bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Numerical response of predators to large variations of grassland vole abundance, long-term community change and prey switches

Patrick Giraudoux[1,*], Aurélien Levret[2], Eve Afonso[1], Michael Coeurdassier[1], Geoffroy Couval[1,2]

1 Chrono-environnement, Université de Bourgogne Franche-Comté/CNRS usc INRA, 25030, Besançon Cedex, France.
2 FREDON Bourgogne Franche-Comté, 12 rue de Franche-Comté, 25480, Ecole-Valentin, France.

* patrick.giraudoux@univ-fcomte.fr

Abstract

Voles can reach high densities with multi-annual population fluctuations of large amplitude, and they are at the base of large and rich communities of predators in temperate and arctic food webs. This places them at the heart of management conflicts where crop protection and health concerns are often raised against conservation issues. Here, a 20-year survey describes the effects of large variations of grassland vole populations on the densities and the daily theoretical food intakes (TFI) of vole predators based on road-side counts. Our results show how the predator community responds to prey variations of large amplitude and how it reorganized with the increase of a dominant predator, here the red fox, which likely impacted negatively hare, European wildcat and domestic cat populations. They also indicate which subset of the predator species can be expected to have a key-role in vole population control in the critical phase of low density of grassland voles. Our study provides empirical support for more timely and better focused actions in wildlife management and vole population control, and shows why it implies evidence-based and constructive dialogue about management targets and options between all stakeholders of such socio-ecosystems.

Introduction

The relationship between people and rodents is an old one and early accounts show clearly that rodents were a destructive agent in the fields and a source of disease for many ancient and current societies [1–4]. Voles can reach high densities with multi-annual population fluctuations of large amplitude, and where they occur they are mainly considered as pests. However often persecuted for this reason [4, 5], their effects on biodiversity is of crucial importance. They are at the base of temperate and arctic food webs, maintaining large and rich communities of predators, and modifying nutrient cycling, soil aeration, and micro-organism assemblages [6]. This places them at the heart of management conflicts where crop protection and health concerns are often raised against conservation issues [5]. Moreover pest control, especially when using chemicals carelessly, by indirect poisoning, can non-intentionally depress the populations of predators able to contribute to the regulation of rodent populations [7, 8].

Predation has been suggested as one of the main drivers of rodent population fluctuations. Theory predict that specialist predators that feed on one or a few kinds of

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

prey can destabilize prey populations because they exert delayed- and direct density dependent mortality on their prey populations, while generalist predators, that feed on a wide variety of prey species, have direct density dependent mortality and therefore stabilize prey populations [9]. However, experimental tests of this prediction, e.g. predator removals and comparative field studies, have provided evidence both supporting and rejecting this hypothesis [10–15]. One of the world's simplest vertebrate predator/prey community is high-arctic tundra ecosystem. Its has only four predators preying upon one rodent species, the collared lemming (*Dicrostonyx groenlandicus*). There the numerical response of the stoat (*Mustela erminea*) drives the population dynamics of the collared lemming by a 1-year delay. this dynamics is concurrently stabilized by strongly density-dependent predation by the arctic fox (*Vulpes lagopus*), the snowy owl (*Bubo scandiacus*), and the long-tailed skua (*Stercorarius longicaudus*) [14, 16]. Studies in Fennoscandia on small mammal population cycles have accumulated support for the predation hypothesis [17]. Population dynamic patterns of the common vole (*Microtus arvalis*) in intensive agricultural landscapes of south-west France are largely consistent with five of six patterns that characterize rodent cycles in Fennoscandia and can be explained by the predation hypothesis [18]. Hence, there is little doubts that in European arctic and temperate ecosystems predation plays a key role in regulating small mammal population dynamics. However, in temperate ecosystems the multiplicity of prey-resources and the larger number of predator species combined to landscape diversity (e.g. the spatial arrangements of optimal and suboptimal habitats for prey and predators) [19, 20] make the disentangling of the detailed processes and the role of each species involved still a challenge [21].

Interactions between populations of various species in systems driven by predation are complex. For instance, based on a 20-year survey of the effects of an epidemic of sarcoptic mange decreasing fox populations in Scandinavia, Lindström *et al.* [22] revealed that red fox (*Vulpes vulpes*) predation was a crucial factor in limiting the populations of hare (*Lepus europeus*), capercaillie (*Tetrao urogallus*), and grouse (*Tetrao tetrix* and *Bonasia bonasia*), as well as fawns per doe of roe deer (*Capreolus capreolus*) in autumn, and in conveying the 3-4 year fluctuations of voles (both bank and field voles (*Myodes glareolus* and *Microtus agrestis*)) to small game. The importance of such prey switchings on prey population dynamics has also been reported since long in northern ecosystems of the Newfoundland, in Canada, where lynxes (*Lynx lynx*), prey on snowshoe hares (*Lepus americanus*), until the hare population crashes. Then, lynxes switch to caribou calves (*Rangifer tarandus*), and the cycle continues [23]. Furthermore, variations in prey and predator population densities also affect parasite transmission and shape disease epidemiology as shown e.g. for the common vole and tularemia in Spain [24] or the montane water vole (*Arvicola terrestris*), the red fox and *Echinococcus multilocularis* in the Jura massif, France [25, 26]. As a whole, those multiple and complex interactions can hardly be investigated in depth by simple modelling [27] or by small-scale experiments that cannot technically take into account all the relevant space-time scales and species involved in the real world and thus be generalized.

