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**A preliminary feasibility assessment  
for the reintroduction of the  
European wildcat to England and Wales**

**Jenny MacPherson**



# Co-authors and contributors

# Content

## Steve Carter

Vincent Wildlife Trust  
3-4 Bronsil Courtyard, Eastnor,  
Ledbury, Herefordshire HR8 1EP  
United Kingdom

## Sébastien Devillard

Université de Lyon UMR CNRS 5558  
LBBE, Biométrie et Biologie Évolutive  
UCB Lyon 1, Bât. Grégor Mendel  
43 bd du 11 novembre 1918  
69622 VILLEURBANNE cedex

## Rosalind Kennerley

Durrell Wildlife Conservation Trust  
Trinity, Jersey, JE3 5BP  
Channel Islands

## Sandrine Ruelle

Office National de la Chasse et de la Faune Sauvage  
UPAD, Montfort, F-01330 Birieux  
France

## Mike Hudson

Durrell Wildlife Conservation Trust  
Trinity, Jersey, JE3 5BP  
Channel Islands

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European wildcats *Felis silvestris silvestris* used to be found throughout mainland Britain but, as was the case with many native carnivores, the population underwent a steep decline through the 19th and early 20th centuries due to loss and fragmentation of its woodland habitat, coupled with hunting and predator control. Today, the wildcat is extinct in England and Wales, and on the verge of extinction in Scotland where hybridisation and introgression with feral domestic cats is prevalent among wild living cats. A recent review of the status of the wildcat in Scotland concluded that its recovery would only be possible with the support of reintroduction projects. Reintroduction of captive bred wildcats from European stock to England and Wales is also being considered, if and where conditions are suitable.

Species reintroductions are increasingly being used as a conservation tool in spite of the often high risks and costs associated with them. Where natural recovery or recolonisation is unlikely and other options are limited, then reintroductions may be necessary. If this is the case, then an initial assessment should look at whether and where this is feasible and most likely to succeed.

This report constitutes a preliminary assessment of the biological feasibility of reintroducing the European wildcat to regions of England and Wales. This was done by modelling and mapping potentially suitable wildcat habitat across England and Wales in the first instance, and by identifying the range of potential risk factors that may negatively impact a wildcat reintroduction. The extent to which a wildcat reintroduction in England or Wales would meet current IUCN guidelines for conservation translocations was also considered. The objectives at this stage were to determine whether and where further, more detailed, assessment should be focused and to make recommendations as to how to progress towards a longer-term objective of restoring wildcats to some of their former range in England and Wales. This is part of a GB-wide strategy for the species and will complement work already being done in Scotland.

Genetically verified wildcat presence locations from a widescale survey across France were used to develop a landscape scale model to identify regions of potentially suitable habitat for wildcats in England and Wales. Of the potential predictor variables, the most significant were broadleaved and mixed woodland, elevation, and agricultural mosaic. These were followed by arable, scrub and natural grassland, all important habitats for prey such as small mammals. Data on wildcat-domestic hybrids were also used to model hybrid habitats.

Model predictions were plotted onto a 10km square grid map of mainland Britain. These suggested that the regions that could warrant further investigation for potential reintroduction sites are in the south-west of England and north and west Wales. There is a clear association between the distribution, numbers and movements of domestic cats and several human and environmental factors. The presence of people has been shown to be the single most important variable. Many areas predicted as being suitable for wildcats in Britain also have high suitability for hybrid cats, so it would be important to select reintroduction sites and to release animals in sufficient numbers to minimise the risk of wildcats mating with domestic cats in the first instance. The biggest risk of hybridisation is likely to be in fragmented habitats where domestic cats are present in rural villages and farms, close to the interface with wildcat habitats.



Beside fragmentation of habitat and hybridisation with feral cats, road mortality is acknowledged as a major threat for wildcats throughout their range. In wildcat reintroduction projects that have been carried out elsewhere in Europe, many of the released animals died on the roads. It is therefore suggested that if reintroductions are considered, they should first be to regions with low densities of roads and traffic, as well as sufficient areas of contiguous high-quality habitat to support relatively high numbers of wildcats. Conflict with other land uses and risks of accidental trapping should also be considered and, in addition to the potential impacts on wildcats, the actual or perceived risks that wildcats may pose to other species need to be evaluated and, where appropriate, mitigation measures developed.

The most recent IUCN guidelines for reintroductions and other conservation translocations stress that matching habitat suitability and availability to the needs of candidate species is central to feasibility and design. They also state that habitat suitability should include assurance that the release of animals and their subsequent movements are compatible with permitted land uses in the affected area. Existing and adjacent land uses (such as agriculture and game shooting) and the attitudes of local communities will be a further indication of the suitability of these areas for releasing wildcats. A full stakeholder and community engagement programme is beyond the scope of the preliminary work presented here, but it is recommended that it has the highest priority in the future. A PhD study is underway, which will carry out interdisciplinary work towards understanding the ecological and social feasibility, as well as the practicalities of wildcat restoration in Britain. This research will inform the next stage of the process.

A captive breeding programme is already established in Scotland with the ultimate aim of supplementing wild living cats there, and Durrell Wildlife Conservation Trust is also developing a captive breeding strategy for this species. There will need to be a co-ordinated approach between Scotland, England and Wales in order to ensure a medium to long-term strategy that balances the goals of wildcat conservation in all three countries with the best use of the finite captive bred stock that will be available. Should releases go ahead, further advice and expertise from conservation geneticists will inform the most appropriate source of captive wildcats to complement the Scottish programme for conservation breeding in England and Wales.

The results presented in this report suggest three areas that might have the optimal combination of high habitat suitability, relatively low (for southern Britain) densities of human population, roads and traffic, and minimal potential conflict with other land uses. These are in north Wales, west Wales and south-west England. It is suggested that these are prioritised for further investigation.



# Crynodeb

Roedd y gath wyllt Ewropeaidd *Felis silvestris silvestris* yn arfer byw ym mhob rhan o dir mawr Prydain. Ond, fel yn achos nifer o anifeiliaid cigysol brodorol, fe leihaodd y boblogaeth yn sylweddol ac yn gyflym yn ystod y 19eg a blynyddoedd cynnar yr 20fed ganrif. Roedd sawl ffactor yn gyfrifol am hyn, yn cynnwys holli ardaloedd eang o goetir yn ddarnau bychain ynghyd â hela a rheoli ysglyfaethwyr. Erbyn heddiw mae'r gath wyllt wedi diflannu'n llwyr o Gymru a Lloegr, ac mae hi ar fin diflannu o'r Alban hefyd gan fod y cathod gwyllt sydd ar ôl yn dueddol o groesi gyda cathod dof lled-wyllt. Dros amser, wrth i'r croesiadau hyn baru drosodd a throsodd gyda chathod dof gall arwahanrwydd genetegol y gath wyllt wanhau a diflannu i bob pwrpas ('introgression' yw'r term Saesneg am hyn). Yn dilyn gwaith a wnaed yn ddiweddar ar statws y gath wyllt yn yr Alban, daethpwyd i'r casgliad mai'r unig ffordd o sicrhau ei dyfodol yn yr Alban fyddai drwy sefydlu prosiectau i'w hail-gyflwyno. Mewn lleoedd addas, ac o dan amodau addas, mae ystyriaeth bellach felly yn cael ei roi i ailgyflwyno cathod gwyllt o darddiad Ewropeaidd, ac a fagwyd mewn caethiwed,, i ardaloedd yng Nghymru a Lloegr.

Mae prosiectau i ailgyflwyno rhywogaethau yn cael eu defnyddio'n gynyddol fel arf cadwraeth, er fod 'na risgiau a chostau sylweddol ynghlwm wrthyn nhw. Os nad yw adferiad naturiol, neu ail-gytrefu naturiol, yn debygol o ddigwydd, ac os yw opsiynau eraill yn gyfyngedig, efallai bydd rhaid ailgyflwyno. Yn yr achosion hyn, dylai asesiadau cychwynnol ystyried a yw hyn yn bosib, ym mha le y gallai fod yn bosib, ac ym mha le y byddai'r ailgyflwyno yn fwyaf tebygol o lwyddo.

Mae'r adroddiad hwn yn asesiad cychwynnol o ddichonoldeb biolegol prosiect i ailgyflwyno'r gath wyllt Ewropeaidd i ardaloedd yng Nghymru a Lloegr. Gwnaed yr asesiad drwy fodelu a mapio cynefinoedd allai fod yn addas i'r gath wyllt ar hyd a lled Cymru a Lloegr, yn y lle cyntaf, a thrwy adnabod yr ystod o ffactorau posib allai effeithio'n andwyol ar brosiect i ailgyflwyno'r gath wyllt. Ystyriwyd hefyd i ba raddau y byddai ailgyflwyno'r gath wyllt i Gymru neu i Loegr yn cwrdd â chanllawiau cyfredol IUCN ar gyfer trawsleoliadau cadwraethol. Yr amcan, ar y pwynt hwn, oedd penderfynu a ddylai asesiad manylach gael ei gynnal, ac ym mha le y dylai hynny ddigwydd - a hefyd i gynnig argymhellion am y dulliau y dylid eu mabwysiadu er mwyn symud tuag at gyflawni'r nod o adfer cathod gwyllt i rai o'r ardaloedd yng Nghymru a Lloegr lle'r oedd yn nhw'n arfer byw. Mae'r gwaith hwn yn rhan o strategaeth ehangach ar draws Prydain ar gyfer y rhywogaeth ac mae'n gydnaws â'r gwaith sydd eisoes yn digwydd yn yr Alban.

Defnyddiwyd cofnodion genetegol sicr o bresenoldeb y gath wyllt yn Ffrainc er mwyn datblygu model ar raddfa tirwedd a fyddai'n galluogi ymchwilyr i adnabod ardaloedd o gynefin allai fod yn addas i gathod gwyllt yng Nghymru a Lloegr. O blith y ffactorau newidiol allai fod yn bwysig o ran darogan dichonoldeb ailgyflwyno, y rhai mwyaf arwyddocaol oedd coetir llydanddail a choetir cymysg, uchder tir, a mosaig amaethyddol. Yn dilyn y rhain 'roedd tir â'r, prysgwydd a glaswelltir naturiol sydd oll yn gynefinoedd pwysig i anifeiliaid fel mamaliaid bychain sy'n fyw i'r gath wyllt. Defnyddiwyd data ar groesiadau rhwng cathod gwyllt a chathod dof hefyd er mwyn modelu cynefinoedd a fyddai'n addas ar gyfer y croesiadau hyn.

Plotiwyd rhagfynegiion y model ar fap grid o sgwariau 10km ar draws tir mawr Prydain. Gwelwyd mai'r ardaloedd allai fod yn werth eu hymchwilio ymhellach, o ran cynnig safleoedd ailgyflwyno, oedd y rheiny yn ne-orllewin Lloegr, gogledd a gorllewin Cymru. Mae cysylltiad amlwg rhwng dosbarthiad, niferoedd a symudiadau cathod dof a nifer o ffactorau dynol ac amgylcheddol.



Presenoldeb pobl yw'r newidyn unigol pwysicaf oll. Mae nifer o ardaloedd allai fod yn addas ar gyfer cathod gwyllt ym Mhrydain hefyd yn addas ar gyfer cathod sy'n groesiadau rhwng cathod gwyllt a dof. Felly fe fyddai'n bwysig dewis safleoedd ailgyflwyno yn ofalus, ac i ollwng digon o anifeiliaid er mwyn lleihau'r perygl o baru rhwng cathod gwyllt a chathod dof yn y lle cyntaf. Mae'r peryg mwyaf o groesi rhwng cathod gwyllt a dof yn debygol o fod mewn cynefinoedd sydd wedi eu hollti'n ddarnau mân - a lle mae cathod dof felly yn bresennol mewn pentrefi a ffermydd gwledig ar gyrion cynefinoedd cathod gwyllt.

Yn ogystal â hollti neu ddarnio cynefinoedd, a chroesi gyda chathod dof lled-wyllt, mae marwolaethau ar ffyrdd hefyd yn fygythiad mawr i gathod gwyllt lle bynnag y maen nhw'n byw. Yn y prosiectau sydd wedi digwydd mewn rhannau eraill o Ewrop i ailgyflwyno cathod gwyllt fe gafodd llawer o'r anifeiliaid a ollyngwyd eu lladd ar ffyrdd. Awgrymir felly, os yw prosiectau ailgyflwyno yn cael eu hystyried, y dylent ddigwydd yn gyntaf mewn rhanbarthau sydd â dwysedd isel o ffyrdd a thraffig, ynghyd ag ardaloedd digonol a di-dor o gynefinoedd ansawdd uchel all gynnal niferoedd gweddol uchel o gathod gwyllt. Dylid ystyried hefyd y peryg o wrthdaro gyda mathau eraill o ddefnydd tir a'r peryg o ddal cathod gwyllt yn ddamweiniol mewn trapiau. Hefyd, fe ddylid asesu'r effaith y gallai cathod gwyllt ei gael ar rywogaethau eraill, a dylid datblygu camau lliniaru lle bo hyn yn addas.

Mae'r canllawiau IUCN mwyaf diweddar ar gyfer ailgyflwyno a dulliau trawsleoli cadwraethol eraill yn pwysleisio bod ystyried addasrwydd ac argaledd cynefinoedd ar yr un pryd ag anghenion y rhywogaeth dan sylw yn ganolog i ddichonoldeb a datblygiad unrhyw brosiect. Maen nhw hefyd yn datgan y dylai gwaith i sicrhau bod cynefin yn addas gynnwys sicrhau fod y cam o ollwng anifeiliaid, a wedyn symudiadau yr anifeiliaid hynny, yn gydnaws gyda'r defnydd tir a ganiateir yn yr ardal dan sylw. Mae defnydd tir yn yr ardaloedd penodol dan sylw, a hefyd ar dir cyfagos (megis amaethyddiaeth a hela gêm), ynghyd ag agweddau cymunedau yn ystyriaethau ychwanegol wrth asesu pa mor addas yw ardaloedd ar gyfer gollwng cathod gwyllt. Mae datblygu a chynnal rhaglen i bontio gyda budd-ddeiliaid a chymunedau y tu hwnt i'r gwaith cychwynnol a gyflwynir yma, ond awgrymir y dylai hyn fod yn flaenoriaeth bwysig yn y dyfodol. Mae 'na brosiect PhD ar y gweill ac fe fydd hwn yn ymgymryd â gwaith rhyng-ddisgyblaethol er mwyn helpu deall dichonoldeb ecolegol a chymdeithasol, a hefyd agweddau ymarferol perthnasol, o ran adfer poblogaethau cathod gwyllt ym Mhrydain. Bydd yr ymchwil hwn yn cael ei ddefnyddio i benderfynu ar y camau nesaf yn y broses.

Mae rhaglen i fagu cathod gwyllt mewn caethiwed eisoes wedi ei sefydlu yn yr Alban, gyda'r nod o atgyfnerthu niferoedd y cathod gwyllt sydd yn byw yno, ac mae'r Durrell Wildlife Conservation Trust hefyd yn datblygu strategaeth fridio mewn caethiwed ar gyfer y rhywogaeth. Bydd angen i'r Alban, Cymru a Lloegr gydweithio a chydlynu gweithgaredd er mwyn sicrhau strategaeth tymor canolig a hirdymor a fydd yn cydbwysu amcanion cadwraeth y gath wyllt yn y dair gwlad gyda'r defnydd gorau o'r stoc cyfyngedig o greaduriaid wedi'u magu mewn caethiwed a fydd ar gael. Os fydd cathod gwyllt yn cael eu gollwng bydd angen rhagor o gyngor gan arbenigwyr geneteg cadwraethol er mwyn helpu adnabod y ffynhonnell fwyaf addas o gathod gwyllt a fagwyd mewn caethiwed er mwyn sicrhau bod y gwaith yn Lloegr a Chymru yn gydnaws gyda'r rhaglen fridio gadwraethol yn yr Alban.

Mae'r canlyniadau a gyflwynir yn yr adroddiad hwn yn awgrymu tair ardal sy'n cynnig, o bosib, y cyfuniad delfrydol o ran cynefin addas, dwysedd cymharol isel (yn ne Prydain) o boblogaeth ddynol, ffyrdd a thraffig, a thebygolrwydd isel o wrthdaro gyda mathau eraill o ddefnydd tir. Yr ardaloedd hyn yw gogledd Cymru, gorllewin Cymru a de-orllewin Lloegr. Awgrymir y dylid canolbwyntio ar yr ardaloedd hyn ar gyfer gwaith ymchwil pellach.



# Introduction

The European wildcat (*Felis silvestris silvestris*) used to be found throughout mainland Britain but, as was the case with many native carnivores, the population underwent a dramatic decline due to loss and fragmentation of its woodland habitat, coupled with hunting and predator control. Today, the last remaining wildcats in Britain outside of captivity are found only in the north of Scotland, where the small number of remaining wild living cats are threatened with genetic extinction due to hybridisation and introgression with feral domestic cats and existing feral-wildcat hybrids. Reintroduction of captive-bred wildcats from European stock to England and Wales has been proposed, if and where conditions are suitable.

Reintroducing species into parts of their former range from which they have been historically extirpated is an increasingly important tool used by conservation managers to counteract biodiversity loss. In spite of the often high risks and costs associated with animal translocations (Seddon, 2010 and Sainsbury and Vaughan Higgins, 2012), in circumstances where natural recovery or recolonisation is unlikely, and other options are limited, then reintroductions may be necessary – in which case, an initial assessment should look at whether and where this is feasible and most likely to succeed.







# The wildcat

The wildcat (*Felis silvestris silvestris*), cath wyllt or cath y coed in Welsh and cat-fiadhaich in Scottish Gaelic, was also known as the wood cat in England because of its association with forest habitats. It is one of our most elusive carnivores and the only native member of the cat family, or *Felidae*, still found in Britain. The wildcat is a European protected species and, as one of our last remaining native predators, can play an important role in maintaining the balance and resilience of a healthy ecosystem (Ritchie *et al.*, 2012).

Despite superficial similarities, the wildcat is genetically distinct from domestic cats, which evolved from the Near Eastern wildcat (*Felis lybica*) rather than the European wildcat (Driscoll *et al.*, 2007). Although striped like a domestic tabby cat, the wildcat has longer legs, is usually larger, more muscular and robust, and has a distinctive bushy, ringed tail with a blunt, black tip. The total length, from nose to tail, can be 82-98cm for males and 73-89cm for females. Male wildcats weigh on average 5-8kg, with females being smaller at around 3.5kg (Condé and Schauenberg, 1971; Harris *et al.*, 2008).

