Census indices for stoats *Mustela erminea* and weasels *Mustela nivalis* in Great Britain from1961 to 2009. Black diamonds are for stoats and grey circles are for weasels. Gamebags are indices of the numbers killed per unit area on game estates. All index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Data reproduced by permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).

Fig. 6. European polecat *Mustela putorius* distribution in Great Britain from 1960 to 2016. Data are from Langley and Yalden (1977), Blandford (1987), Tapper (1992), Birks and Kitchener (1999), Birks (2008) and Croose (2016). Black circles indicate presence. Grey triangles indicate polecat-ferret hybrids. All presence points were scaled to hectads.

Fig. 7. Timeline of interventions providing legal protection for native mammalian carnivores in Great Britain.

967 SUPPORTING INFORMATION

968 Additional supporting information may be found in the online version of this article at
969 the publisher's website.

970 **Appendix S1.** Changes in the ranges of wildcat *Felis silvestris*, European pine marten
971 *Martes martes* and European polecat *Mustela putorius.* a) Distances (in km) from the
972 central points of species ranges in 1975 to all positive hectads using 95th percentile
973 gamma statistic (after Preuss et al. 2014) and b) results of linear models analysing the
974 rates of expansion (in km).

975 **Appendix S2.** Recent population estimates for native mammalian carnivores in Great
976 Britain. Population estimates are the combined totals for England, Scotland and Wales
977 unless otherwise stated. Reliability is scored differently by Mathews et al (2018), where
978 <=1 indicates very poor reliability of estimate and 4 = very good reliability of estimate,
979 and Harris et al (1995), where 1 is most reliable estimate and 5 the least reliable
980 estimate.

981 **Appendix S3.** National distribution surveys of native mammalian carnivores in Great
982 Britain, 1960 – 2017.

983 **Appendix S4.** National and international legislation providing protection for native
984 mammalian carnivores in Great Britain.

985 **Appendix S5.** Incidences of secondary exposure to contaminants in native British
986 mammalian carnivores in Europe.

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