However, stakeholders in such systems are often protagonists of endless debates about regulation adoption and management decisions, each of them advocating for the control of one among many possible of the population targets and subsequent options for management. This debate is recurrently illustrated by controversies about large and mesopredator culling (e.g. wolf, fox, etc.) for 'desirable' prey protection (e.g. sheep, hare, etc.) as opposed to their protection for their role as regulator of 'undesirable' prey such as overpopulating cervids or small mammal pests [5, 28]. Due to the fascination they exert over the general public, the control of large or medium carnivores is generally unpopular whatever the reasons. By contrast the broad social acceptability of the control or exploitation of other species (e.g. rodents, lagomorphs), due to their lack of

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

charisma or low public visibility, and the lobbying of pro/anti, may lead to social consensus or political decisions that hinder evidence-based and targetted management options, and can even jeopardize biodiversity conservation (e.g. the protection of species of conservation value critically endangered sometimes threaten by prey switches) [29].

Instruments to help set local, national and global priorities in biodiversity conservation, pest and game management and disease control can be severely handicapped by a lack of sound observational data, collected through fieldwork [30], especially in complex multi-species and multi-functional systems where modelling fails (e.g. theoretical sub-systems oversimplified for mathematical convenience or lack of relevant external validation) and where experiments cannot be performed on space-time scales relevant for many of the species involved (large home-range, slow growth rate, etc.) for obvious practical and sometimes ethical reasons. However, our knowledge of the ecology and population dynamics of many common species and communities is still limited. Field-based investigations, including somehow despised 'observational' or 'correlative' studies are powerful allies of synthetic and comparative studies [30], providing crucial data that enable us to better identify key-factors driving those systems and inform decision-making across scales, design tests and modelling at the appropriate place and time, and make adaptive management, necessarily linked to adaptive monitoring [31], possible.

Such an approach has been successfully carried out in the Jura massif for small mammal pest control [32]. In this region of mid-altitude mountains (250-1718m), in the 1950s, grassland was covering only 20-60% of farmland whatever the altitude. Farmers in higher altitude areas (above 500 m a.s.l) specialized in milk production in the 1960s for the production of a number of Protected Geographical Indication cheese (Comté, Morbier, Mont d'Or, Bleu de Gex). This led to convert ploughed fields into permanent grassland and subsequently to increase the proportion of permanent grassland up to 75-100% of farmland in these areas, with, additionally, an increase in grass productivity from 2-3 tonnes of dry matter.ha^{-1}.year^{-1} in the 1950s to 4-9 tonnes nowadays (milk production itself shifted from less than 2000 liters.cow^{-1}.year^{-1} in 1951 to currently about 7000 liters in average (range 5400-8500)). As soon as the 1970s, this shift resulted in triggering massive outbreaks of a grassland vole species, the montane water vole, with 5-6 year cycles propagating over the grasslands of the Jura massif under the form of a travelling wave [33, 34]. In the same area, it also favoured outbreaks of the common vole, another grassland vole, however non-cyclic [6]. A number of field studies and modelling have shown that population dynamics of the two species was shaped by landscape features, with hedgerow networks and wood patches dampening the population dynamics and by contrast open grassland landscapes amplifying the outbreaks [33, 35–40]. Those observations permitted to shift rodent control from late and chemical-only (with devastating side-effects on non-targeted wildlife) in the 1980-1990s [41], to early and more environmentally-friendly multi-factorial control in the 2000s [7, 8] using an integrated approach based on the key factors previously identified in observational studies [32]. The successful results of this shift in practices with regard to pest control can be considered as a quasi-experiment, and confirmed that the correlations identified in earlier studies were not spurious. Those field studies also indicated that the population dynamics of all of the rodent species in the area were synchronic, with concomitant low density phases [42, 43]. Hence, after a tipping point in the 1960s from mixed agriculture to specialized milk production, the regional socio-ecosystem stabilized since the 1970s, with cyclic outbreaks of montane water vole and outbreaks of common vole. Those outbreaks provide regularly massive quantity (up to > 80kg.ha^{-1}) of prey for carnivores and birds of prey in grassland and by contrast low densities of secondary prey-resources less accessible (vegetation and/or anti-predation behaviour) like forest, marsh and fallow small mammals (maximum

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

about 3kg.ha^{-1}) (e.g. bank vole, wood mice, (*Apodemus* sp.), field vole, etc.), with periodic (5-6 years) concomitant low densities in every habitats.