Like many carnivores, wildcats are solitary and territorial, and live at a low population density (Corbett, 1979). Male home ranges will overlap with the ranges of one or more females, but female home ranges are usually exclusive (Corbett, 1979), although related females seem to tolerate some spatial overlap in specific habitats with a high abundance of prey (Beugin *et al.*, 2016). The size of home ranges can vary depending on prey availability and habitat quality (Easterbee *et al.*, 1991; Corbett, 1979; Daniels, 1997; Scott *et al.*, 1993b). For male wildcats, these were found to be between 8-18km<sup>2</sup> in an area where rabbit abundance was low, compared with c1.8km<sup>2</sup> where rabbit population density was high. In optimal habitat, it has been suggested that densities of 3-5 wildcats per 10km<sup>2</sup> are achievable (Sunquist and Sunquist, 2002).

Woodlands and areas with dense thickets of gorse or juniper are good habitat for wildcats, providing both shelter and den sites (Easterbee *et al.*, 1991; Kilshaw, 2011). Rocky areas, log and brush piles or gaps under tree root plates all make good den sites, particularly for females during the breeding season. Wildcats need some open patches of habitat, such as rough grassland or riparian areas, for hunting. However, when moving around their territories, they often use woodland or scrub and stream edges for cover (Corbett, 1979; Easterbee *et al.*, 1991; Daniels, 1997; Macdonald *et al.*, 2010; Sunquist and Sunquist, 2002). Agricultural land and scrubland can also provide important hunting habitat for wildcats because they support a high density of rabbit and small mammal prey (Lozano *et al.*, 2003), but wildcats avoid heavily urbanised areas, areas of intensive agriculture and exposed coasts (Easterbee *et al.*, 1991; Daniels, 1997; Kilshaw *et al.*, 2016).

Rabbits (*Oryctolagus cuniculus*) are a favoured prey (Malo *et al.*, 2004; Lozano *et al.*, 2006) but where or when rabbits are scarce, wildcats eat mainly small mammals, such as voles *Microtus* spp. and wood mice *Apodemus sylvaticus* (Moleón and Gil-Sánchez, 2003; Lozano *et al.*, 2006). Birds, invertebrates, reptiles and carrion will also be eaten in smaller quantities (Moleón and Gil-Sánchez, 2003; Biró *et al.*, 2005).

Like most cat species, wildcats are solitary except when breeding. Mating generally takes place from January to March with litters of 1-8 kittens born in April-May. Wildcats usually produce only one litter a year but, if this is lost, females can come into oestrus again, which means that litters can be born up until August. Kittens are weaned at 12 weeks and stay with their mother until about five months old (Kilshaw, 2011; Daniels *et al.*, 2002). Where numbers are low and there are few other wildcats with which to mate, wildcats can interbreed with the domestic cat, producing fertile hybrid offspring (Balharry *et al.*, 1994; Hubbard *et al.*, 1992; Oliveira *et al.*, 2008b; Kitchener *et al.*, 2005; Senn *et al.*, 2019).

## Past and present distribution and population trends

The European wildcat, *Felis silvestris silvestris*, is a member of the polytypic species group *Felis silvestris*, which is geographically widespread across central and southern Europe, Africa and central Asia (Figure 1).

*Felis silvestris* is comprised of three (Kitchener and Rees, 2009) or more (Driscoll *et al.*, 2007) distinct interfertile subspecies, with clearly defined geographic and ecological distributions. The European wildcat *F. silvestris silvestris* shows a strong preference for temperate woodland (Yamaguchi *et al.*, 2015), whereas the Asian wildcats *Felis silvestris ornata* (and related subspecies) and African wildcats *Felis silvestris lybica* are found in dry steppe, savanna, bush and semi-desert habitats (Kitchener and Rees, 2009 and references therein). Mitochondrial DNA suggests five major biogeographic matrilineages: namely European wildcat *F. s. silvestris*; Southern African wildcat *F. s. cafra*; Asian wildcat *F. s. ornata*; Near Eastern wildcat *F. s. lybica* (from which the domestic cat is derived); and the Chinese Desert cat *F. s. bieti* (Driscoll *et al.*, 2007). The distributions of these are shown in Figure 2.

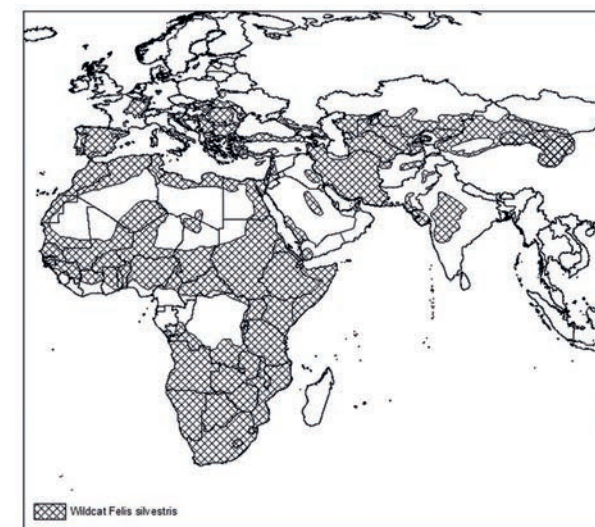


Figure 1 African and Eurasian distribution of the wildcat *Felis silvestris*. NatureServe and IUCN (International Union for Conservation of Nature) 2007. *Felis silvestris*. The IUCN Red List of Threatened Species. Version 2018-2. <https://www.iucnredlist.org> [Downloaded on 24 April 2019].

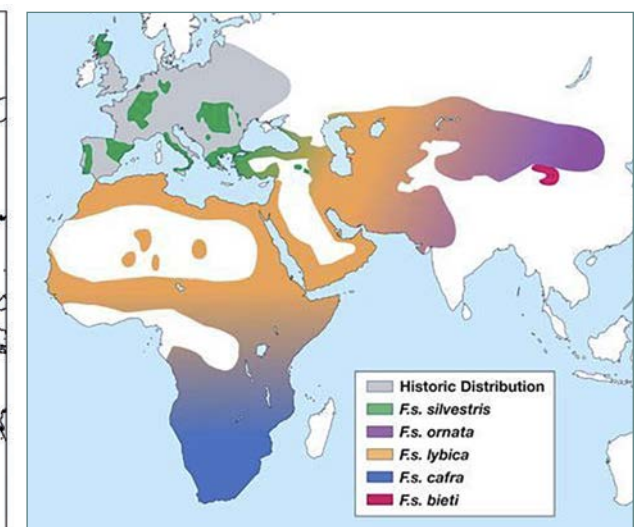


Figure 2 African and Eurasian distribution of the five clades of the *Felis silvestris* complex (*F. s. silvestris*, *F. s. ornata*, *F. s. lybica*, *F. s. cafra* and *F. s. bieti*) defined by mitochondrial DNA evidence (from Marr, 2017).



The International Union for the Conservation of Nature (IUCN) currently lists the wildcat as Least Concern, because of large and stable populations in the east of its range. However, while the wildcat may be the most widespread and numerous *felid* in Europe, it is seriously threatened in some areas by hybridisation with domestic cats and also by risks from feline disease, road collisions, fragmentation and loss of habitats through development or changes in land management.

Wildcats were once widespread across much of Europe with the exception of Fennoscandia. However, since the late 1700s, severe declines and local extirpations occurred due to a combination of habitat loss, hunting and predator control. These have resulted in the distribution seen today, shown in green and grey in Figure 2. This fragmented pattern means that wildcat populations are isolated at both regional and local scales, and many are facing real extinction risks. Therefore, preserving all the European populations will maximise the long-term viability of the specie

The species is listed in Appendix II of CITES (UNEP-WCMC, 2006) and legally protected under the Bern Convention (Appendix II, 1979) and the European Habitats Directive 92/43/EEC (Commission, 1992). As a result of this protection, wildcat populations in some parts of Europe have begun to recover (Stahl and Artois, 1994), however, hybridisation with feral domestic cats continues to be a major threat. In some parts of the wildcat's distribution, including Scotland, it is acknowledged that, as a result of hybridisation, very few genetically pure wildcats remain (Macdonald *et al.*, 2004; Battersby, 2005; Senn *et al.*, 2019). The wildcat in Scotland is currently listed as Vulnerable on the IUCN Red List of Threatened Species. It is also protected under the Wildlife and Countryside Act 1981 (as amended), included on the Scottish biodiversity list and is a priority species in Scotland for the UK Biodiversity Action Plan.

### Agents of decline and threats in Britain

Wildcats used to be found throughout mainland Britain but underwent a steady reduction in range from the middle ages due to loss of woodland habitat, hunting and persecution as vermin. Consequently, the species was probably extinct in England and Wales by the late 1800s, by which time it had also disappeared from the southern counties of Scotland. As game shooting increased in popularity at around this time, the number of gamekeepers on hunting estates increased and wildcats, along with other predators, were killed in huge numbers to maximise gamebird productivity (Balharry and Daniels, 1998; McOrist and Kitchener, 1994). The wildcat, in common with the pine marten, *Martes martes*, managed to survive in the remote north-west of Scotland, where low human population density meant that levels of persecution were also low (Easterbee *et al.*, 1991). After the 1914-18 war, the intensity of predator control declined, reforestation began and the wildcat population in Scotland started to recover so that by 1946 they are thought to have recolonised much of the range known to be occupied today (Langley and Yalden, 1977; Easterbee *et al.*, 1991; Kitchener, 1992; Hetherington *et al.*, 2016). Although how much of this apparent recovery was due to the presence of wildcat phenotype hybrids, is not known. Since the 1960s, the population has declined and, with current numbers estimated to be between 30 and 430 individuals and decreasing, in spite of considerable conservation effort, the wildcat in Scotland is now considered to be at the brink of extinction. The most recent review of the status of the species concluded that '... the recovery of the wildcat in Scotland will only be possible with the support of reintroduction/reinforcement projects, and that the remaining "pure Scottish wildcats" ... should be combined with wildcats from continental Europe.' (Breitenmoser *et al.*, 2019). Reintroductions of wildcat in England and/or Wales are also being considered if it is feasible to do so according to current IUCN guidelines.



# Objectives and geographical scope of the present study

Reintroduction of captive bred wildcats from European stock into parts of England (Gow and Cooper, 2018) and Wales is currently being proposed as a potential management tool to minimise the risk of extinction in Britain, to enhance the long-term survival of the species, and to maintain and enhance native biodiversity in England and Wales. The report presented here constitutes a preliminary assessment of the biological feasibility of reintroducing the European wildcat *Felis sylvestris* to regions of England and Wales through:

- modelling and mapping potentially suitable wildcat habitat across England and Wales;
- identifying the range of potential risk factors that may negatively impact a wildcat reintroduction;
- a preliminary assessment of the extent to which a wildcat reintroduction in England or Wales will meet IUCN Conservation Translocation guidelines;
- a preliminary assessment of the feasibility of obtaining sufficient numbers of 'good quality' wildcats for release into the wild.

The objectives at this stage were to determine whether and where further, more detailed, assessment should be prioritised, and to make recommendations as to how to progress towards a longer-term objective of restoring wildcats to their former range in England and Wales. This will entail a detailed biological and social feasibility study, as well as an evaluation of potential risks and benefits. This is part of a GB-wide strategy for the species and will complement work already being done in Scotland by Scottish Wildcat Action.

The IUCN Guidelines for Reintroductions and other conservation translocations (IUCN, 2013), state that the principal aim of any reintroduction must be to yield '... a measurable conservation benefit at the level of a population, species or ecosystem.' However, reintroductions are carried out for a number of biological (eg, species or ecosystem restoration) and non-biological (cultural, political and ethical) reasons (Converse *et al.*, 2013). Identifying these motivations and a clear set of objectives from the outset is vital in order to define the appropriate indicators, assess and choose relevant management actions, and ensure monitoring is adequately focused.

In the simplest terms, a specific set of reintroduction decisions include whether, where, when and how to translocate and establish an endangered species in a part of its historical range that it does not currently occupy. Nevertheless, decisions around reintroductions are frequently made more challenging by the presence of multiple and often competing objectives. These include maximising the likelihood of establishment of a new population, maintaining the genetic diversity within captive breeding programmes, keeping costs to a minimum, providing socio-economic benefits or preventing negative impacts to the recipient ecosystem and to other land users.

For these reasons, many authors and practitioners advocate the use of a decision-analytic approach for conservation problems including reintroductions. Decision analysis has been defined as '... a formalisation of common sense for decision problems which are too complex for informal use of common sense.' (Keeney, 1982). Within this framework, decisions are objective driven and approached as an iterative sequence of steps, the first of which is to define clear objectives and measures of success. Then a set of potential alternative actions can be identified and assessed. For each potential alternative, predictions can be made of the outcomes of candidate actions in relation to the stated objectives, and any trade-offs and uncertainty can be evaluated. Finally, the optimal action(s) can be implemented and the results monitored.



# Biological feasibility



Translocations need rigorous justification with clearly defined goals and objectives. The associated risks should be identified and assessed, and criteria defined for monitoring and measuring the project's performance. If the decision is taken that wildcat reintroductions to England and/or Wales are appropriate, then decisions will need to be made regarding where to source individuals, exactly where to release individuals and how to manage the translocation. These decisions will form the basis of future reintroduction plans. A working group should be tasked with developing these decisions and this should include key stakeholders, who should be involved from the start in formulating a goal statement setting out the intended result and the intended conservation benefit in quantifiable terms. The actions taken to achieve the objectives can then be specified and should be measurable (enabling monitoring and assessment of progress), with suggested time scales, indications of expected resources required, and notes on who is responsible for the implementation.

In recent years, there has been an exponential increase in the number of conservation reintroductions worldwide (Seddon *et al.*, 2007), and there have been a number of reviews published of reintroduction/translocation success in particular taxa (Griffiths and Pavajeau, 2008; White Jr *et al.*, 2012; Germano and Bishop, 2009) and of reintroduction biology in general (Ewen *et al.*, 2012). Previous reviews of the outcomes of conservation translocations have often reported low rates of success, ie (Fischer and Lindenmayer, 2000; Wolf *et al.*, 1996). Low habitat suitability and poor release site selection are reasons frequently given for failure (Wolf *et al.*, 1996; Cook *et al.*, 2010; Armstrong *et al.*, 2002), therefore, significant effort should be put into evaluating suitable release areas before considering going ahead with translocations. By definition, serious scientific uncertainty is an issue in reintroduction efforts because the species is being reintroduced into an environment that it does not currently occupy. It cannot be assumed that historical sites offer suitable habitat and it may often be inappropriate to reintroduce within the former range (Seddon, 2010). The more time that has elapsed between local extinction and a planned reintroduction, the greater the likelihood that the habitat will no longer be suitable. This means there is a need to evaluate habitat suitability regardless of historical occupancy. Sites should not be selected on the basis that a species used to be there or that the site looks right. Detailed knowledge of the ecology of a species can provide information on the likely current suitability of a proposed release site, but modelling enables that knowledge to be put into a landscape context, projected into a range of current and future scenarios, and compared against a number of objectively assessed alternative sites.



Across Europe, the wildcat has been reported as being able to use a variety of habitats ranging from dense coniferous forest to mosaics of agricultural land and scrubland (Corbett, 1979; Sunquist and Sunquist, 2002; Lozano *et al.*, 2003). This has been attributed to the species having different habitat requirements to satisfy different daily activities, particularly resting and hunting (Corbett, 1979; Klar *et al.*, 2008; Monterroso *et al.*, 2009; Hobson, 2012). In spite of this, the European wildcat is often still regarded as a typical forest species (Lozano *et al.*, 2006). Previous studies of wildcat habitat use have shown a positive association with forest edge, water courses, edge of rivers, marginal agricultural habitats with rough grassland, moorland and meadows (Corbett, 1979; Sunquist and Sunquist, 2002; Lozano *et al.*, 2003); all habitats likely to be rich in small mammal prey. Conversely, Klar *et al.* (2008) found that wildcat presence was negatively associated with human settlements, roads and arable fields, and other studies report that the probability of wildcat presence decreases in heather moorland, at higher altitudes and in habitats with fewer grassland blocks or secondary watercourses (Easterbee *et al.*, 1991; Daniels *et al.*, 2001; Silva *et al.*, 2013b). In Scotland, priority wildcat conservation habitats include rough or improved grassland, interspersed with mixed or conifer woodland. Kilshaw *et al.* (2016) found that the probability of wildcat occupancy increased with higher proportions of mixed woodland with less forest edge (Kilshaw *et al.* 2016).

Ecological Niche Models (ENMs) (Warren *et al.*, 2010; Warren and Seifert, 2011), sometimes called Species Distribution Models (SDMs) (Kramer-Schadt *et al.*, 2013; Syfert *et al.*, 2013; Fourcade *et al.*, 2014) or Habitat Suitability Models (HSMs) (Koreň *et al.*, 2011; Bellamy *et al.*, 2013), correlate a set of species presence locations with environmental covariates to estimate habitat associations. ENMs can be used to predict distributions or habitat suitability in unsurveyed areas, and can also be a useful tool to help identify candidate reintroduction sites for endangered species (Martinez-Meyer *et al.*, 2006; Osborne and Seddon, 2012). However, in spite of their widespread use in ecology, relatively few studies to date have used them for this purpose (Peterson *et al.*, 2011).

MaxEnt (Phillips *et al.*, 2006) is one of the most commonly used ENM techniques and has been used to model suitable habitat for various species (Phillips *et al.*, 2006; Ward, 2007; Gibson *et al.*, 2007; Stabach *et al.*, 2009; Hernandez *et al.*, 2008). It has been shown to perform better than other presence-only and presence-absence modelling techniques (Elith *et al.*, 2006; Hernandez *et al.*, 2006).