If landscape effects on vole populations have been assumed by deduction to be in part mediated by predation [20, 35, 44, 45] in this unique system, some field and modelling studies have focused on the functional response of predators, e.g. the barn owl (*Tyto alba*) and the red fox [27, 46–48], but none on their population dynamics. However, predator management generates controversy regularly in such system, where their role and the ecosystem services/disservices [49] they render are perceived like contrasted. Socially assumed to contribute to small mammal pest regulation, they are also blamed for maintaining other species in predation sinks, such as small game or some species of conservation value vulnerable to predation (e.g. wading birds, capercaillie, etc.), for damage to hen house, etc. However, observations to corroborate those perceptions are often anecdotal, often with no context, and call for sound data on which objectively ground adaptive management. Although the density of small and medium-size mustelids can hardly be estimated using simple techniques, other predator species can more easily be censused by road-side counts. The variation in this predator community structure over the time span of large fluctuations of prey abundance has not been documented yet in this system, limiting both comparisons with ecosystems described in other part of the world where small mammal outbreaks occur [4] or with more simple food webs of northern ecosystems. Moreover here, a large scale inadvertent experiment was offered by the chemical control of vole populations in the 1990s, leading to a dramatic decrease of the fox population and its gradual recovery the following years after a shift in vole control practices [7].

The aim of this 20-year study is to describe the effects of large variations of grassland vole populations on their predator community and of the long term increase of the fox population in such system. It aims at understanding (i) how a predator community respond to prey variations of large amplitude, (ii) how this community reorganizes with the increase of a dominant predator, here the red fox, (iii) which subset of the predator species can be expected to have a key-role in vole population control in the critical phase of low density of grassland voles. Better understanding the links between grassland vole population variations and predator responses will allow more timely and better focused management actions for all stakeholders in multifunctional socio-ecosystems.

Material and methods

Study area

The study was carried out around the Pissenavache hamlet (46.95°N, 6.29°E) in Franche-Comté, France, in an area of 3425 ha (2646 ha of farmland, 1094 ha of forest, 167 ha of buildings), at an average altitude of 850-900 m above sea level (Fig. 1 and 2). There, 100% of the farmland was permanent grassland used for pasture and (high grass) meadow for cattle feeding in winter (minimum 6 months, November-March), with a productivity ranging 5-6.5 tonnes of dry matter.ha^{-1}.an^{-1} under the specifications of the European Protected Geographical Indication of the locally produced Comté cheese. A KML file with the bounding box of the study area is provided in Supplementary Material S1 kml file.

Road-side counts

Predator and hare (*Lepus europeus*) populations have been monitored from June 1999 to September 2018 (20 years) using night and day road-side counts. Each sampling consisted in driving a car with 4 people (the driver, a data recorder and two observers)

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Fig 1. Location of the study area. a, general location in France; b, study area (red square) and communes including it; c, land cover, road side counts and small mammal transect, P1 and P2 indicate the directions of Fig. 2 photos. Until 2009, a road side count segment was driven straight along the dotted line, but in 2010 mud prevented to use this bypass and slightly changed the itinerary (n-shaped solid line around the dotted line). Commune boundaries were derived from OpenStreetMap and land use from 'BD Carto' provided freely for research by the *Institut Géographique National*, modified based on field observations.

Fig 2. General views of the study area. Top, from the road-side count road at P1 (see Fig. 1); bottom, from P2 with the Pissenavache hamlet, a segment of the road-side count road can be seen in the background (photos PG, 20/02/2019).

along a fixed track at less than 20 km/h. The length of the track was 18.6 km from 1999 to 2009, then 19.6 km due to a slight variation in the itinerary (Fig. 1). Observations were made using 100-W spotlights by night and binoculars for species identification. Distinction between domestic cats (*Felis silvestris catus*) and European wildcats (*Felis silvestris silvestris*) was made visually considering phenotypic criteria (relative to pelage and morphology) without possible distinction of hybrid individuals. Double counting was unlikely because transects were relatively straight, space open (Fig. 2) and observers were careful about animal movements. Sampling was carried out on 3 successive nights (4 when meteorological conditions prevented to achieve a sampling) called a 'session'. The same track was also driven by daylight in the early morning. Most often 3-4 sessions a year were carried out corresponding to seasons, but 1 session in autumn only since 2016. Day road-side counts were stopped in 2017 (see Supplementary Material S2 Excel file for details). Each observation was recorded on a paper map (IGN 1/25000). A Kilometric Abundance Index (KAI) was calculated for each session as the maximum number of animals recorded km^{-1} (thus providing a lower limit for the number of animals present). For the period 2001-2006, only the total counts without the localizations of the observations were available. Thus, only the 1999-2000 and 2007-2018 observations could be georeferenced in 2019.

Small mammal relative densities

Transects

Small mammal (*A. terrestris*, *M. arvalis* and *Talpa europea*) relative abundance was assessed using a transect method adapted from [50–52]; a 5 m-wide transect across the study area was divided into intervals 10 m long and the proportion of intervals positive for fresh indices (tumuli, molehill, runway, feces, cut grass in holes) was taken as an index of abundance. Total transect length was 11.6 km (Fig. 1). Sampling was carried out once a year in april 2007, then in august from 2008 to 2010, then at least twice a year generally in spring and in autumn from 2011 to 2018 (see Supplementary Material S3 Excel file for details).

A. terrestris communal scores

In order to get abundance assessments on a larger space-time scale, abundance was also assessed at the commune-scale by technicians of the FREDON of Bourgogne Franche-Comté (a technical organization for plant pest prevention and control contracted by the Ministry of Agriculture [53]), in the 7 communes crossed by the

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

road-side count itinerary (Fig. 1). Assessments were made in autumn since 1989 (Supplementary Material S3 Excel file). The FREDON assessment uses a ranking system that ranges from 0 to 5: 0 - no *A. terrestris* sign in any parcel within the commune; 1 - low or no *A. terrestris* tumuli, voles and moles (*T. europea*) cohabiting the same tunnel systems; 2 - *A. terrestris* tumuli present in some parcels within the commune and mole burrow systems still present in some parcels; 3 -*A. terrestris* tumuli present in some parcels within the commune, few or no mole burrow systems present in the commune; 4 - *A. terrestris* colonies established in the majority of meadows and within pastures; 5 - all of the commune is colonized by *A. terrestris*. The FREDON index does not directly translate to transect-based indices, partly because it is applied at the commune scale and not the parcel scale, but Giraudoux et al. [52] have shown that levels 0-1 correspond to densities < 100 voles.ha^{-1}, level 2 to 100-200 voles.ha^{-1}, and levels 3-5 to > 200 voles.ha^{-1}. For a given year, the median score of the 7 communes was taken as a score of abundance.

Grassland prey resource

In order to better visualize grassland rodent populations variations on the same scale and fill the gap when transects data were lacking, taking into account that *M. arvalis* body mass is four times smaller than *A. terrestris*'s in average [54], the dynamics of prey resource abundance in grassland has been indexed (i) over the time span when transects were carried out, summing the relative abundance of *A. terrestris* and of *M. arvalis* divided by four, divided by the maximum of this sum over the series and (ii) before this time span, using the FREDON score divided by its maximum score (5). The amplitude of the high density phase is biased to an unknown extend with this method (e.g. arbitrarily summing weighted relative abundances, chained with standardized FREDON scores), but not the time-locations of the low density phases. Thus, the alternation between high density and low density phases was robustly and correctly represented over the time series as an abundance index, in the best possible way given the data, for further comparisons.

Complementary data

In France, bromadiolone, an anticoagulant rodenticide, has been used to control water vole populations since the 1980s, with deleterious effects on non-target wildlife including vole predators [8]. In the early 2000s, the development of an integrative pest management (IPM) approach [32] led to decrease dramatically the quantity of bromadiolone applied by farmers and their non-intentional effects [7, 8]. By law, the delivery of bromadiolone baits for vole control to farmers is under strict FREDON supervision and usage declaration compulsory in order to ensure traceability [55]. Data on bromadiolone quantities used in the 7 communes of the study area were provided by the FREDON of Bourgogne Franche-Comté.

Theoretical daily food intakes (TFI) per predator species were computed following Crocker *et al.*'s method [56] with small mammals considered as prey. Average body mass when missing was estimated based on the *Encyclopédie des carnivores de France* [57–60], the Handbook of Birds of Europe, the Middle East and North Africa [61] and the Encyclopedia of Life (`https://eol.org`).

Statistical analyses

Statistical and spatial analyses were performed in R (version 3.6.2) [62] with the packages Distance [63], pgirmess [64], rgdal [65], rgeos [66], using QGIS 3.10 [67] complementarily. The standard errors of small mammal relative abundances assessed

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

from transects were computed across 1000 bootstrap replicates [68]. We examined the effect of grassland prey abundance indices and seasons upon the number of animals observed in the road-side counts using generalized linear models with a Poisson error distribution of the form $n = a_0 + a_1 ln(x_1) + a_2 x_2 + a_3 x_3 + \epsilon$, with n, the number of observations, x_1, the length of the itinerary, x_2, the season, x_3, the prey abundance index, a_i, the model coefficients, ϵ, the residuals. To avoid the overestimation of degrees of freedom that might come from time series data (here irregular and intrinsically autocorrelated), statistical inference was computed using permutation tests. The grassland prey resource index corresponding to each road-side count was linearly interpolated over time between the two bracketing abundance index estimates.