A reliable set of species presence locations are required for ENMs. However, hybridisation has complicated wildcat survey and monitoring throughout the species' range (Kilshaw *et al.* 2016; Macdonald *et al.* 2004). This is particularly true in Scotland, where the population has undergone such an extreme bottleneck and is now at such low numbers that, even were sufficient data on 'pure' wildcat presence locations available, environmental features alone are unlikely to be the limiting factor in wildcat presence. Wildcats have been protected in France since 1976 and recent studies have shown that, while hybridisation with feral domestic cats does occur, a significant pool of genetically pure wildcats still persists in France (O'Brien *et al.*, 2009; Say *et al.*, 2012). For this reason, we used genetically verified data for wildcat (and wildcat hybrid) presence locations from a widescale survey across France to develop a landscape scale model with MaxEnt to identify and prioritise regions of potentially suitable habitat for wildcat reintroductions to England and Wales. Britain and France are both in the temperate oceanic climate zone of northern Europe (Peel *et al.*, 2007), and have a similar range of environmental conditions and land cover classes. Therefore, the region from which presence data used for training the model were collected was sufficiently similar to the region onto which the model was projected for this extrapolation to be valid. This was tested by cross-validation and Multivariate Environmental Similarity Surface (MESS) maps in MaxEnt to look at estimates of how the environmental space in predicted places compares with that of the training data (Elith *et al.*, 2010).



# Methods

Habitat suitability was modelled at the 10km square resolution for all of mainland Britain and France. Presence locations were grid references in France where a hair sample or carcass, confirmed by DNA testing as either wildcat, hybrid or domestic, had been collected during recent surveys between 1988-2016 [for details, see (Say et al., 2012; Léger *et al.*, 2008)]. The sampling area covered 51% of metropolitan France, divided into grid cells of 10x7km<sup>2</sup>. Surveys were carried out by officers of the National Hunting and Wildlife Agency (ONCF), professionals of various hunting associations, and by trained naturalists. The survey specifically reported and/or collected specimens with wildcat phenotypes. This meant that domestic cats were probably under sampled and therefore were not used in the analyses.

The precision of sample locations was variable but was recorded to a minimum resolution of the commune, the smallest administrative unit in France. This is approximately 10km<sup>2</sup> and so this resolution was used for the analysis of landcover and other environmental variables (EVs).

Land cover classes were derived from the CORINE 2012 datasets (European Environment Agency, 2007) and manipulated in ArcMap 10.2. The 44 pan-European land cover classes were extracted for the countries of mainland France and Britain, and reclassified into land cover variables that were deemed to be biologically relevant for wildcats (see Table 2 for details). Coniferous woodland and broadleaved/mixed woodland were separated into two different variables because of likely differences in prey availability, understorey structure and human disturbance (likely to be higher in commercial coniferous forests related to timber extraction). The cumulative area of each re-classified land cover type was summed onto a 10x10 km square grid. One landcover type (bare ground), which was present in less than 20% of grid squares, was excluded from the models because it has been shown that including rare cover classes can increase the level of background noise in environmental data. This can lead to predictions that are biased towards local conditions and make it less acceptable to extrapolate model predictions to other areas (McCune *et al.*, 2002). Road density and mean altitude per 10km square were derived from DIVA-GIS datasets (<http://www.diva-gis.org/Data>) for Britain and mainland France. Human population density per 10km square was derived from the European Environment Agency raster dataset representing the 1km<sup>2</sup> population density for the year 2001 on a 100m grid for Europe (<http://www.eea.europa.eu/data-and-maps/data/population-density-disaggregated-with-corine-land-cover-2000-2>).

MaxEnt 3.4.1 (Phillips and Dudík, 2008) software was used for model fitting. A random 70 percent of presence locations was used for model training, with the remaining 30 percent used for model testing. The maximum number of iterations was increased to 1,000 and the maximum number of background points used to 50,000. All other settings were left at default with cross validation. Model fit was assessed using Receiver Operator Characteristic (ROC) curve analysis and the average Area Under the Curve (AUC) values across all of the replicated runs. AUC values greater than 0.9 are classed as very good, with 0.7-0.9 being good and an AUC of less than 0.7 classed as uninformative (Swets, 1988). The significance of each environmental variable in explaining the variance in the presence location data was evaluated from Jackknife plots. Pairwise correlations were calculated for all EVs using ENM tools (Warren *et al.*, 2010) to exclude one variable of a pair if they were strongly correlated (correlation co-efficient >0.5).

# Results and discussion

From a total of 557 samples, 364 were confirmed by DNA analysis as wildcat, with 107 hybrids and a further 86 that were domestic cat. The geographic spread of wildcat and hybrid locations used in the models is shown in Figure 3.

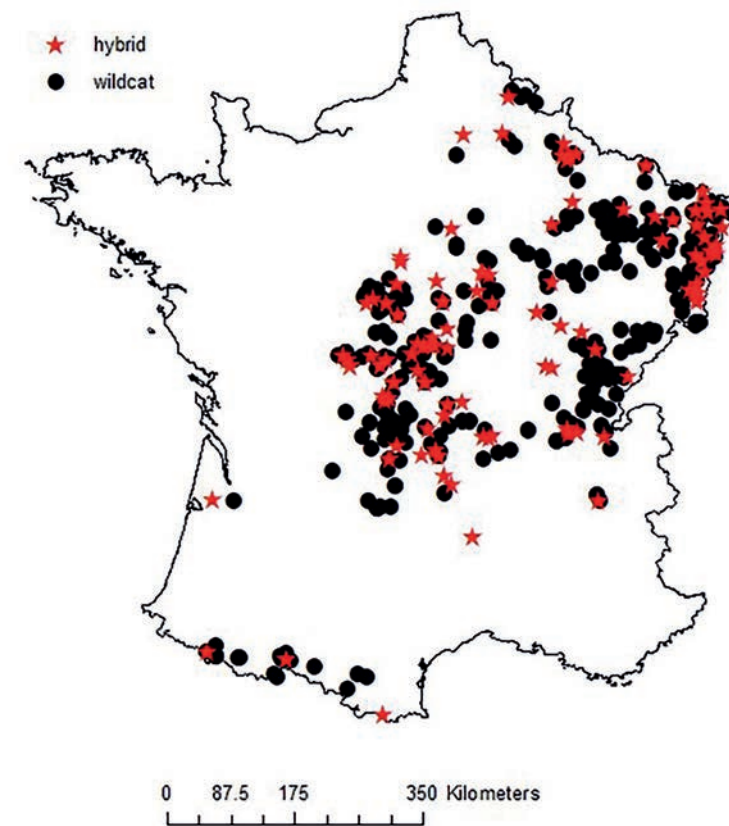


Figure 3 Wildcat and hybrid presence locations used for model training and testing.

A series of models was run with all potential EVs included, and then with each of those that accounted for the lowest percent contribution to the model dropped and added, in turn, to refine the final set of candidate models. Population density was correlated with urban landcover ( $r= 0.63$ ) and so models were run with either one or the other included, to look at the effect on model fit. Road density was thought to be a potential bias, as many of the samples were collected as roadkill carcasses. Therefore, each of the final set of candidate models was run both with and without road density included as a bias file to account for the possible effect of this on sampling effort.



Table 1 Model evaluation metrics for the final set of models

	Urban	Population density	Road density	Roads included as bias	AIC	AUC <sub>Train</sub>	AUC <sub>Test</sub>
1	✓	×	×	×	7005.36	0.89	0.84
2	✓	×	×	✓	7031.514	0.89	0.84
3	×	✓	×	✓	6937.012	0.88	0.84
4	×	✓	×	×	6937.626	0.88	0.84
5	✓	×	✓	×	6059.918	0.89	0.84
6	×	✓	✓	×	6009.261	0.89	0.86
7	✓	×	✓	✓	6403.467	0.87	0.82
8	×	✓	✓	✓	6205.355	0.85	0.81

As recommended by Warren *et al* (2010), Akaike Information Criteria were used to compare the final set of models. The model with the lowest AIC score was considered the best of the candidate models (Burnham and Anderson, 2002). This also had the highest ROC AUC on both training and testing, although there was quite low variation in AUC values among the final eight best models (shown in Table 1).

To identify potentially suitable areas for wildcat reintroductions, the best fit model was projected across the entire study area, which included all of mainland France and mainland Britain. Output using the complementary log log link (cloglog) function was used as this is more appropriate for estimating probability of presence (used here as an indicator of predicted habitat suitability) than the previous MaxEnt default of logistic transformation (Phillips *et al.*, 2017).



Photo: ©Helen Haden

## Wildcat model

The model for wildcats with the lowest AIC and highest mean AUCs included population density and road density, along with all the other environmental variables shown in Table 2. From 100 replicate runs, this model had an average AUC of 0.86 (s.d. 0.05) on the test records not included in model construction. At the threshold of minimum training presence, the TSS for this model was 0.6. This model was used for projecting to Britain to look at where the model predicted the highest habitat suitability for wildcats.

Table 2 Description of environmental variables and their mean contribution to the final model for wildcats (100 iterations)

Variable	Description	Contribution %
Broadleaf mix	Summed area (ha) of 10km square with broadleaf and mixed woodland	62.1
Mean elevation	Mean elevation per 10km square	13.9
Agri-mosaic	Summed area (ha) of 10km square with heterogeneous agricultural land	5.4
Arable	Summed area (ha) of 10km square with arable and crop cover	4.7
Scrub	Area (ha) of 10km square with transitional woodland scrub cover	4.4
Natural grassland	Area (ha) of 10km square with natural grassland cover	4.1
Conifer	Area (ha) of 10km square with conifer woodland	1.4
Wetland	Area (ha) of 10km square with bogs, marshland and other wetland	1.3
Water	Summed area (ha) of 10km square with water bodies and water courses	0.7
Road density	Summed length (km) of major roads within 10km square	0.7
Population density	Human population density per 10km square	1.0
Moor and heath	Area (ha) of 10km square with moors and heathland	0.3

Although there were 12 potential predictor variables included in the final model, six of these accounted for almost 95% contribution to model performance. The most significant of these was broadleaved and mixed woodland. Elevation was the next most significant variable, followed by agri-mosaic, arable, scrub and natural grassland (Table 2).

Jackknife tests were run on training gain, test gain and AUC. The environmental variable with the highest gain when used in isolation was broadleaf/mix woodland, which therefore appears to have the most useful information by itself. The environmental variable that decreased the gain the most when omitted was mean elevation, which therefore appears to have the most information not present in the other variables.

MESS map analysis was carried out to check the validity of using the model for projecting to mainland Britain. MESS maps indicate, for each cell, the extent to which predictors are outside of their training range. No cells in the projected area were found to have one or more environmental variables outside the range present in the training region.



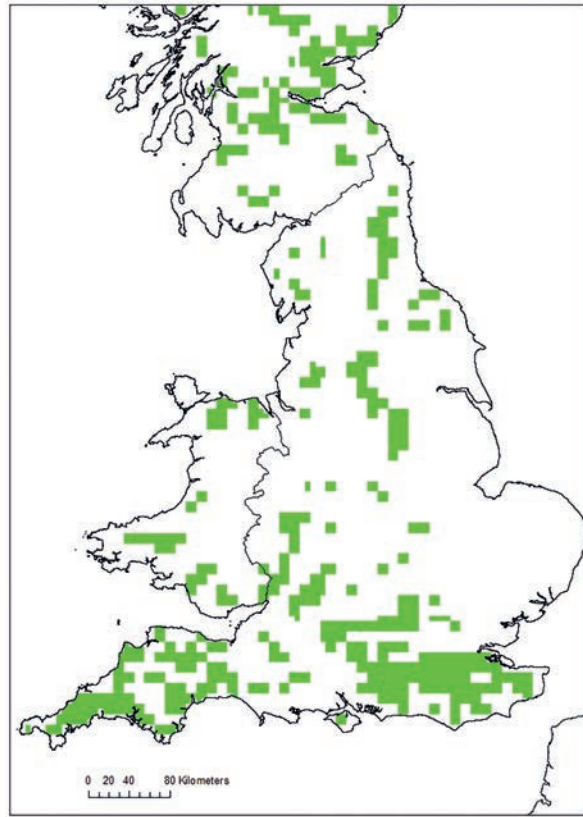


Figure 4 Habitat suitability map for the wildcat in southern Britain based on MaxEnt model predictions. (10km squares above the threshold of minimum training presence are shown in green).

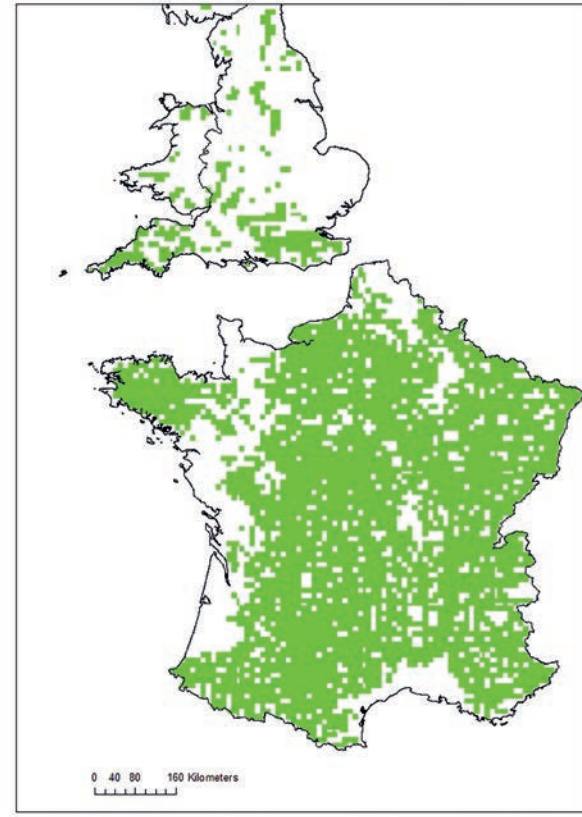


Figure 5 Model predicted suitable areas in Britain and France (10km squares with values above minimum training presence threshold shown in green).

Model predictions were plotted onto a 10km square grid map of mainland Britain (Figure 4) showing 10km squares with predicted suitability values above the threshold of minimum training presence.

The number of model-predicted 10km squares that were above the minimum training presence threshold is fairly low and relatively fragmented in England and Wales, compared with France (shown in Figure 5). There is a cluster in the south-east of England, but this has a very high human population density and heavily used road network, not shown in Figure 4. There is also a block in the Pennines, but potential issues of conflict with other land uses in this area are discussed later. Regions that could warrant further, more detailed investigation for potential reintroduction sites are in the south-west of England and north and west Wales.

### Wildcat-domestic hybrid model

The same methods were used for model training, testing and selection with presence locations for confirmed wildcat/domestic hybrids. The candidate model with the lowest AIC retained the same variables as that for wildcat. The mean AUC on test data was 0.83 (s.d 0.17) for hybrids. The first two environmental variables that accounted for the highest percent contribution to the hybrid model were also broadleaf/mixed woodland and mean elevation. However, arable was the landcover with the third highest percent contribution, followed by agri-mosaic and natural grassland (shown in Table 3).

Limited data have been published on the environmental factors affecting hybrid distribution, however it is thought that hybrids have similar habitat use to wildcats but utilise human resources, unlike wildcats (Germain *et al.*, 2008; Kilshaw *et al.*, 2016). Therefore, hybrids may play a significant role in further increasing hybridisation by bridging landscapes that largely separate feral cats from wildcats.

Table 3 Description of environmental variables and their mean contribution to the final model for hybrids.

Variable	Description	Contribution %
Broadleaf mix	Summed area (ha) of 10km square with broadleaf and mixed woodland	50
Mean elevation	Mean elevation per 10km square	12.3
Arable	Summed area (ha) of 10km square with arable and crop cover	10.2
Agri-mosaic	Summed area (ha) of 10km square with heterogeneous agricultural land	6.9
Natural grassland	Area (ha) of 10km square with natural grassland cover	5.6
Road density	Summed length (km) of major roads within 10km square	3.9
Conifer	Area (ha) of 10km square with conifer woodland	3.5
Water	Summed area (ha) of 10km square with water bodies and water courses	3.5
Moor and heath	Area (ha) of 10km square with moors and heathland	2.1
Wetland	Area (ha) of 10km square with bogs, marshland and other wetland	1.2
Scrub	Area (ha) of 10km square with transitional woodland scrub cover	0.7
Population density	Human population density per 10km square	0.1

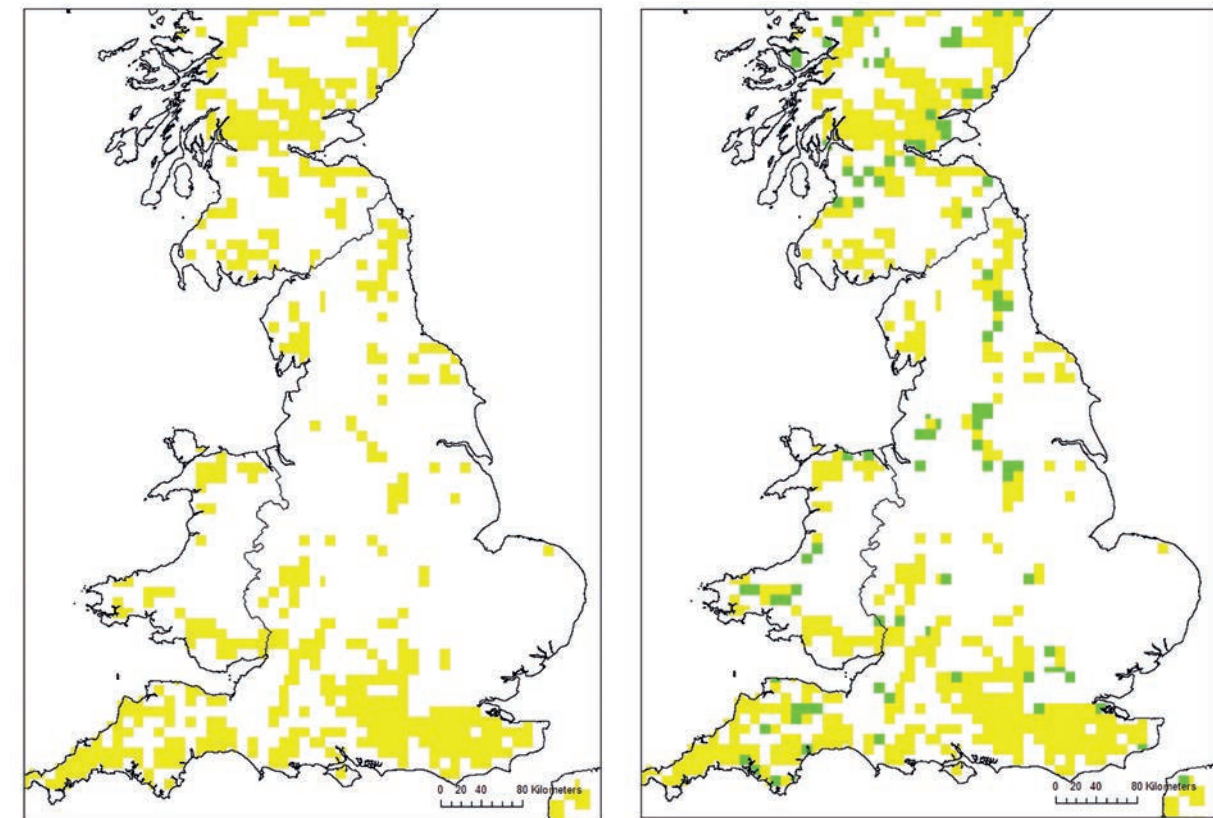


Figure 6 Habitat suitability maps for hybrids in southern Britain based on MaxEnt model predictions. Only 10km squares above the threshold of minimum training presence are shown in yellow for hybrids. On the right, these are overlaid onto 10km squares predicted as suitable for wildcats in green, showing how few of these are not overlapped by suitable hybrid habitats.



We used two methods to test whether the ENMs for wildcat and for hybrids are identical or no more similar than expected if localities are drawn at random from the environmental background. Niche similarity tests were carried out using ENMTools version 1.4.4 (Warren *et al.*, 2010). Schoener's D index and the similarity statistic (I) were calculated for each grid cell of the model projections for wildcats and for hybrids. These tests summarise similarity of projected suitability scores for each grid cell of a shared landscape and range from 0 (ENMs highly divergent) to 1 (ENMs identical) (Warren *et al.*, 2008).  $D=0.8$  and  $I=0.96$ , suggesting significant niche overlap between the two models. This concurs with the findings of other studies (Germain *et al.*, 2008; Biró *et al.*, 2005) and, given the high degree of spatial overlap between the presence location datasets for wildcats and hybrids (shown in Figure 3), this is not unexpected. However, it does highlight that the areas predicted as being suitable for wildcats in Britain would also have a high suitability for hybrid cats, so it would be important to select reintroduction sites and release animals in sufficient numbers to minimise the risk of wildcats mating with domestic cats in the first instance. In addition to this, a campaign to raise awareness of the issues of hybridisation with and disease transmission from domestic and feral cats will be crucial.



# Potential risk factors

## Domestic/feral cats and human habitation

There is a clear association between the distribution, numbers and movements of domestic cats and several human and environmental factors (Ferreira *et al.*, 2011). The presence of people has been shown to be the single most important variable. The number of owned (pet) cats in the UK was estimated at 8 million in 2017. In addition to this, it is estimated that there is a minimum of 813,000 feral cats in the UK (Woods *et al.*, 2005), although animal welfare charity, Cats Protection, believes this is likely to be much higher at approximately 1.5 million.

Cities and towns (and the almost unlimited food supplies that they provide) allow for the presence of large numbers of feral cats, numbers of which follow the gradient of availability of human related food resources and refuge, from urban and suburban areas to rural areas (Bradshaw *et al.*, 1999). However, heavily urbanised areas are unlikely to be used by wildcats and so probably represent less of a hybridisation risk than smaller rural settlements.



Photo: ©Julia Bracewell

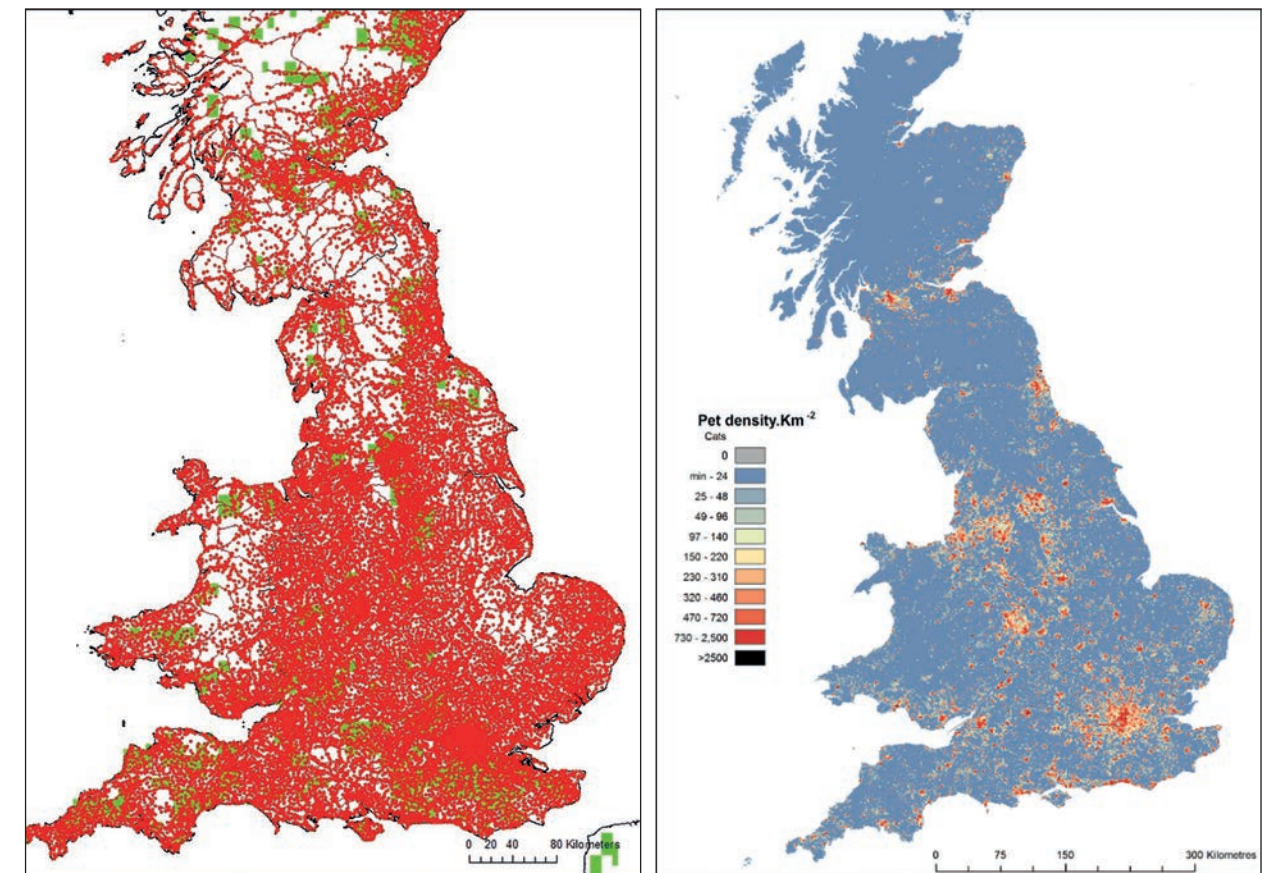


Figure 7 Model predicted suitable wildcat habitat in Britain (green) in relation to cities, towns and other settlements (in red) on the left and, on the right, map showing estimated pet cat densities across the country (from Aegerter *et al.*, 2017). Contains OS data ©Crown copyright and database right (2019)



Small rural villages or even isolated houses or farms represent a bridge allowing the intrusion of cats into the surrounding areas. Ferreira *et al.* (2011) found that the presence and number of domestic cats in their study area was dependent on the presence of people and the resources provided by them, and that the area around farms was the preferred land use type for these cats.

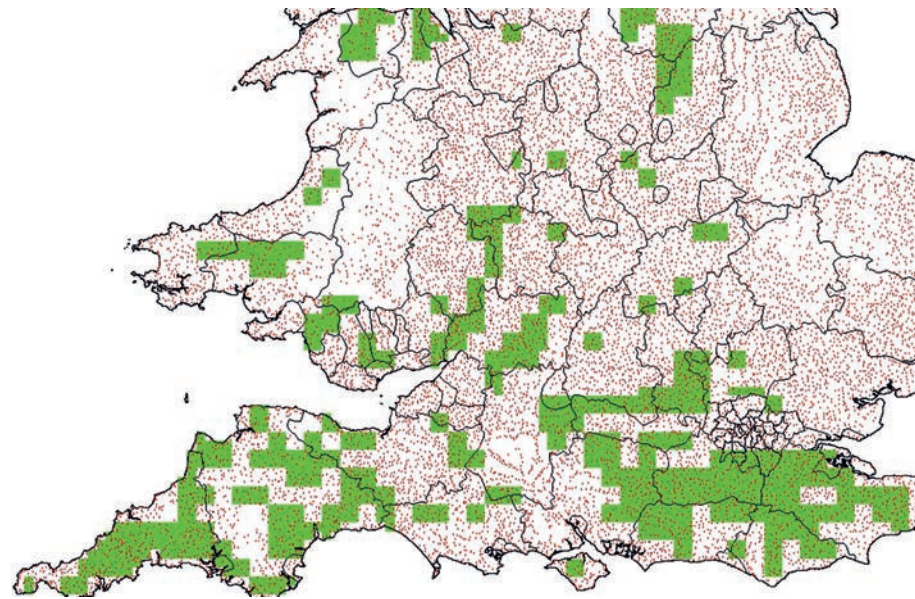


Figure 8 Potentially suitable wildcat areas in southern Britain (shown in green) in relation to settlements other than major towns and cities. Contains OS data ©Crown copyright and database right (2019)

This was found in a study in northern France, where domestic cats centred their home ranges in a village or around farms (Germain *et al.*, 2008). However, Ferreira *et al.* (2011) found that, while home ranges of radio-tagged feral cats were centred on inhabited farms, males travelled up to 6.8km (mean 3.8km) away from farms during the mating season. Nonetheless, they still used human settlements as a stepping-stone to make these longer distance movements. The biggest risk of hybridisation is therefore likely to be in fragmented habitats where domestic cats are present in rural farms and villages, close to the interface with wildcat habitats, where some individuals will make forays into areas where they are likely to encounter and may interbreed with wildcats.

This may be further facilitated in southern Britain by the relatively mild climate. The distance domestic cats move away from farms has been shown to increase with temperature, leading some authors to suggest that hybridisation should be more frequent in regions characterised by mild winter than in colder regions. Once hybrids are present, they may then play a key role in exacerbating further hybridisation of the population by behaving as wildcats and by sharing at least a part of their range with them as well as with domestic cats. It is thought that behavioural barriers between hybrids and wildcats may not exist because of their similarity in morphology, home range characteristics and spatial behaviour (Germain *et al.*, 2008). The map shown in Figure 8 illustrates that there are no areas in southern Britain where suitable wildcat habitat is not in close proximity to some level of human settlement.

### Road mortality

Wildlife mortality due to road traffic has increased over recent decades and is a major threat for many medium-sized carnivores across Europe (Van der Zee *et al.*, 1992; Philcox *et al.*, 1999; Jancke and Giere, 2011). Beside habitat loss and hybridisation with feral cats, road mortality is acknowledged as a major threat for wildcats throughout the species' range in Europe (Stahl and Artois, 1994; Pierpaoli *et al.*, 2003; Lecis *et al.*, 2006; Klar *et al.*, 2009).

Roads and other major infrastructure can also act as significant barriers to gene flow and, although wildcats have the capability of dispersal across major anthropogenic and natural landscape barriers, genetic analysis has shown that these structures still lead to an effective isolation of populations (Hartmann *et al.*, 2013; Klar *et al.*, 2009). When they are able to do so, wildcats avoid human made structures such as roads (Klar *et al.*, 2009; Silva *et al.*, 2013b) and one study found that the probability of wildcat habitat use decreased at distances less than 200m from roads (Klar *et al.*, 2008). Roads affect the survival of many carnivores (Kramer-Schadt *et al.* 2004; Reynolds-Hogland & Mitchell 2007) and are likely to be an important source of mortality affecting the viability of newly released and establishing wildcat populations. Some of the regions in Britain predicted as having habitat suitable for wildcats also have a very high density of roads as shown in Figure 9.

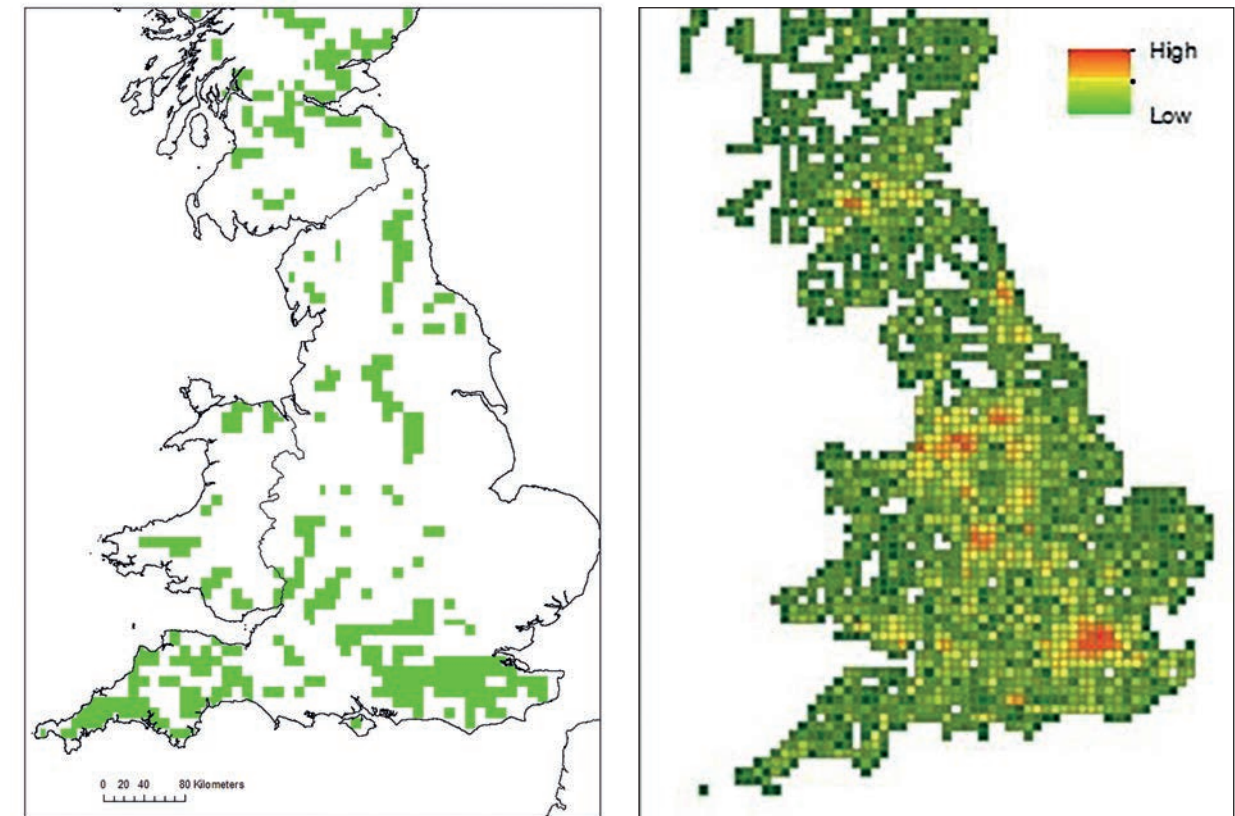


Figure 9 Model predicted habitat suitability for wildcats in Britain (in green on left) and road density/10km<sup>2</sup> (on the right).



In wildcat reintroduction projects that have been carried out elsewhere in Europe, many of the released animals have died on the roads (Nowell and Jackson, 1996). Rates of wildlife road mortality are influenced, not just by road density but by habitat suitability and landscape structure, as well as road and traffic characteristics (Gunson *et al.*, 2011). Narrow and sinuous roads with low to medium traffic volumes that pass through high quality habitat are often particularly problematic (Grilo *et al.*, 2012). There seems to be a threshold in traffic volume above which a barrier effect is apparent which, for larger carnivores is reported as being approximately 2,000-5,000 vehicles per day (Alexander *et al.*, 2005). However, this may be species specific: for example, stone martens have been recorded regularly crossing a four-lane highway with nightly traffic volumes of 2,000 vehicles (Grilo *et al.*, 2012) with the result that road mortality was a significant threat to the population. Across Britain, there is wide regional variation in annual traffic volume as seen in Figure 10.



Region	Vehicle miles (billions) 2018
South-east England	54.9
East England	38.7
North-west England	35.7
South-west England	33.2
West Midlands	31.6
Scotland	29.7
Yorkshire and the Humber	27.8
East Midlands	27.7
London	18.4
Wales	18.3
North-east England	12.3

Figure 10 Showing regional variation in traffic flow (vehicle miles driven per region) in 2018. Actual figures on the right. [Reproduced from the Department for Transport website <https://roadtraffic.dft.gov.uk/regions>].

Local, as well as seasonal, variation in vehicle traffic flows should be assessed. As wildcats are vulnerable to mortality as a result of road traffic accidents, animals exploring an unfamiliar landscape following release while establishing new home ranges are likely to be even more at risk. Roads with high traffic volumes and those which pass through woodland probably represent the highest threat (Grilo *et al.*, 2012). Therefore, these factors should be quantified and taken into account when selecting release sites.

It is recommended that detailed information on road characteristics combined with annual volume of traffic is used to calculate the relative likelihood of wildcat mortality due to road traffic accidents. Even a low rate of additional mortality will significantly increase extinction risk and jeopardise the establishment of a newly reintroduced population. It is therefore suggested that translocations should first be to regions with sufficient areas of contiguous high-quality habitat to support relatively high numbers, and where likelihood of road and other causes of mortality are low.

## Effects of disturbance

Worldwide, ecotourism and recreational activities are growing, especially in protected natural areas (Balmford *et al.*, 2009). For the conservation of the wildcat and other species, it is therefore important to know the impact these increased recreational activities may have on animals at the physiological level. This could be useful in the preservation of existing wildcat populations and in the selection of future reintroduction sites. Studies of how human disturbance affects wild *felids* have been based on behavioural changes (Kerley *et al.*, 2002; Ngoprasert *et al.*, 2007; Jerosch *et al.*, 2010), as well as using physiological parameters to assess the responses of captive *felids* to human presence (Montanha *et al.*, 2009; Terio *et al.*, 2004). Piñeiro *et al.* (2012) looked at whether increased physiological stress levels in wildcats were a response to levels of disturbance from tourist numbers. The study found that wildcat faecal cortisol metabolite concentrations were higher in areas of a natural park when the number of visitors was higher. Visitor numbers in natural areas tend to be highest in spring and summer, which is the breeding season for wildcats when females are pregnant. An increase in physiological stress during this sensitive period could negatively impact reproductive success. This has been observed in other mammals (Arck *et al.*, 1995; Nepomnaschy *et al.*, 2006). Therefore, recreational use and seasonal variation in visitor numbers should also be considered during the selection process for reintroduction sites.