The shortest distance of observations to the road-side count itinerary, to the nearest forest and to the nearest building were computed [65, 66] and their distribution examined. In order to test whether the proximity of some habitats might explain the observed distributions, mean distance to forest and to building were compared to mean distances obtained from 1000 simulations of the same number of random positions as the number of observations in the strip observed along the itinerary.

In order to obtain density estimates, distance to the itinerary data were analysed using conventional distance sampling with a truncation distance [69–71] including 90% of the observations for each species at the minimum. Avoidance behaviour along the road being detected for most species, we used hazard-rate detection functions fitted to the data. This function type has a more pronounced shoulder compensating for the bias due to avoidance [63]. Models with a seasonal effect as covariate were compared with concurrent models with no covariate using the Akaike Index Criterion [72].

Results

Small mammal density and prey resource variations

Fig. 3a shows the cyclic variations of *A. terrestris* from 1989 to 2018. Predators communities have been monitored during the last four cycles, but the local populations dynamics of small mammals during the last three cycles only (Fig. 3b). A clear synchrony of the low density phase between rodent species was observed, while *T. europea* and *A. terrestris* peaks were in phase opposition. In term of prey resource, low density phases contrast with the phases of large abundance of grassland voles (Fig. 3c).

Fig 3. Small mammal population dynamics. Numbers with arrows indicate high density peaks in the communes including the study area; a, dotted grey line, *A. terrestris* FREDON scores; red line and red scale, quantity of bromadiolone (g) applied for *A. terrestris* control in the communes of the study; b, abundance index based on transects, vertical bars are 95% confidence intervals (grey scale and dotted line relate to the *A. terrestris* FREDON scores for comparison); c, estimated variations of grassland prey resource, the rug on the x axis represents road-side count events.

Time variations of predator and hare relative abundances

Twenty seven species for the day road side counts and 24 for the night were observed, corresponding to 19,010 and 7,355 individual observations respectively, and to 58 sessions for each count type ($\simeq$ 348 night or day counts in total) (see Supplementary material S2 Excel file). Some were occasional visitors and likely play a marginal role on vole prey (e.g. grey herons (*Ardea cinerea*) could regularly be observed preying on voles in grassland). Others, such as some mustelids (stoat (*Mustela erminea*), least weasel (*M.*

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

nivalis), stone marten (*Martes foina*), pine marten (*M. martes*)) were elusive and hardly detected by road-side counts. Among them, the following species were both observed frequently enough over time and considered of interest for this study: for day road-side counts, the carrion crow (*Corvus corone*), the common buzzard (*Buteo buteo*), the red kite (*Milvus milvus*), the kestrel (*Falco tinnunculus*), the domestic cat (*Felis silvestris catus*), the hen harrier (*Circus cyaneus*); for night road-side counts, the European hare (*Lepus europeus*), the red fox (*Vulpes vulpes*), the domestic cat (*Felis silvestris catus*), the European wildcat (*Felis silvestris silvestris*), the long-eared owl (*Asio otus*), the European badger (*Meles meles*).

Fig. 4 shows the dynamics of diurnal species. For each species KAI differences between seasons were found statistically significant except the domestic cat (Table 1 and Fig. 5).

Fig 4. Day road-side counts. Black circles at the bar top identify autumn counts. The grey line in the background shows the variations of grassland prey abundance (the scale is the same in every plot). The letters above identify the sessions available and selected to estimate densities based on distance sampling during high (ˆ) or low (o) abundance period.

Table 1. Statistical significance ($p(H_0)$) of the model coefficients obtained by permutations, and model r-squared. Numbers between parentheses are values when one outlier is dropped (see results). n.s., not significant.

count type	species	season	prey abundance	r^2
day	carrion crow	< 0.001	n.s.	0.68
	common buzzard	0.002	< 0.001	0.59
	red kite	0.001	0.05	0.44
	kestrel	< 0.001	0.09 (0.01)	0.62 (0.66)
	domestic cat	n.s.	n.s.	-
	hen harrier	0.009	0.08 (0.02)	0.52 (0.51)
night	hare	n.s	0.007	0.42
	red fox	n.s	n.s.	-
	domestic cat	< 0.001	n.s.	0.54
	wildcat	n.s.	< 0.001	0.42
	long-eared owl	n.s.	n.s.	-
	European badger	n.s.	n.s.	-

Fig 5. Biplots of diurnal KAIs as a function of grassland prey index. sp (green), spring; su (dark wheat), summer; au (red), autumn; wi (blue), winter. Lines correspond to the Poisson model for each season.