## Potential conflict with other land uses

In addition to the potential impacts on wildcats, the actual or perceived risks that wildcats may pose to other species need to be assessed and, where possible, mitigation measures developed.

Feral domestic cats can be a problem for poultry keepers and land managers rearing game birds. Lethal control of feral cats is a legitimate and legal activity, provided it is carried out humanely. Gamekeepers carry out legal predator control to reduce feral cat numbers, (89% of surveyed shoots culled feral cats where they were present, (NGO, 2011) but the difficulty in separating a protected wildcat from a non-protected feral cat (or a potential hybrid) is a serious problem. In the first instance, it would be preferable to select release sites well away from any potential conflict with shooting estates or large poultry rearing businesses (recent densities of which are shown in Figure 11).

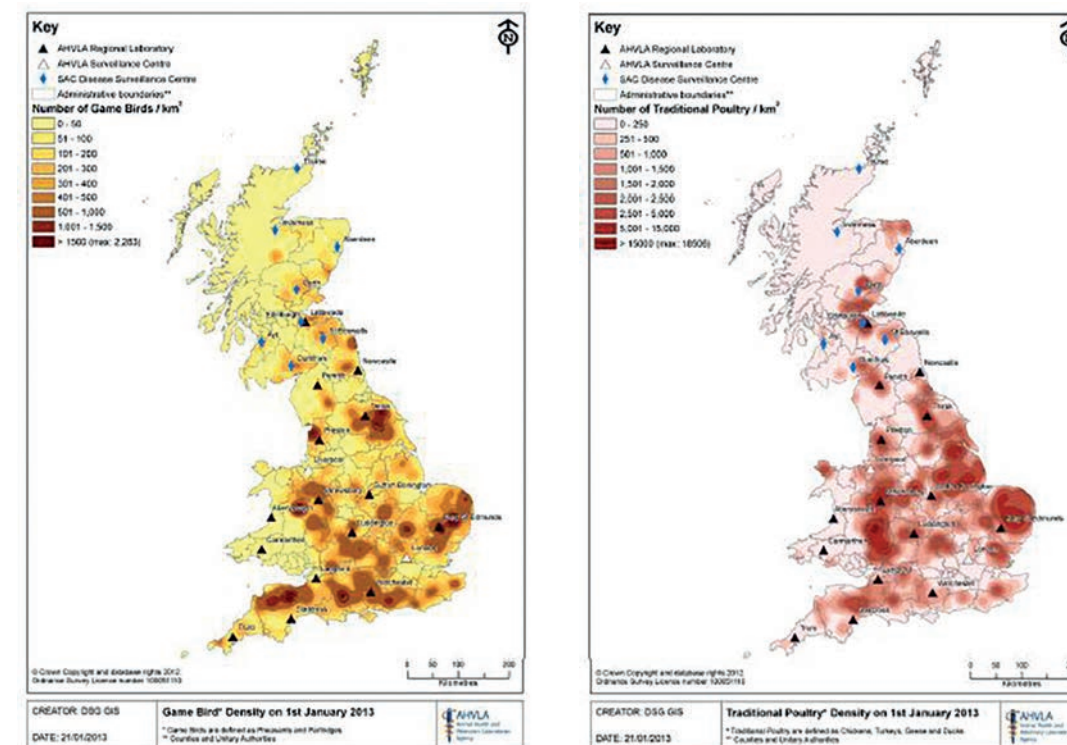


Figure 11 Maps showing 2013 regional densities of gamebirds (pheasants and partridges)/km<sup>2</sup> (left) and poultry/km<sup>2</sup> (right) [From AHVLA Great Britain Poultry Register Statistics 2013 <https://www.gov.uk/government/statistics/great-britain-poultry-register-statistics>].



In the longer term, a publicity campaign should aim to raise awareness of the presence of true wildcats outside of Scotland, the measures that can be taken both to keep wildcats out of pheasant and poultry pens, and how to distinguish between wild and feral cats for the purposes of legal predator control.

Predator control on pheasant shoots is relatively low key nowadays, as it is generally more cost effective to rear and release larger numbers of birds than use resources on predator management, but for wild shoots, this is not the case (S. Tapper pers. comm.). Moorland management for grouse shoots is heavily dependent on keeping predators to a minimum, so it is to be expected that reintroductions of wildcats would not be welcomed in regions where grouse are present and driven grouse shooting is an important element of the local economy. These areas are shown in the maps in Figure 12.

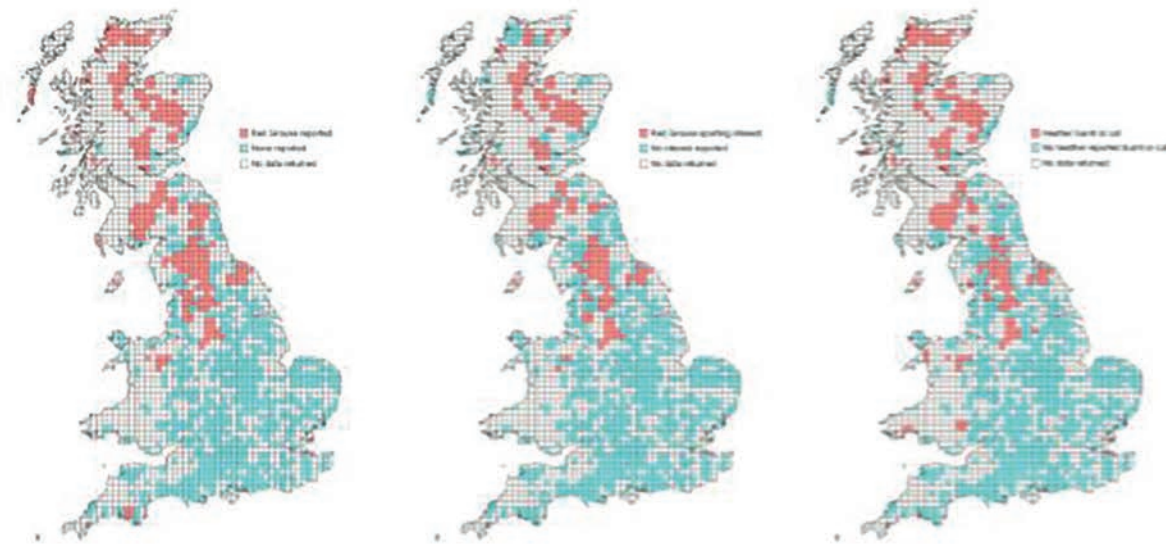


Figure 12 The presence of red grouse (shown in red on the left), together with its sporting interest (in red on the right) [From (NGO, 2011)].



# Conclusions and further work

The aim of this study was to identify and prioritise regions at a landscape scale, within which to focus the search for potentially suitable areas for wildcat reintroductions. This was done by using a niche-based modelling technique at a broad landscape scale.

The advantage of the method is that it requires only presence data to develop the model. True absence data for elusive species with low detection probabilities, such as most small carnivores, are impossible to verify. This is made even more complicated for wildcats by the issue of morphologically similar hybrids. Hybridisation has created a 'morphological cline' where characteristics such as size and pelage show a continuum from purebred wildcats to the domestic house cat (Davis and Gray, 2010; Mattucci, 2014). This makes identification from morphology alone very difficult. Microsatellite markers suggest that there are around 5-10 percent cryptic hybrids in most European populations (Mattucci *et al.*, 2016), meaning that presence locations from sightings or camera trap images cannot be verified. This was accounted for in the present study by only using presence locations from animals or samples that had been genetically tested before being classified as either pure wildcats or hybrids.

The final model performed reasonably well, with AUC values between 0.8-0.9 considered good but not excellent, suggesting that the method is suitable for screening at this relatively coarse scale to identify optimal regions for reintroductions. MaxEnt is relatively insensitive to spatial errors (up to c.5km) however, analyses should not be conducted with location data that are less precise than environmental data (Graham *et al.*, 2008). Environmental variables should be converted to the precision of the location data, as they were in this case.

Most of the available information on wildcat habitat use is derived from fine scale approaches, either in terms of resolution or extent (Silva *et al.*, 2013a). Coarse-scale studies, such as this one (and, eg, Ferreira, 2010) are scarce throughout Europe, despite the importance of understanding the determinants that constrain species presence at multiple scales (Wiens, 1989). However, species use habitats differently at a wide range of difference scales (Graf *et al.*, 2005; Cushman and McGarigal, 2004) and, in order to produce a realistic HSM, it is vital that habitat and other features are included at spatial resolutions that are relevant to the species of interest, based on its ecology and life history strategy.

Even when the correct variables are included in the model, if the scale at which scale-dependant characteristics operate is incorrect, this can lead to a dramatically different interpretation of which factors are actually influencing species occurrence (Shirk *et al.*, 2014; Bellamy *et al.*, 2013; Girvetz and Greco, 2009). As there is no *a priori* way of inferring the grain and extent at which each environmental predictor is most strongly related to species presence (Shirk *et al.*, 2014), habitat suitability modelling is moving towards increasingly complex multiscale models to reveal the true grain at which species respond to the landscape. Several recent studies conducted on mammals (Wasserman *et al.*, 2012; Bellamy *et al.*, 2013; Shirk *et al.*, 2014; Mateo Sánchez *et al.*, 2014) have demonstrated the effectiveness of multi-scale approaches (Vergara *et al.*, 2016). These allow more



accurate and fine-scale predictions of species occurrence and habitat suitability by systematically varying the scale of analysis to find the dominant scale at which each variable operates to build the models (Shirk *et al.*, 2012). It is recommended that this approach be used with a subset of the presence location data that have the highest spatial resolution, rather than to the nearest 10km square that encompassed the whole dataset and was used here. Finer-scale models should also incorporate prey availability once field surveys have been undertaken.

European wildcat distribution is known to be influenced by the distribution of prey, particularly that of the European rabbit, *Oryctolagus cuniculus* (Corbett, 1979; Lozano *et al.*, 2003; Malo *et al.*, 2004). This is especially obvious in parts of Southern Europe where rabbits constitute a large proportion (70% of biomass) of the wildcat's diet (Gil-Sánchez, 1998; Malo *et al.*, 2004). A preference for rabbits has been shown by studies comparing the diet of wildcats at sites where rabbits are present or absent, with the presence of the species resulting in far lower quantities of small mammals being consumed (Malo *et al.*, 2004; Lozano *et al.*, 2006). A habitat selection analysis carried out in Portugal (Monterroso *et al.*, 2009) showed that abundance of rabbits was one of the most important factors shaping the species distribution.

However, although rabbits are a preferred prey species across the wildcat's range, wildcats can persist in areas where rabbits are scarce or absent by preying on other species such as small mammals or birds (Scott *et al.*, 1993a; Lozano *et al.*, 2006). Studies from Scotland have shown that wildcats vary their diet in relation to prey availability, preferentially preying on rabbits when and where they occur (Corbett, 1979; Hobson, 2012), but switching to other prey, mainly small mammals, where rabbits are absent or at low densities (Scott *et al.*, 1993a). The preference for rabbits over small mammal species may be because they provide higher energetic returns in terms of biomass. Therefore, rabbits are an optimal prey item. Theory predicts that, for a predator like a wildcat weighing 4-5kg (Stahl and Léger, 1992), a food intake of c. 1000g per day is optimal (Carbone *et al.*, 1999). This equates to approximately two to three adult rabbits or four juveniles to fulfil its energetic needs. In contrast, a wildcat would need about 30 small rodents (mice and voles) daily to fulfil its energetic requirements.

Catchability is also a key parameter in prey selection (Stephens and Krebs, 1986). Although catching small rodents may generally be less demanding than catching rabbits, as a result of myxomatosis and the more recent Rabbit Haemorrhagic Disease (RHD) virus now present throughout Europe, rabbits may have become easier to catch when suffering from the effects of either disease. Corbett (Corbett, 1979) found that young rabbits and rabbits with myxomatosis were preyed heavily upon in relation to their availability by both wildcats and domestic cats. The young and diseased rabbits displayed different anti-predator responses to cats in comparison with adult rabbits, which made them more vulnerable and easier to catch. Paradoxically, while apparently making rabbits easier prey to catch, myxomatosis and RHD have also made them much scarcer in the last 60 years and, crucially for the purposes of this study, impossible to predict with any accuracy. Myxomatosis, which was first reported on mainland Britain in 1953 (Armour and Thompson, 1955) caused a dramatic decrease in rabbit populations throughout the country. However, subsequently, less virulent strains were present and an increase in genetic resistance to the disease was reported in 1977 (Ross and Sanders, 1984). The wild rabbit population was thought to have increased substantially after the mid-1970s (Trout *et al.*, 1986) but was still restricted by the disease in the 1980s (Trout *et al.*, 1992). High variations in local rabbit abundances have been observed throughout the UK, with myxomatosis thought to be a primary factor, as outbreaks do not occur in every population in every year (Trout *et al.*, 2000).

RHD was first confirmed in a domestic rabbit in 1992 and by 1994 it had caused significant declines in wild rabbit populations of the south-east of England (Forrester *et al.*, 2009). The disease has significantly impacted wild rabbit populations throughout the world, however, within Europe, outbreaks have been most virulent in Spain (Forrester *et al.*, 2009). This has resulted in dramatic declines in several of Spain's charismatic species as a result of reduced prey populations following this disease, notably the Iberian lynx, *Lynx pardinus*, which is completely dependent on rabbits, and the Imperial eagle. The impact of RHD on the rabbit population in Britain has not been as severe as elsewhere, which is thought to be due to a non-pathogenic RHD-like virus having been present in the region, resulting in a resistance to the disease being developed (Trout *et al.*, 1997; Calvete, 2006).

There is substantial site-to-site variation in rabbit numbers related to habitat and landscape factors, however, year-to-year variation within sites has been shown to be greater, likely as a result of the impacts of disease outbreaks (Trout *et al.*, 2000). This is why environmental variables related to rabbit presence were not included as indices of prey availability in the model presented here, but this will need to be considered in selecting sites and regions for reintroductions.

Species distribution models are calibrated on the realised niche of a species, relying on the assumption that location data used in the model are representative of its true requirements and that appropriate predictor variables have been used in the model. These are then used to predict areas that meet the requirements of the ecological niche of a species and therefore its potential distribution. The assumption that location data are representative of the fundamental niche of a species can be a problem if using data for a declining species. Some regions of its potential distribution may not be inhabited because it is being excluded by a competitor (eg, red squirrel in the presence of grey squirrel) or predator (as in the case of water vole and American mink), because it cannot disperse into an area because of geographical barriers to dispersal, or because the species has been extirpated from an area for some reason. The data used here were from an expanding population of wildcats. The distribution shown by the data in Figure 3 represents an estimated range increase of approximately 30% compared with data on the distribution of the species published in 1984 (SFEP, 1984). Specimens detected in the newly colonised area are both wildcats and hybrids, indicating that the extension of the wildcat range in France is not solely due to hybrids, as previously suggested (Lecis *et al.*, 2006).

Source-sink dynamics are another factor that may result in a species being recorded as present in unsuitable (sink) habitats, which do not provide the environmental conditions needed to support a viable population, but which may be visited or frequently re-colonised by individuals from a nearby source habitat that does support a viable population. In this case, presence locations will not represent suitable habitat or the fundamental niche of the species (Pulliam, 2000). This can also be an issue if remnant populations have been forced into refuges of sub-optimal habitat, in which case current ranges can be an unreliable indicator of habitat requirements. This is likely to be the case for wildcats in Scotland at the present time as an artefact of wildcat distribution during the species' nadir. It is certainly the case that where very few occurrence records are available, these are unlikely to provide a sufficient sample to identify the range of environmental conditions occupied by the species. The number of presence locations used for the present study was sufficiently large ( $n_{\text{wildcat}}=364$  and  $n_{\text{hybrid}}=107$ ) and collected from expanding populations across a wide enough geographical area and range of environmental conditions to support confidence in the predictions of habitat suitability from the final model. This is supported by the values for AUC for both final models and TSS values for the specified thresholds.



Model extrapolation should be treated with caution when making predictions for areas with environmental values that are beyond the range of the data used to construct the model. This was assessed by using multivariate environmental similarity surface (MESS) maps (Elith *et al.*, 2010). These provide an indication of the similarity of the range of environmental variables in the projected region compared with the training region. MESS maps were carefully interpreted by visual inspection of the outputs, which showed that the areas within which presence data used for building the model were collected are similar enough to the area over which the model was extrapolated, in this case to permit confidence in the model predictions. We used the minimum training presence or lowest presence threshold (LPT)(Pearson *et al.*, 2007) to define potentially suitable areas.

All Presence-only based HSM methods are based on the assumption that the entire study area has been systematically and randomly sampled (Elith *et al.*, 2010). The effect of sampling bias in model performance is increasingly acknowledged and several correction methods have recently been proposed to improve model accuracy (Fourcade *et al.*, 2014). If the areas predicted by the model as the most suitable tightly match those with the highest density of species records, then this can indicate effects of sampling bias. Each of our candidate models was run both with and without the inclusion of a bias file to account for the possible bias of having a high proportion of roadkill samples in our dataset. However, the inclusion of a bias file reduced the model performance very slightly but not significantly. In effect, by summing the area of each land class and EV within 10km grid squares, the model is not analysing the exact point locations at which wildcats were found, which may be affected by where the surveyors looked, but at the characteristics of the 10km squares in which wildcats were detected. At this scale there seems to be little effect of survey bias. At a smaller scale this might not have been the case.

The high percentage contribution to the model of mean elevation is interesting. In Scotland, favourable environmental conditions reported for wildcats include areas of altitude between 100-650m a.s.l. and with a cold climate (mean minimum annual temperature of -5° to -10°C). In other parts of their range, wildcats have been observed at elevations up to 1200 m a.s.l. but they move between elevations depending on snow cover (Mermod and Liberek, 2002)

Both habitat and elevation can restrict species' range and have been shown to be important in explaining the distribution of species. It is argued that species do not respond directly to elevation but rather to changes in abiotic variables regulated by elevation (Hof *et al.*, 2012). However, elevation can provide a useful surrogate for other variables such as temperature, prey density and productivity, which is why it was included here. The response curves showed a positive relationship with increasing elevation up to a point and then levelling off. Central Wales and the Cambrian mountains had surprisingly low predicted suitability for wildcats in our model, despite having been identified as highly suitable for pine martens (MacPherson *et al.*, 2014). Pine martens prey on the same small mammals, have similar habitat requirements to wildcats (Balharry, 1993) and are reported as an indicator species for the presence of wildcats in Scotland (Kilshaw *et al.*, 2016). However, the areas in Wales predicted here as suitable for wildcats differed from those for pine martens in an earlier study. This may be as a result of the relatively high proportions of upland, coniferous woodland and few areas of lowland, agri-mosaic habitats in the region. The strong association with broadleaved woodland found in the model concurs with other studies (Kilshaw *et al.*, 2016; Silva *et al.*, 2013a).

The summed area of each aggregated land cover class was used here: this included waterbodies and watercourses. However, more detailed models incorporating distance-based analyses to significant features such as watercourses, settlements and roads could be used at a finer scale to verify and refine the selection of release sites.

Wildcats have been shown to avoid moorland in Scotland (Kilshaw *et al.*, 2016), which is consistent with the negative association with moor and heath in the model presented here. This has implications for dispersal and shows that models of habitat suitability can also highlight how connected or isolated potentially suitable areas are and provide an understanding of how landscape might influence the spread of species (Ovaskainen, 2004; La Morgia *et al.*, 2011). This will impact on the viability of wildcat populations as numbers increase and release sites approach carrying capacity. Spatially explicit population viability modelling (eg, HexSim) can be used to identify likely future scenarios and predict spread in different areas.

The most recent guidelines for reintroductions and other conservation translocations from the IUCN (IUCN, 2013) stress that matching habitat suitability and availability to the needs of candidate species is central to feasibility and design. They also state that habitat suitability should include assurance that the release of animals and their subsequent movements are compatible with permitted land uses in the affected area. Existing and adjacent land uses (such as agriculture and game shooting), fine scale habitat structure and the attitudes of local communities will be a further indication of the suitability of these areas for releasing wildcats. Suitable habitat should now be investigated further in the areas highlighted by the present study as having sufficiently suitable habitat. Further analyses and field surveys of these priority areas are needed next to validate their suitability for future wildcat reintroductions and evaluate the level of potential conflicts with existing land uses, anthropogenic threats, such as high risk of mortality from traffic, and other potential causes.

## Social feasibility

It is well understood that conservation interventions, such as animal reintroductions, cannot hope to succeed without engagement with all stakeholders and, crucially, local communities. Community engagement is not just a useful part of the translocation process but should be one of the objectives. Translocations provide a way of engaging with the public by making them collaborators in the project and, as such, have the potential to change negative opinions of scientists and conservation managers. Providing people with the opportunity to take an active part in conservation projects, to learn more about the species involved and see tangible results can be a powerful antidote to the perception that conservation is exclusive and prioritises wildlife over people (a particular problem in the, often polarised, re-wilding debate). It is, therefore, important that meaningful community participation should be one of the main outputs of a translocation alongside its management and scientific objectives. A full stakeholder and community engagement programme is beyond the scope of the work presented here, but it is recommended that it has the highest priority in the future of the programme.

## Regulatory compliance

The Convention on the Conservation of European Wildlife and Natural Habitats (1979), also known as the Bern Convention, was the first wildlife treaty to encourage signatories to reintroduce native species as a method of conservation. Under Article 11(2), the Contracting Parties undertake: '... to encourage the reintroduction of native species of wild flora and fauna when this would contribute to the conservation of an endangered species, provided that a study is first made in the light of the experiences of other Contracting Parties to establish that such reintroductions would be effective and acceptable.' The more



recent Convention on Biological Diversity 1992 reaffirmed an international commitment to the recovery of species. Article 9(c) of the Convention creates an obligation to reintroduce threatened species, by requiring that 'Each Contracting Party shall, as far as possible and as appropriate, and predominantly for the purpose of complementing in situ measures... adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions.'

However, the obligations to reintroduce species as set out in the Bern Convention and the Biodiversity Convention, are not enshrined in European law. By the time Article 11(2) was translated into European law, as Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora, the meaning had been altered (Rees, 2001). The Directive merely requires (under Article 22), that 'Member States shall: (a) study the desirability of reintroducing species in Annex IV that are native to their territory where this might contribute to their conservation, provided that an investigation, also taking into account experience in other Member States or elsewhere, has established that such reintroduction contributes effectively to re-establishing these species at a favourable conservation status and that it takes place only after proper consultation of the public concerned.' The original obligation to encourage the reintroduction of native species has here been diluted into an obligation simply to study the desirability of reintroducing them. Nonetheless, the UK Government's recently published 25-year Environment plan explicitly states the objective of '... providing opportunities for the reintroduction of native species' as part of a developing Nature Recovery Network (Government, 2018). It remains to be seen how committed they are to this objective.



Photo: ©Helen Haden

## Captive breeding and source animals

Captive breeding and reintroduction have saved a number of species from extinction. In addition, captive animals can be used for research and to answer questions important to conservation, and to help advance and refine techniques for reintroductions, such as the provision of artificial den sites or improving capture methods. However, captive breeding for reintroduction is expensive in time, space, and money, and can be risky (eg, see Snyder *et al.*, 1996).

Questions that need to be answered include where to source animals for a significant captive breeding programme, and what resources are required to ensure enough animals are produced each year to release in sufficient numbers.

Should wildcat reintroductions be recommended in future, a large-scale captive breeding programme will be required, with all of the associated costs, staff and breeding stock. A detailed and fully costed captive breeding plan will be produced with appropriate partners in the next stage.

## Preliminary assessment of potential wildcat reintroductions against IUCN guidelines

Conservation Translocation is defined as '... the intentional movement and release of a living organism where the primary objective is a conservation benefit.' The aim of conservation translocations is to create self-sustaining populations that will be resilient in the long term. Translocation is an important tool for species that are in imminent danger of, or have already undergone, local extinction. However, translocations should not be undertaken lightly and should only be used if specific conditions can be met.

The Reintroduction and Invasive Species Specialist Groups of the International Union for Conservation of Nature (IUCN) have published guidelines that have been developed over a number of years with input from experienced practitioners. These are designed to be applicable to all types of conservation translocations (IUCN, 1995, IUCN, 2013). They are based on principle rather than example and are intended as a series of checks and balances to ensure that any translocation is justified because it will result in a quantifiable conservation benefit and will not cause adverse side effects of greater impact.

The guidelines can be distilled into a number of questions that need to be asked when planning and carrying out any conservation translocation (Seddon *et al.*, 2014). Here, we assess the concept of reintroducing wildcats to areas in England and Wales against these questions (numbers in parentheses are those of the annex to which each relates).

**Before resorting to translocations, have alternative courses of action been considered? (3.3)** Translocations for reinforcement and reintroduction are important tools for wildlife conservation used by conservation managers. However, translocating animals entails inherent risks. Wherever possible, the preferred option should be to manage species where they still occur and, where possible, to facilitate natural recolonisation to areas from which they have been extirpated. This can be by less invasive management methods such as restoring habitat, creating corridors and improving connectivity and/or by identifying and addressing the issues that caused the decline, be they trapping, disease, or hybridisation.

A recent review of the conservation status and assessment of conservation activities for the wildcat in Scotland over the past fifteen years has been published (Breitenmoser *et al.*, 2019). The review details the huge amount of work that has been carried out by a number of projects, notably Scottish Wildcat Action (SWA), and all that has been accomplished. This includes survey and monitoring, as well as raising awareness of the issues around wildcat conservation in Scotland (see details in Breitenmoser *et al.*, 2019). As a consequence of SWA's work, there are more reliable data available and a more



realistic understanding of the situation, with the review finding that ‘... earlier assessments of the situation of the wildcat in Scotland were too optimistic.’

In 2004, extrapolation from data available at the time led to an estimate of 3,500 wild living cats across Scotland, with only 400 individuals likely to be considered phenotypically wildcat based on ‘classic pelage characteristics’ (Macdonald *et al.*, 2004). A decade later, extrapolations from camera trapping data carried out across Northern Scotland over 23 sites by Kilshaw *et al.* (2016), resulted in an estimate of just 115-314 cats that display wild or mostly wild phenotypes.

It is now accepted that the wildcat population in Scotland is too small, too fragmented and too hybridised to be viable. The Breitenmoser (2019) report concluded that ‘... all the robust information available indicates that the wildcat in Scotland is at the verge of extinction.’

#### **Can the past causes(s) of decline and extinction be identified and addressed? (3.2)**

The cause of the decline in wildcats in Britain is widely attributed to intensive predator control associated with the rise in sport shooting, along with loss and fragmentation of suitable woodland habitat (Langley and Yalden, 1977). There has been a significant reduction in game keeping since the early 1900s (Tapper, 1992) and wildcats now have full legal protection under the Wildlife and Countryside Act, 1981. Gamekeeping practice has also changed considerably over the last century, and lethal control is closely targeted on a small number of pest species. However, there is still the issue of wildcats being confused with feral cats during legal predator control and the potential for this to impact on a newly reintroduced population if there is insufficient awareness of the issue.

Woodland cover in Britain is currently back to a similar level as in the 11th century (Watts, 2006), so the availability of woodland habitat for wildcats is at its highest for many years. However, most authors agree that wildcats require a mosaic of habitats and, in recent years, there has been a simplification of habitat types in the UK. Humans have modified ecosystems more in the last 50 years than in any comparable period. Land use and habitat change often result in simplification of the ecosystem to increase the economic value of one ecosystem service, usually provisioning services such as food production. Extensive modifications, such as conversion to intensive agricultural land, can alter ecosystems and reduce their capacity to provide a broad range of services. This may have an impact over a geographical scale wider than that of the original modification.

#### **Can potential future causes of decline/extinction be identified and addressed?**

(3.2.3; 5.3.2)

It is not sufficient to simply address the causes of the original population decline, as new potential threats may have arisen since that could prevent establishment of a restored population. It is also necessary to anticipate future threats and to assess the potential impact of these.

There have been large changes in the landscape since wildcats were widespread and common. It is anticipated that there will continue to be changes in land use in the future, including further increases in urban expansion, roads and vehicle traffic, particularly in the more densely populated parts of the UK. This needs to be accounted for in more detailed assessments of the areas identified by habitat suitability modelling as potential reintroduction regions.

#### **Is enough known about the biology and ecology of the species to inform the selection of release area(s)? (5.1)**

Selection of suitable release sites within appropriate release regions is of paramount importance. It has been shown that release into unsuitable habitat is a major cause of failure in translocations (Magdalena Wolf *et al.*, 1998). There is a large body of published literature on the biology, ecology and habitat use of the wildcat across northern Europe, which has been reviewed and discussed here.

#### **Are there sufficient areas of suitable habitat to sustain viable populations? (5.3)**

Releases into areas with low chances of success are counter-productive and may also be considered an animal welfare issue (Harrington *et al.*, 2013). The release region should have a large enough carrying capacity to accommodate an increase in population size and to sustain a viable population in the long term. Tried and tested modelling methods have been used in the first instance to identify areas of potentially suitable habitat. The models were parameterised with data from an expanding population of wildcats in a region (northern Europe) that has sufficiently similar environmental conditions to those in potential reintroduction regions. The most recent available GIS data have been used to further examine some of the potentially suitable reintroduction regions, and these are discussed. It is suggested that these data be ground-truthed with detailed fieldwork and further interrogation over the coming months before proceeding with further reintroduction plans. Further GIS modelling of habitat networks is recommended to identify probable routes for expansion from any potential reintroduction sites.

#### **Are plans in place to formally integrate stakeholder concerns and social acceptability into all phases and a participatory process for all groups that might be involved in or affected by releases? (6.7)**

Other land users and stakeholders should be consulted from the beginning to understand the potential human impacts and consequences of a translocation. The support of local stakeholders is an important factor in deciding whether it is acceptable to proceed. In light of recent, high-profile proposals to reintroduce Eurasian lynx (*L. lynx*) to Britain, many may view the smaller, more recently present, wildcat as a more preferable native *felid* for restoration to the contemporary British fauna. However, this cannot be taken for granted, and work to consult and engage with landowners and communities in any potential release region must be the highest priority. This should begin well in advance of any proposed reintroduction and local communities must be involved from the outset in a transparent and structured decision-making process.

Conflict management will not just be around the issues of potential predation: trap-neuter-vaccinate-return (TNVR) will be necessary, which can be controversial, and much can be learned from the experience of Scottish Wildcat Action in this area. Working with animal welfare charities will be vital. For example, with the Cats’ Protection League (CPL) and Royal Society for the Prevention of Cruelty to Animals (RSPCA), both of which have experience of promoting the responsible ownership of pet cats, neutering stray and feral cats, and helping with disease prevention.

***A PhD project began in September 2019 at the University of Exeter in partnership with Vincent Wildlife Trust and Durrell Wildlife Conservation Trust. This will carry out interdisciplinary work towards understanding the ecological and social feasibility and practicalities of wildcat restoration in Britain, and will inform the next stage of the process.***



### Has there been an evaluation of the risk that translocated animals may pose to the conservation interests of other species and habitats? (5; 6)

The guidelines state that the possible ecological roles of the focal species in any new environment should be carefully evaluated and that there should be an assessment of the risk that the translocated animals might pose to the conservation interests of other species or habitats in release areas. Globally, it is acknowledged that (domestic) cats are responsible for killing a huge number and range of other wildlife (Baker *et al.*, 2005), which includes small mammals and birds (Woods *et al.*, 2005; Blancher, 2013), many of which are endangered. In contrast to the native wildcat, domestic cats can achieve densities far higher than the natural carrying capacity of their environment because they are fed by humans and are not reliant on prey availability to meet their daily energy requirements (Beckerman *et al.*, 2007). The impact of the native wildcat would be expected to be minimal. However, this cannot be assumed. Once a shortlist of potential reintroduction sites has been agreed on, detailed risk assessments should be carried out for each, and the information used in the decision-making process on which, if any, is the most appropriate/acceptable.

In addition to the risks, the assessment of any translocation proposal should also identify potential benefits including ecological, social and economic impacts.

### Can enough animals be taken from a genetically appropriate source population or populations without detrimental effects? (5.5)

When sufficient stock is available, wild-born animals are preferable to captive-born animals for translocations (Griffith *et al.*, 1989), and releasing captive-bred carnivores is only recommended when there are no other alternatives (Miller *et al.*, 1999). Wild carnivores generally show higher survival and better adaptation to new environments than captive bred animals (Jule *et al.*, 2008). However, translocating sufficient numbers of wild caught individuals will not be possible for wildcats. Results of population viability analyses suggest a minimum of 40 animals is needed for a viable population of wildcats (Littlewood *et al.*, 2014). It will be necessary, therefore, to develop a captive breeding programme in England and Wales if reintroductions are to go ahead.

Captive breeding for reintroduction and reinforcement is a well-established conservation measure (McGowan *et al.* 2017; IUCN-SSC 2013), and release of captive bred animals is a conservation intervention that now needs to be considered in detail, providing there are suitable areas with minimal risk of hybridisation and other threats. Since the IUCN Policy Statement on Captive Breeding (1987) was published by the IUCN-SSC Captive Breeding Specialist Group, it has been recommended that when the population of vertebrate taxa falls below 1,000 individuals, swift cooperation between conservationists and captive breeding specialists takes place.

Captive breeding is a well-developed field in conservation and one in which Durrell Wildlife Conservation Trust has a long and successful history. With this wealth of expertise in intensive species-recovery programmes, in particular in captive breeding and species reintroductions, Durrell Wildlife Conservation Trust is developing a captive breeding strategy for the wildcat. This strategy document will be presented as a separate document in 2020. Scottish Natural Heritage (SNH) with the Royal Zoological Society of Scotland (RZSS) has established a captive breeding programme with the aim of supplementing the remaining wild-living wildcats in Scotland. There is a need for a co-ordinated approach between Scotland, England and Wales in order to ensure a medium to long-term strategy that balances the goals of wildcat restoration in all three countries with the best use of the finite captive bred stock that will be available.

Source populations should show characteristics based on genetic provenance, morphology, physiology and behaviour that are appropriate in comparison with remaining wild populations. A recent study of wildcat phylogeny found that British wildcat samples grouped together within a matrilineage with west Germany/central Europe. The results of the study suggest that ‘... the geographic origin of Holocene British wildcats can therefore be identified as the NW coast of France or Belgium and the likeliest glacial refugia for this species are the Iberian or Italian peninsulae.’ (Marr, 2017). Further discussion and expertise from conservation geneticists is needed as to the most appropriate origin of captive wildcats to complement the Scottish programme for conservation breeding in England and Wales and releases across Britain. The objectives of the programmes in all three countries should be aligned.

### Recommendation of priority areas

The results presented here suggest three areas that might have the optimal combination of high habitat suitability, relatively low (for southern Britain) densities of human population, roads and traffic, and minimal potential conflict with other land uses. These are in north Wales, west Wales and south-west England. It is suggested that these are prioritised for further investigation.

The potential impacts on wildcats of the increased traffic flow and physiological stress of seasonal increases in visitor numbers at popular destinations should be considered in some of these regions, particularly north Wales (Snowdonia National Park), north Devon and Cornwall, which are all popular tourist destinations in the summer months.

Evidence from the continent, where some wildcat populations are now expanding, shows that it is possible to maintain the genetic integrity of wildcat populations even in landscapes shared with domestic cats (Steyer *et al.*, 2018). Studies across the range of the European wildcat have shown that there is a high degree of variability in the extent of admixture and introgression with domestic cats. High levels (up to 45%) of hybridisation have been reported in Hungary and Scotland (Randi, 2008; Beaumont *et al.*, 2001; Daniels *et al.*, 2001; Pierpaoli *et al.*, 2003; Lecis *et al.*, 2006), while low levels (between 0 and 2%) of interbreeding with domestic cats have been shown in Germany, Italy and Portugal (Lecis *et al.*, 2006; Pierpaoli *et al.*, 2003; Randi *et al.*, 2001; Oliveira *et al.*, 2008a). The direction of the gene flow also varies, with some studies reporting a gene flow from domestic cats to wildcats (Oliveira *et al.*, 2008b; Nussberger *et al.*, 2014; Quilodrán *et al.*, 2019), while others show the opposite with a detected flow from wildcats to domestic cats (Hertwig *et al.*, 2009).