For instance, common buzzard KAI was highly significantly correlated to grassland prey index, with KAI 2.2 times higher in autumn than in spring. In spring, during the breeding season, KAI were 4.3 times larger in the peak phase than in the low density phase of grassland vole populations. Red kite's correlation p-value was equal to and kestrel and hen harrier's above but not far from the critical threshold generally accepted of $p(Ho) \leq 0.05$. This lack of significance for the latter two species held from one outlier, when a relatively large number of birds was observed in Summer 1999 in a period when prey estimates were not available locally from transects but derived from the FREDON scores on a communal scale. Dropping this observation from the data set

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

would lead to reject Ho at $p = 0.01$ and $p = 0.02$, respectively, and to conclude formally on a correlation between the number of observations of those species and grassland prey abundance.

Fig. 6 shows the dynamics of nocturnal species. We did not detect numerical response statistically significant to seasons or grassland prey index for red fox, badger and long-eared owl abundance. Domestic cat did not correlate to grassland prey index but to seasons, with lower counts in winter. Hare and wildcat KAIs were significantly correlated to grassland prey index but seasonal variations could not be detected (Table 1 and Fig. 7). Fox and hare KAIs were highly and negatively correlated to each other ($p < 0.001$). Furthermore, a model of hare abundance as response variable including grassland prey index and fox KAI as independent variables showed that controlling for grassland prey, hare abundance did not significantly correlate to fox KAI at a probability ≤ 0.05 (however with an observed p-value of 0.07).

Fig 6. Night road-side counts. Black circles at the bar top identify autumn counts. The grey line in the background shows the variations of grassland prey abundance (the scale is the same in every plot). The letters above identify the sessions available and selected to estimate densities based on distance sampling during high (ˆ) or low (o) abundance period.

Fig 7. Biplots of nocturnal KAIs as a function of grassland prey index. sp (green) spring; su (dark wheat), summer; au (red), autumn; wi (blue), winter. Biplots in black have no seasonal effect. Lines correspond to the Poisson model.

Red fox and badger showed significantly higher abundance in average in the last half of the time series, and hare, wild and domestic cat, long-eared owl and hen harrier significantly lower (one-tailed permutation tests on mean, $p < 0.001$) (Fig. 4 and 6).

Spatial variations

Observations were truncated at a distance of 300 m and 350 m from the track for night and day road-side counts respectively, accounting for 92% and 93% of their total number. Among all species in the open grassland strip along the itinerary, only the common buzzard with regard to forest and buildings, and the red fox with regard to buildings were randomly distributed. Carrion crow, red kite, kestrel and hare were observed at a greater distance to forest than expected from a random distribution; hen harrier, red fox, wildcat, long-eared owl, badger at a smaller distance; wildcat, long-eared owl and badger at a greater distance to buildings; carrion crow, red kite, kestrel, domestic cat, hen harrier at a smaller distance (Tab. 2). 75% of the observations of domestic cat were made at less than 500 m of buildings by night and at less than 250 m by day (Fig. 8). No change in any of those patterns was observed between the first and the second half of the time series.

Fig 8. Distance to buildings of domestic cats for the night and day road-side counts ($n_{obs} = 320$ and $n_{obs} = 101$, respectively).

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Table 2. Mean distance (in meters) of observations to forest and buildings; random locations is the mean distance obtained from 1000 random replicates of the same number of geographical coordinates as the observations in the observation strip; the permutation test being one-tailed, p(Ho) is the number of random mean distance equal or above, or equal or below, the observed mean distance, divided by 1000. n.s., not significant. Forest effect could not be computed for the domestic cat due to its strong aggregation in and around villages

		forest			buildings		
count type	species	observed	p(Ho)	effect	observed	p(Ho)	effect
day	carrion crow	319	< 0.001	-	852	< 0.001	+
	common buzzard	n.s.	n.s.	=	n.s.	n.s.	=
	red kite	304	0.02	-	894	< 0.001	+
	kestrel	327	< 0.001	-	896	0.002	+
	domestic cat	-	-	?	193	< 0.001	++
	hen harrier	236	< 0.001	+	920	0.01	+
	random locations	292			953		
night	hare	299	0.05	-	874	0.008	+
	red fox	253	< 0.001	+	n.s.	n.s.	=
	domestic cat	-	-	?	354	< 0.001	++
	wildcat	248	0.002	+	1113	< 0.001	-
	long-eared owl	229	0.003	+	1043	0.03	-
	badger	229	0.008	+	1125	0.001	-
	random locations	284			939		

Estimation of predator and hare densities, and theoretical food intake (TFI)

Comparing detection models with 'season' as covariate with models with no covariates led to reject the hypothesis of a seasonal effect on the detection function for every species (detection functions are presented in Supplementary material S4 Word file and S5 Word file). Based on the visual examination of KAI dynamics, for each species, we identified periods when the indices could be considered similarly high or similarly low with regard to the amplitude of variations and categorize them as sub-samples of 'low' or 'high' densities (see Fig. 4 and 6). Table 3 gives conversion coefficients from KAI to densities, the maximum density values observed, and summarizes the estimations obtained by distance sampling by density categories ('low' or 'high'). Considering the relative aggregation of the domestic cat close to buildings, we provide one density estimate for the entire study area, and another for a buffer of 300 m (night) or 250 m (day) around buildings.

Fig. 9 shows the population density variations of the predator community during the study period for all species when both day and night road-side counts were available. Raw numbers and graphs on biomass and daily TFI variations are provided in Supplementary material S6 Excel file, S7 Word file and S8 Word file. The main features of the dynamics hold in the importance of the carrion crow (range 4.4-56.9% of the total TFI), the common buzzard (range 4.7-48.6% of the total TFI) and the red kite (0-54.5% of the total TFI) along the entire time span, and the gradual increase of the red fox from 1999 to 2010 (Fig. 9). The numerical importance of the carrion crow apart, three key periods could be identified: 1999-2004 with red fox density extremely low not exceeding 0.2 ind.km^{-2}, the community being numerically dominated by cats (domestic and wild) and common buzzards, 2005-2009 with an increasing density of foxes, and 2010-2016 when fox densities were higher and stabilized at an average of 2.7 ind.km^{-2}. Foxes represented only 5.5% of the predator biomass (2.8% of the total TFI) in 1999-2004 but reached 29.5% (31.4% of the TFI) in 2010-2016. Whatever the period

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Table 3. Comparison of density estimates (n.km^{-2}) derived from all species data and distance sampling. Lower and upper densities correspond to estimations during low or high density period (see Fig. 4 and 6); CI95%, 95 % confidence interval; coef., conversion coefficient from KAI (n.km^{-1}) into density (n.km^{-2}) ; max($\hat{D}$), maximum density observed; n, number of sessions; $\hat{D}$, density estimate. *, domestic cat densities in a 500 m (night) or 250 m (day) buffer around buildings (including 75% of domestic cat observations, see results).

				lower densities				upper densities			
						CI95%				CI95%	
count type	species	coef.	max($\hat{D}$)	n	$\hat{D}$	lower limit	upper limit	n	$\hat{D}$	lower limit	upper limit
day	carrion crow	2.0	28.2	27	3.3	2.6	4.2	8	16.4	12.0	22.5
	common buzzard	2.1	15.7	25	1.6	1.3	2.0	10	8.5	6.0	12.0
	red kite	2.1	9.2	31	0.6	0.4	0.9	4	7.4	5.4	10.1
	kestrel	2.3	3.0	23	0.3	0.2	0.4	6	2.4	2.1	2.9
	domestic cat	3.3	1.4	23	0.4	0.3	0.5	12	1.0	0.8	1.3
	domestic cat*	-	18.8	-	3.4	2.5	4.5	-	9.1	6.8	12.0
	hen harrier	1.9	0.3	28	0.03	0.01	0.1	7	0.2	0.1	0.3
night	hare	2.4	3.2	29	0.7	0.5	0.8	7	2.0	1.3	3.0
	red fox	2.5	4.8	7	0.1	0.01	0.3	17	2.6	2.2	3.2
	domestic cat	2.9	2.1	22	0.7	0.6	0.9	14	1.7	1.4	2.0
	domestic cat*	-	7.4	-	2.4	1.9	3.1	-	5.9	4.9	7.0
	wildcat	2.3	1.1	33	0.4	0.3	0.5	3	0.9	0.7	1.2
	long-eared owl	2.5	1.9	30	0.1	0.07	0.2	6	0.8	0.4	1.7
	badger	2.3	0.9	33	0.1	0.1	0.2	3	0.8	0.6	1.1

and relative densities of species, the average TFI in the three periods was close to 4 (3.8-4.2) kg.km^{-2}.day^{-1}. The largest predator densities were reached during the high density peaks of the grassland vole populations, with a maximum observed in the autumn 2008, with 60 ind.km^{-2} (carrion crow making 48% of this total) and a daily TFI of 10.7 kg.km^{-2}.day^{-1} (39.3% from carrion crow).

Fig 9. Variations in densities for each species (n.km^{-2}). Variations in biomass (kg.km^{-2}) and theoretical daily food intake (kg.km^{-2}.day^{-1}) are presented in Supplementary material S7 Word file and S8 Word file.