Hybridisation and introgression are expected in two circumstances – under severe declines, when wildcat numbers are so low that opportunities for mating with conspecifics are scarce (French *et al.*, 1988) and, as a consequence of range expansion, where individuals dispersing away from the core population are more likely to encounter heterospecifics, in this case domestic cats, at the colonisation front. Studies that support this have been reported for wildcats (Nussberger *et al.*, 2014; Randi, 2008) and other species, eg, Costa *et al.*, 2013; Godinho *et al.*, 2011.

However, less clear patterns of hybridisation have also been reported for wildcats (Steyer *et al.*, 2018; Say *et al.*, 2012). When habitat fragmentation is low and/or populations are sufficiently robust, spatial overlap between wildcats and domestic cats may be fairly limited (Germain *et al.*, 2008; Gil-Sánchez *et al.*, 2015), in which case hybridisation would result only from occasional encounters. Nonetheless, in areas with highly fragmented habitat or high human population densities, wildcats may be forced into closer proximity to human associated habitat where domestic cats are more abundant and therefore interactions between wild and domestic cats will be more common.



Klar *et al.* (2008) showed that wildcats avoided human structures, however, both Scott *et al.* (1993) in Scotland, and Jerosch *et al.* (2010) found that wildcats might tolerate the presence of humans through habituation. It is important to better understand the relationship between wildcats and human presence in areas that are heavily influenced by humans, as these regions may be particularly prone to hybridisation due to contact with domestic cats (Nowell and Jackson, 1996; Daniels *et al.*, 1998; Yamaguchi *et al.*, 2004; O'Brien *et al.*, 2009; Macdonald *et al.*, 2010).

Initial reintroduced wildcat populations will, of necessity, be relatively small and therefore likely to be much more vulnerable to hybridisation at this stage. Therefore, it is of paramount importance that reintroductions are initially to regions of high habitat suitability where human (and by association) domestic and feral cat density is lowest.

Despite the fact that the amount of broad-leaved and mixed woodland was the most important variable for wildcats at the 10km square scales, wildcats may benefit from heterogeneity within the landscape at finer scales. It is reported that wildcats use a wide variety of habitats, displaying both individual and seasonal variation in habitat selection (Oliveira *et al.*, 2018). Lozano *et al.* (2003) found that wildcats were mainly associated with mosaics of scrublands and pasturelands at a landscape scale or to areas where shrub cover was high at a microhabitat scale. Watercourse abundance was also associated with wildcat occurrence, as was rabbit abundance. Scrubland is rich in prey such as rodents and rabbits and also provides shelter. In a heterogeneous landscape in northern France, with a fine scale mosaic of habitats, home ranges of related female wildcats were found to be spatially close and even, in some cases, overlapping, leading the authors to suggest that prey might be sufficiently abundant in this type of landscape for females to tolerate range overlap (Beugin *et al.*, 2018). Reintroductions to highly productive landscapes will be important in order to maximise breeding success and survival of kittens and to maintain wildcat populations at densities above a threshold at which hybridisation is likely.

Decisions now need to be made regarding (1) if and where to release individuals (2) where to source individuals and (3) how to plan and manage the translocation. These decisions will form the basis of future reintroduction plans.



Figure 13 Example of the heterogeneous mosaic of woodland, river valleys and small fields in one of the regions predicted as having high habitat suitability for wildcats.

# References

- Aaris-Sørensen, J., 1995, January. Road-kills of badgers (*Meles meles*) in Denmark. In *Annales Zoologici Fennici* (pp. 31-36). Finnish Zoological and Botanical Publishing Board.
- Aegerter, J., Fouracre, D. & Smith, G. C. 2017. A first estimate of the structure and density of the populations of pet cats and dogs across Great Britain. *PloS one*, 12, e0174709.
- Alexander, S. M., Waters, N. M. & Paquet, P. C. 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. *Canadian Geographer/Le Géographe canadien*, 49, 321-331.
- Arck, P. C., Merali, F. S., Stanisz, A. M., Stead, R. H., Chaouat, G., Manuel, J. & Clark, D. A. 1995. Stress-induced murine abortion associated with substance P-dependent alteration in cytokines in maternal uterine decidua. *Biology of reproduction*, 53, 814-819.
- Armour, C. J. & Thompson, H. V. 1955. Spread of myxomatosis in the first outbreak in Great Britain. *Annals of applied Biology*, 43, 511-518.
- Armstrong, D. P., Davidson, R. S., Dimond, W. J., Perrott, J. K., Castro, I., Ewen, J. G., Griffiths, R. & Taylor, J. 2002. Population dynamics of reintroduced forest birds on New Zealand islands. *Journal of Biogeography*, 29, 609-621.
- Baker, P. J., Bentley, A. J., Ansell, R. J. & Harris, S. 2005. Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, 35, 302-312.
- Balharry, D. 1993. Factors affecting the distribution and population density of pine martens (*Martes martes L.*) in Scotland. PhD, University of Aberdeen.
- Balharry, D. & Daniels, M. J. 1998. Wild living cats in Scotland. SNH Research Survey and Monitoring Report.
- Balharry, E., Staines, B. W., Marquiss, M., Kruuk, H. & Branch, C. 1994. Hybridisation in British mammals. JNCC report, 154.
- Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M. & Manica, A. 2009. A global perspective on trends in nature-based tourism. *PLoS biology*, 7, e1000144.
- Battersby, J. (Ed) & Tracking Mammals Partnership (2005). UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough.
- Beaumont, M. A., Barratt, E. M., Gottelli, D., Kitchener, A. C., Daniels, M. J., Pritchard, J. K. & Bruford, M. W. 2001. Genetic diversity and introgression in the Scottish wildcat. *Molecular ecology*, 10, 319-336.
- Beckerman, A. P., Boots, M. & Gaston, K. J. 2007. Urban bird declines and the fear of cats. *Animal Conservation*, 10, 320-325.
- Bellamy, C., Scott, C. & Altringham, J. 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *Journal of Applied Ecology*, 50, 892-901.
- Beugin, M-P., Leblanc, G., Queney, G., Natoli, E. & Pontier, D. 2016. Female in the inside, male in the outside: insights into the spatial organization of a European wildcat population. *Conservation genetics*, 17, 1405-1415.
- Beugin, M-P., Salvador, O., Leblanc, G., Queney, G., Natoli, E. & Pontier, D. 2018. Contrasted hybridization patterns between two local populations of European wildcats in France. *BioRxiv*, 342576.
- Biró, Zs., Lanszki, J., Szemethy, L., Heltai, M. & Randi, E. 2005. Feeding habits of feral domestic cats (*Felis catus*), wild cats (*Felis silvestris*) and their hybrids: trophic niche overlap among cat groups in Hungary. *Journal of Zoology*, 266, 187-196.
- Blancher, P. 2013. Estimated number of birds killed by house cats (*Felis catus*) in Canada. *Avian Conservation and Ecology*, 8.



Bradshaw, J. W. S., Horsfield, G. F., Allen, J. A. & Robinson, I. H. 1999. Feral cats: their role in the population dynamics of *Felis catus*. Applied Animal Behaviour Science, 65, 273-283.

Breitenmoser, U., Lanz, T. & Breitenmoser-Würsten, C. 2019. Conservation of the wildcat (*Felis silvestris*) in Scotland: Review of the conservation status and assessment of conservation activities.

Burnham, K. P. & Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Ecological Modelling. Springer Science & Business Media, New York, New York, USA.

Calvete, C. 2006. Modeling the effect of population dynamics on the impact of rabbit hemorrhagic disease. Conservation Biology, 20, 1232-1241.

Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature, 402, 286.

Commission, C. O. T. E. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities. Series L, 206, 7-49.

Condé, B. & Schauenberg, P. 1971. Le poids du Chat forestier d'Europe (*Felis silvestris* Schreber, 1777). Rev. Suisse Zool, 78, 295-315.

Converse, S. J., Moore, C. T., Folk, M. J. & Runge, M. C. 2013. A matter of tradeoffs: reintroduction as a multiple objective decision. The Journal of Wildlife Management, 77, 1145-1156.

Cook, C. N., Morgan, D. G. & Marshall, D. J. 2010. Reevaluating suitable habitat for reintroductions: lessons learnt from the eastern barred bandicoot recovery program. Animal Conservation, 13, 184-195.

Corbett, L. K. 1979. Feeding ecology and social organisation of wildcats (*Felis silvestris*) and domestic cats (*F. catus*) in Scotland. Unpublished PhD thesis, Aberdeen University.

Costa, M., Fernandes, C., Birks, J. D., Kitchener, A. C., Santos-Reis, M. & Bruford, M. W. 2013. The genetic legacy of the 19th-century decline of the British polecat: Evidence for extensive introgression from feral ferrets. Molecular ecology, 22, 5130-5147.

Cushman, S. A. & McGarigal, K. 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. Oikos, 105, 117-124. Daniels, M. J., Balharry, D., Hirst, D., Kitchener, A. C., & Aspinall, R. J. 1998. Morphological and pelage characteristics of wild living cats in Scotland: implications for defining the 'wildcat'. Journal of Zoology, 244, 231-247.

Daniels, M. J. 1997. The biology and conservation of the wildcat in Scotland. University of Oxford.

Daniels, M. J., Beaumont, M. A., Johnson, P. J., Balharry, D., Madonald, D. W. & Barratt, E. 2001. Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat. Journal of Applied Ecology, 38, 146-161.

Daniels, M. J., Wright, T. C., Bland, K. P. & Kitchener, A. C. 2002. Seasonality and reproduction in wild-living cats in Scotland. Acta theriologica, 47, 73-84.

Davis, A. R. & Gray, D. 2010. The distribution of Scottish wildcats (*Felis silvestris*) in Scotland (2006-2008). Scottish Natural Heritage Commissioned Report No. 360.

Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., Harley, E. H., Delibes, M., Pontier, D. & Kitchener, A. C. 2007. The Near Eastern origin of cat domestication. Science, 317, 519-523.

Easterbee, N., Hepburn, L. V. & Jeffries, D. J. 1991. Survey of the status and distribution of the wildcat in Scotland, 1983-1987, Nature Conservancy Council for Scotland.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettemann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S., & Zimmerman, N. E. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129-151.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. & Yates, C. J. 2010. A statistical explanation of MaxEnt for ecologists. Diversity and distributions, 17, 43-57.

European Environment Agency 2007. CORINE land cover data.

Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. 2012. Reintroduction biology: integrating science and management, Wiley Online Library.

Ferreira, J. P., Leitão, I., Santos-Reis, M. & Revilla, E. 2011. Human-related factors regulate the spatial ecology of domestic cats in sensitive areas for conservation. PLoS One, 6, e25970.

Ferreira, J. P. 2010. Integrating anthropic factors into wildcat *Felis silvestris* conservation in Southern Iberia landscapes. PhD, University of Lisbon.

Fischer, J. & Lindenmayer, D. B. 2000. An assessment of the published results of animal relocations. Biological conservation, 96, 1-11.

Forrester, N. L., Boag, B., Buckley, A., Moureau, G. & Gould, E. A. 2009. Co-circulation of widely disparate strains of rabbit haemorrhagic disease virus could explain localised epidemics in the United Kingdom. Virology, 393, 42-48.

Fourcade, Y., Engler, J. O., Rödder, D. & Secondi, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PloS one, 9, e97122.

French, D. D., Corbett, L. K. & Easterbee, N. 1988. Morphological discriminants of Scottish wildcats (*Felis silvestris*), domestic cats (*F. catus*) and their hybrids. Journal of Zoology, 214, 235-259.

Germain, E., Benhamou, S. & Poulle, M-L. 2008. Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. Journal of Zoology, 276, 195-203.

Germano, J. M. & Bishop, P. J. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology, 23, 7-15.

Gibson, L., Barrett, B. & Burbidge, A. 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. Diversity and Distributions, 13, 704-713.

Gil-Sánchez, J. M. 1998. Dieta comparada del gato montés (*Felis silvestris*) y la jineta (*Genetta genetta*) en un área de simpatria de las Sierras Subbéticas (SE España). Miscel·lània Zoològica, 21, 57-64.

Gil-Sánchez, J. M., Jaramillo, J. & Barea-Azcón, J. M. 2015. Strong spatial segregation between wildcats and domestic cats may explain low hybridization rates on the Iberian Peninsula. Zoology, 118, 377-385.

Girvetz, E. H. & Greco, S. E. 2009. Multi-scale predictive habitat suitability modeling based on hierarchically delineated patches: an example for yellow-billed cuckoos nesting in riparian forests, California, USA. Landscape Ecology, 24, 1315-1329.

Godinho, R., Llana, L., Blanco, J. C., Lopes, S., Álvares, F., Garcia, E. J., Palacios, V., Cortés, Y., Talegón, J. & Ferrand, N. 2011. Genetic evidence for multiple events of hybridization between wolves and domestic dogs in the Iberian Peninsula. Molecular Ecology, 20, 5154-5166.

Government, H. M. 2018. A Green Future: Our 25 Year Plan to Improve the Environment. HM Government.

Gow, D. & Cooper, P. 2018. A strategy for the reintroduction of the wild cat (*Felis silvestris*) to England.

Graf, R. F., Bollmann, K., Suter, W. & Bugmann, H. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. Landscape Ecology, 20, 703-717.

Graham, C. H., Elith, J., Hijmans, R. J., Guisan, A., Townsend Peterson, A., Loiselle, B. A. & Group, N. P. S. D. W. 2008. The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology, 45, 239-247.

Griffith, B., Scott, J. M., Carpenter, J. W. & Reed, C. 1989. Translocation as a species conservation tool: status and strategy. Science, 245, 477-480.

Griffiths, R. A. & Pavajeau, L. 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conservation Biology, 22, 852-861.

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernado, J., Reto, D., Lourenço, R., Santos-Reis, M., & Revilla, E. 2012. Individual spatial responses towards roads: implications for mortality risk. PLoS One, 7, e43811.

Gunson, K. E., Mountrakis, G. & Quackenbush, L. J. 2011. Spatial wildlife-vehicle collision models: a review of current work and its application to transportation mitigation projects. Journal of environmental management, 92, 1074-1082.

Harrington, L. A., Moehrensclager, A., Gelling, M., Atkinson, R. P., Hughes, J. & Macdonald, D. W. 2013. Conflicting and complementary ethics of animal welfare considerations in reintroductions. Conservation Biology, 27, 486-500.



Harris, S., Yalden, D. W. & Society, M. 2008. Mammals of the British Isles: Handbook, Mammal Society.

Hartmann, S. A., Steyer, K., Kraus, R. H., Segelbacher, G. & Nowak, C. 2013. Potential barriers to gene flow in the endangered European wildcat (*Felis silvestris*). Conservation Genetics, 14, 413-426.

Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., Soto, A., Swenson, J. J., Tovar, C. & Valqui, T. H. 2008. Predicting species distributions in poorly-studied landscapes. Biodiversity and Conservation, 17, 1353-1366.

Hernandez, P. A., Graham, C. H., Master, L. L. & Albert, D. L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography, 29, 773-785.

Hertwig, S. T., Schweizer, M., Stepanow, S., Jungnickel, A., Böhle, U-R. & Fischer, M. S. 2009. Regionally high rates of hybridization and introgression in German wildcat populations (*Felis silvestris*, *Carnivora*, *Felidae*). Journal of Zoological Systematics and Evolutionary Research, 47, 283-297.

Hetherington, D., Bryce, J. & Cole, M. 2016. The Species Action Framework Handbook. In: Gaywood, M. J., Boon, P. J., Thompson, D. B. & Strachan, I. M. (eds.) The Species Action Framework Handbook. Battleby, Perth: Scottish Natural Heritage.

Hobson, K. J. 2012. An investigation into prey selection in the Scottish wildcat (*Felis silvestris silvestris*). MSc, Imperial College London.

Hof, A. R., Jansson, R. & Nilsson, C. 2012. The usefulness of elevation as a predictor variable in species distribution modelling. Ecological Modelling, 246, 86-90.

Hubbard, A. L., McOris, S., Jones, T. W., Boid, R., Scott, R. & Easterbee, N. 1992. Is survival of European wildcats (*Felis silvestris*) in Britain threatened by interbreeding with domestic cats? Biological Conservation, 61, 203-208.

IUCN 1995. Guidelines for reintroductions. Gland, Switzerland: Reintroduction Specialist Group.

IUCN 2013. Guidelines for Reintroductions and Other Conservation Translocations. Gland, Switzerland: IUCN Species Survival Commission.

Jancke, S. & Giere, P. 2011. Patterns of otter *Lutra lutra* road mortality in a landscape abundant in lakes. European journal of wildlife research, 57, 373-381.

Jerosch, S., Götz, M., Klar, N. & Roth, M. 2010. Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): Implications for its conservation. Journal for Nature Conservation, 18, 45-54.

Jule, K. R., Leaver, L. A. & Lea, S. E. G. 2008. The effects of captive experience on reintroduction survival in carnivores: a review and analysis. Biological conservation, 141, 355-363.

Keeney, R. L. 1982. Decision analysis: an overview. Operations research, 30, 803-838.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B. & Hornocker, M. G. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology, 16, 97-108.

Kilshaw, K. 2011. Scottish wildcats, Scottish Natural Heritage.

Kilshaw, K., Montgomery, R. A., Campbell, R. D., Hetherington, D. A., Johnson, P. J., Kitchener, A. C., Macdonald, D. W. & Millspaugh, J. J. 2016. Mapping the spatial configuration of hybridization risk for an endangered population of the European wildcat (*Felis silvestris silvestris*) in Scotland. Mammal Research, 61, 1-11.

Kitchener, A. 1992. The Scottish wildcat (*Felis silvestris*): decline and recovery. In: Cats. Ed. by P. Mansard. Hastings: The Ridgeway Trust for Endangered Cats, 21-41.

Kitchener, A. C. & Rees, E. E. 2009. Modelling the dynamic biogeography of the wildcat: implications for taxonomy and conservation. Journal of Zoology, 279, 144-155.

Kitchener, A. C., Yamaguchi, N., Ward, J. M. & Macdonald, D. W. A diagnosis for the Scottish wildcat (*Felis silvestris*): a tool for conservation action for a critically-endangered felid. Animal Conservation forum, 2005. Cambridge University Press, 223-237.

Klar, N., Fernández, N., Kramer-Schadt, S., Herrmann, M., Trinzen, M., Büttner, I. & Niemitz, C. 2008. Habitat selection models for European wildcat conservation. Biological Conservation, 141, 308-319.

Klar, N., Herrmann, M. & Kramer-Schadt, S. 2009. Effects and mitigation of road impacts on individual movement behavior of wildcats. The journal of wildlife management, 73, 631-638.

Koreň, M., Find'ó, S., Skuban, M. & Kajba, M. 2011. Habitat suitability modelling from non-point data: the case study of brown bear habitat in Slovakia. Ecological Informatics, 6, 296-302.

Kramer-Schadt, S. T., Revilla, E., Wiegand, T., Breitenmoser, U.R. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. Journal of Applied Ecology. 2004 Aug;41(4):711-23.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A. K., Augeri, D. M., Cheyne, S.M., Hearn, A.J., Ross, J., Macdonald, D.W., Mathai, J., Eaton, J., Marshall, A.J., Rustam, G.S., Bernard, R., Alfred, H. Samejima, R., Duckworth, H.J.W., Belant, C.B.W., Hofer, J. L. & Wilting, A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions, 19, 1366-1379.

La Morgia, V., Malenotti, E., Badino, G. & Bona, F. 2011. Where do we go from here? Dispersal simulations shed light on the role of landscape structure in determining animal redistribution after reintroduction. Landscape ecology, 26, 969-981.

Langley, P. J. W. & Yalden, D. W. 1977. The decline of the rarer carnivores in Great Britain during the nineteenth century. Mammal Review, 7, 95-116.

Lecis, R., Pierpaoli, M., Birò, Z. S., Szemethy, L., Ragni, B., Vercillo, F. & Randi, E. 2006. Bayesian analyses of admixture in wild and domestic cats (*Felis silvestris*) using linked microsatellite loci. Molecular Ecology, 15, 119-131.

Léger, F., Stahl, P., Ruetten, S. & Wilhelm, J-L. 2008. La répartition du chat forestier en France: évolutions récentes. Faune sauvage, 280, 24-39.

Littlewood, N. A., Campbell, R. D., Dinnie, L., Gilbert, L., Hooper, R., Iason, G., Irvine, J., Kilshaw, K., Kitchener, A. C., Lackova, P., Newey, S., Ogden, R., & Ross, A. 2014. Survey and scoping of wildcat priority areas. Scottish Natural Heritage.

Lozano, J., Moleón, M. & Virgós, E. 2006. Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. Journal of Biogeography, 33, 1076-1085.

Lozano, J., Virgós, E., Malo, A. F., Huertas, D. L. & Casanovas, J. G. 2003. Importance of scrub-pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (*Felis silvestris*). Biodiversity & Conservation, 12, 921-935.

Macdonald, D. W., Daniels, M. J., Driscoll, C., Kitchener, A. C. & Yamaguchi, N. 2004. The Scottish Wildcat: Analyses for Conservation and an Action Plan.,(Wildlife Conservation Research Unit: Oxford, UK.).

Macdonald, D. W., Yamaguchi, N., Kitchener, A. C., Daniels, M. J., Kilshaw, K. & Driscoll, C. 2010. Reversing cryptic extinction: the history, present and future of the Scottish Wildcat. Biology and conservation of wild felids, 471-492.

MacPherson, J. L., Croose, E., Bavin, D., O'Mahony, D., Somper, J. & Buttriss, N. 2014. Feasibility assessment for reinforcing pine marten numbers in England and Wales. Ledbury: The Vincent Wildlife Trust.

Magdalena Wolf, C., Garland Jr, T. & Griffith, B. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological conservation, 86, 243-255.

Malo, A. F., Lozano, J., Huertas, D. L. & Virgós, E. 2004. A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? Journal of Zoology, 263, 401-407.

Marr, M. M. 2017. Faunal response to abrupt climate change: the history of the British mammal fauna from the Lateglacial to the Holocene. Doctor of Philosophy PhD, Royal Holloway University of London.

Martinez-Meyer, E., Peterson, A. T., Servín, J. I. & Kiff, L. F. 2006. Ecological niche modelling and prioritizing areas for species reintroductions. Oryx, 40, 411-418.

Mateo Sánchez, M. C., Cushman, S. A. & Saura, S. 2014. Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). International Journal of Geographical Information Science, 28, 1531-1546.

Mattucci, F. 2014. Conservation genetics of European wildcat (*Felis silvestris silvestris*): a wide and integrating analysis protocol for admixture inferences and population structure. PhD, University of Bologna.



Mattucci, F., Oliveira, R., Lyons, L. A., Alves, P. C. & Randi, E. 2016. European wildcat populations are subdivided into five main biogeographic groups: consequences of Pleistocene climate changes or recent anthropogenic fragmentation? Ecology and evolution, 6, 3-22.

McCune, B., Grace, J. B. & Urban, D. L. 2002. Analysis of ecological communities, MjM software design Gleneden Beach, OR.

McGowan, P.J., Traylor-Holzer, K. and Leus, K., 2017. IUCN guidelines for determining when and how ex situ management should be used in species conservation. Conservation Letters, 10(3), pp.361-366.

McOrist, S. & Kitchener, A. C. 1994. Current threats to the European wildcat, *Felis silvestris*, in Scotland. Ambio (Sweden).

Mermod, C. P. & Liberek, M. 2002. The role of snowcover for European wildcat in Switzerland. Zeitschrift für Jagdwissenschaft, 48, 17-24.

Miller, B., Ralls, K., Reading, R. P., Scott, J. M. & Estes, J. Biological and technical considerations of carnivore translocation: a review. Animal Conservation forum, 1999. Cambridge University Press, 59-68.

Moleón, M. & Gil-Sánchez, J. M. 2003. Food habits of the wildcat (*Felis silvestris*) in a peculiar habitat: the Mediterranean high mountain. Journal of Zoology, 260, 17-22.

Montanha, J. C., Silva, S. L. & Boere, V. 2009. Comparison of salivary cortisol concentrations in Jaguars kept in captivity with differences in exposure to the public. Ciência Rural, 39, 1745-1751.

Monterroso, P., Brito, J. C., Ferreras, P. & Alves, P. C. 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. Journal of Zoology, 279, 27-35.

Nepomnaschy, P. A., Welch, K. B., McConnell, D. S., Low, B. S., Strassmann, B. I. & England, B. G. 2006. Cortisol levels and very early pregnancy loss in humans. Proceedings of the National Academy of Sciences, 103, 3938-3942.

NGO 2011. Gamekeepers and Wildlife. Darlington: National Gamekeepers' Organisation.

Ngoprasert, D., Lynam, A. J. & Gale, G. A. 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. Oryx, 41, 343-351.

Nowell, K. & Jackson, P. 1996. Wild cats: status survey and conservation action plan, IUCN Gland.

Nussberger, B., Wandeler, P., Weber, D. & Keller, L. 2014. Monitoring introgression in European wildcats in the Swiss Jura. Conservation genetics, 15, 1219-1230.

O'Brien, J., Devillard, S., Say, L., Vanthomme, H., Léger, F., Ruetter, S. & Pontier, D. 2009. Preserving genetic integrity in a hybridising world: are European Wildcats (*Felis silvestris silvestris*) in eastern France distinct from sympatric feral domestic cats? Biodiversity and Conservation, 18, 2351-2360.

Oliveira, R., Godinho, R., Randi, E. & Alves, P. C. 2008a. Hybridization versus conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian Peninsula? Philosophical Transactions of the Royal Society B: Biological Sciences, 363, 2953-2961.

Oliveira, R., Godinho, R., Randi, E., Ferrand, N. & Alves, P. C. 2008b. Molecular analysis of hybridisation between wild and domestic cats (*Felis silvestris*) in Portugal: implications for conservation. Conservation Genetics, 9, 1-11.

Oliveira, T., Urra, F., López-Martín, J. M., Ballesteros-Duperón, E., Barea-Azcón, J. M., Moleón, M., Gil-Sánchez, J. M., Alves, P. C., Díaz-Ruiz, F., Ferreras, P. & Monterroso, P. 2018. Females know better: Sex-biased habitat selection by the European wildcat. Ecology and evolution, 8, 9464-9477.

Osborne, P. E. & Seddon, P. J. 2012. Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. In: Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (eds.) Reintroduction Biology: Integrating Science and Management. Wiley.

Ovaskainen, O. 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. Ecology, 85, 242-257.

46 Pearson, R. G., Raxworthy, C. J., Nakamura, M. & Townsend Peterson, A. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of biogeography, 34, 102-117.

Peel, M. C., Finlayson, B. L. & McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and earth system sciences discussions, 4, 439-473.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M. & Araújo, M. B. 2011. Ecological niches and geographic distributions (MPB-49), Princeton University Press.

Philcox, C. K., Grogan, A. L. & Macdonald, D. W. 1999. Patterns of otter (*Lutra lutra*) road mortality in Britain. Journal of applied Ecology, 36, 748-761.

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. & Blair, M. E. 2017. Opening the black box: an open-source release of Maxent. Ecography, 40, 887-893.

Phillips, S. J., Anderson, R. P., Dudík, M. & Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling, 190, 231-259.

Phillips, S. J. & Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31, 161-175.

Pierpaoli, M., Birò, Z., Herrmann, M., Hupe, K., Fernandes, M., Ragni, B., Szemethy, L. & Randi, E. 2003. Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. Molecular Ecology, 12, 2585-2598.

Piñeiro, A., Barja, I., Silván, G. & Illera, J. C. 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildlife Research, 39, 532-539.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology letters, 3, 349-361.

Quilodrán, C. S., Nussberger, B., Montoya-Burgos, J. I. & Currat, M. 2019. Hybridization and introgression during density-dependent range expansion: European wildcats as a case study. Evolution.

Randi, E. 2008. Detecting hybridization between wild species and their domesticated relatives. Molecular ecology, 17, 285-293.

Randi, E., Pierpaoli, M., Beaumont, M., Ragni, B. & Sforzi, A. 2001. Genetic identification of wild and domestic cats (*Felis silvestris*) and their hybrids using Bayesian clustering methods. Molecular Biology and Evolution, 18, 1679-1693.

Rees, P. A. 2001. Is there a legal obligation to reintroduce animal species into their former habitats? Oryx, 35, 216-223.

Reynolds-Hogland, M.J. and Mitchell, M.S., 2007. Effects of roads on habitat quality for bears in the southern Appalachians: a long-term study. Journal of Mammalogy, 88(4), pp.1050-1061.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G. X. & McDonald, R. A. 2012. Ecosystem restoration with teeth: what role for predators? Trends in ecology & evolution, 27, 265-271.

Ross, J. & Sanders, M. F. 1984. The development of genetic resistance to myxomatosis in wild rabbits in Britain. Epidemiology & Infection, 92, 255-261.

Sainsbury, A. W. & Vaughan-Higgins, R. J. 2012. Analyzing disease risks associated with translocations. Conservation Biology, 26, 442-452.

Say, L., Devillard, S., Léger, F., Pontier, D. & Ruetter, S. 2012. Distribution and spatial genetic structure of European wildcat in France. Animal Conservation, 15, 18-27.

Scott, R., Easterbee, N. & Jefferies, D. A radio-tracking study of wildcats in western Scotland. Seminar on the biology and conservation of the wildcat, 23-25 September 1992 1993a Nancy, France. Council of Europe, Strasbourg, France, 94-97.

Scott, R., Easterbee, N. & Jefferies, D. A radio-tracking study of wildcats in western Scotland. Proc. Seminar on the biology and conservation of the wildcat, 1993b.

Seddon, P. J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology, 18, 796-802.

Seddon, P. J., Armstrong, D. P. & Maloney, R. F. 2007. Developing the science of reintroduction biology. Conservation biology, 21, 303-312.

Seddon, P. J., Moehrensclager, A. & Ewen, J. 2014. Reintroducing resurrected species: selecting DeExtinction candidates. Trends in ecology & evolution, 29, 140-147.

Senn, H. V., Ghazali, M., Kaden, J., Barclay, D., Harrower, B., Campbell, R. D., Macdonald, D. W. & Kitchener, A. C. 2019. Distinguishing the victim from the threat: SNP-based methods reveal the extent of introgressive hybridization between wildcats and domestic cats in Scotland and inform future in situ and ex situ management options for species restoration. Evolutionary applications, 12, 399-414.



SFEPM 1984. Atlas des mammifères sauvages de France, Paris, SFEPM.

Shirk, A. J., Raphael, M. G. & Cushman, S. A. 2014. Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). *Ecological Applications*, 24, 1434-1444.

Shirk, A. J., Wasserman, T. N., Cushman, S. A. & Raphael, M. G. 2012. Scale dependency of American marten (*Martes americana*) habitat relations [Chapter 12]. In: Aubry, Keith B.; Zielinski, William J.; Raphael, Martin G.; Proulx, Gilbert; Buskirk, Steven W., eds. *Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis*. Cornell University Press. p. 269-283., 269-283.

Silva, A. P., Kilshaw, K., Johnson, P. J., Macdonald, D. W. & Rosalino, L. M. 2013a. Wildcat occurrence in Scotland: food really matters. *Diversity and Distributions*, 19, 232-243.

Silva, A. P., Rosalino, L. M., Johnson, P. J., Macdonald, D. W., Anderson, N. & Kilshaw, K. 2013b. Local-level determinants of wildcat occupancy in Northeast Scotland. *European journal of wildlife research*, 59, 449-453.

Snyder, N.F., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D. and Miller, B., 1996. Limitations of captive breeding in endangered species recovery. *Conservation biology*, 10(2), pp.338-348.

Stabach, J. A., Laporte, N. & Olupot, W. 2009. Modeling habitat suitability for Grey Crowned-cranes (*Balearica regulorum gibbericeps*) throughout Uganda. *International Journal of Biodiversity and Conservation*, 1, 177-186.

Stahl, P. & Artois, M. 1994. Status and Conservation of the Wildcat (*Felis silvestris*) in Europe and around the Mediterranean Rim. *Nature and Environment Series 69*. Strasbourg: Council of Europe Press.

Stahl, P. & Léger, F. 1992. Le chat sauvage d'Europe: (*Felis silvestris* Schreber, 1777), Société française pour l'étude et la protection des mammifères.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging theory*, Princeton University Press.

Steyer, K., Tiesmeyer, A., Muñoz-Fuentes, V. & Nowak, C. 2018. Low rates of hybridization between European wildcats and domestic cats in a human-dominated landscape. *Ecology and Evolution*, 8, 2290-2304.

Sunquist, M. & Sunquist, F. 2002. European wildcat *Felis silvestris silvestris*. *Wild Cats of the World*, 85-91.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science*, 240, 1285-1293.

Syfert, M. M., Smith, M. J. & Coomes, D. A. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PloS one*, 8, e55158.

Tapper, S. C. 1992. *Game heritage: an ecological review from shooting and gamekeeping records*, Game Conservancy Fordingbridge, UK.

Terio, K. A., Marker, L. & Munson, L. 2004. Evidence for chronic stress in captive but not free-ranging cheetahs (*Acinonyx jubatus*) based on adrenal morphology and function. *Journal of Wildlife Diseases*, 40, 259-266.

Trout, R. C., Chasey, D. & Sharp, G. 1997. Seroepidemiology of rabbit haemorrhagic disease (RHD) in wild rabbits (*Oryctolagus cuniculus*) in the United Kingdom. *Journal of Zoology*, 243, 846-853.

Trout, R. C., Langton, S., Smith, G. C & Haines-Young, R. H. 2000. Factors affecting the abundance of rabbits (*Oryctolagus cuniculus*) in England and Wales. *Journal of Zoology*, 252, 227-238.

Trout, R. C., Ross, J., Tittensor, A. M. & Fox, A. P. 1992. The effect on a British wild rabbit population (*Oryctolagus cuniculus*) of manipulating myxomatosis. *Journal of Applied Ecology*, 679-686.

Trout, R. C., Tapper, S. C. & Harradine, J. 1986. Recent trends in the rabbit population in Britain. *Mammal Review*, 16, 117-123.

Van der Zee, F., Wiertz, J., Ter Braak, C., Van Apeldoorn, R. & Vink, J. 1992. Landscape change as a possible cause of the badger *Meles meles* L. decline in the Netherlands. *Biological Conservation*, 61, 17-22.

Vergara, M., Cushman, S. A., Urra, F. & Ruiz-González, A. 2016. Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula. *Landscape Ecology*, 31, 1241-1260.

Ward, D. F. 2007. Modelling the potential geographic distribution of invasive ant species in New Zealand. *Biological Invasions*, 9, 723-735.

Warren, D. L., Glor, R. E. & Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution: International Journal of Organic Evolution*, 62, 2868-2883.

Warren, D. L., Glor, R. E. & Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, 33, 607-611.

Warren, D. L. & Seifert, S. N. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological applications*, 21, 335-342.

Wasserman, T. N., Cushman, S. A., Wallin, D. O. & Hayden, J. 2012. Multi scale habitat relationships of *Martes americana* in northern Idaho, USA. Res. Pap. RMRS-RP-94. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 21 p., 94.

Watts, K. 2006. British forest landscapes: the legacy of woodland fragmentation. *Quarterly Journal of Forestry*, 100, 273-279.

White Jr, T. H., Collar, N. J., Moorhouse, R. J., Sanz, V., Stolen, E. D. & Brightsmith, D. J. 2012. Psittacine reintroductions: common denominators of success. *Biological Conservation*, 148, 106-115.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional ecology*, 3, 385-397.

Wolf, C. M., Griffith, B., Reed, C. & Temple, S. A. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation biology*, 10, 1142-1154.

Woods, M., McDonald, R. A. & Harris, S. 2005. Predation of wildlife by domestic cats in Great Britain. *Mammal Review*.

Yamaguchi, N., Kitchener, A., Driscoll, C. & Nussberger, B. 2015. *Felis silvestris*. The IUCN Red List of Threatened Species 2015: e. T60354712A50652361. URL: [http://dx. doi. org/10.2305/IUCN](http://dx.doi.org/10.2305/IUCN). UK.

Yamaguchi, N., Kitchener, A. C., Driscoll, C. A., Ward, J. M. & Macdonald, D. W. Craniological differentiation amongst wild-living cats in Britain and southern Africa: natural variation or the effects of hybridisation? *Animal Conservation forum*, 2004. Cambridge University Press, 339-351.





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