Table 4 summarizes results at the grassland vole populations peaks of the autumns 2003, 2008 and 2012, and at the low density phases of autumn 1999, spring 2007, autumn 2010 and spring 2014. In the autumn 1999, the first 4 species totalling 91% of the TFI were the carrion crow, the common buzzard, the domestic cat (night) and the kestrel. The common buzzard was still among those first four species in the next low density phase (spring 2007), but the proportion of TFI from birds of prey still decreased, and was preceded by the fox, the carrion crow, the domestic cat and the wildcat in autumn 2010 and spring 2014, these species making together 86% and 84% of the TFI. However, a large proportion of domestic cats roaming at less than 500 m of the buildings, far from villages where domestic cats were virtually absent, fox, carrion crow and wildcat alone made 86% of the TFI. During the first two high density phases, the carrion crow, the common buzzard, the red kite and the domestic cat (night) made 81 and 91% of the TFI, and in autumn 2012 during the third high density phase, the fox, the common buzzard, the carrion crow and the domestic cat (day) alone made 81% of the TFI. Table 4 also shows that the TFI ranged between 1.5 and 2.7 kg.km^{-2}.day^{-1} in the low density phases and between 6.9 and 10.7 kg.km^{-2}.day^{-1} in the high density

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

peaks, thus the TFI was multiplied by 7.1 at the maximum whilst grassland small mammal population biomass was multiplied by thousands.

Table 4. Density (ind.km^{-2}) and theoretical daily food intake, TFI (kg.km^{-2}.day^{-1}) in the low (LD) and high (HD) density phases of grassland vole populations. Numbers between parentheses are percentages.

	species	1999 (LD) autumn	2003 (HD) autumn	2007 (LD) spring	2008 (HD) autumn	2010 (LD) autumn	2012 (HD) autumn	2014 (LD) spring
density	carrion crow	14.9 (61.4)	19.4 (44.4)	3.1 (39.8)	28.6 (48)	12.9 (61.7)	7.9 (26.5)	3.6 (37.6)
	common buzzard	3.3 (13.8)	11 (25.3)	1.2 (16)	16.1 (27)	1.4 (6.6)	9.4 (31.5)	0.7 (7.7)
	kestrel	2.9 (11.9)	2 (4.6)	0.3 (3.3)	2.8 (4.6)	1 (4.5)	3 (10)	0.1 (1.2)
	red kite	0.2 (0.9)	5 (11.4)	0.3 (4.3)	8.5 (14.3)	0.4 (2)	1.4 (4.6)	0.4 (4.4)
	domestic cat (day)	0.5 (2.2)	0.5 (1.2)	0.5 (6.9)	0.9 (1.5)	0.3 (1.6)	1.2 (3.9)	0.3 (3.5)
	hen harrier	0.4 (1.7)	0.2 (0.5)	0 (0)	0.1 (0.2)	0.1 (0.5)	0.2 (0.6)	0 (0)
	red fox	0.1 (0.5)	0.8 (1.8)	0.5 (6.9)	0.4 (0.7)	3 (14.4)	4.9 (16.4)	2.8 (28.9)
	wildcat	0 (0)	1.6 (3.6)	0.4 (4.8)	0.5 (0.8)	0.8 (3.9)	0.7 (2.3)	0.6 (6)
	long-eared owl	0.3 (1.1)	1 (2.2)	0 (0)	0.1 (0.2)	0 (0)	0.4 (1.3)	0 (0)
	badger	0 (0)	0.1 (0.3)	0.1 (1.6)	0 (0)	0.1 (0.6)	0.2 (0.8)	0.1 (1.2)
	domestic cat (night)	1.6 (6.5)	2.1 (4.7)	1.3 (16.5)	1.6 (2.7)	0.9 (4.3)	0.6 (2)	0.9 (9.4)
	total	24.3	43.7	7.7	59.5	20.9	29.9	9.6
	total without crow	9.4	24.3	4.6	30.9	8.0	22.0	6.0
TFI	carrion crow	2.2 (55.1)	2.9 (34.2)	0.4 (23.5)	4.2 (39.3)	1.9 (40.9)	1.2 (16.7)	0.5 (18.5)
	common buzzard	0.6 (15.3)	2 (24.1)	0.2 (11.7)	2.9 (27.4)	0.3 (5.4)	1.7 (24.7)	0.1 (4.7)
	kestrel	0.2 (5.7)	0.2 (1.9)	0 (1)	0.2 (2)	0.1 (1.6)	0.2 (3.4)	0 (0.3)
	red kite	0.1 (1.3)	1.2 (14.3)	0.1 (4.2)	2 (19.2)	0.1 (2.2)	0.3 (4.7)	0.1 (3.5)
	domestic cat (day)	0.2 (4.8)	0.2 (2.3)	0.2 (10)	0.3 (3)	0.1 (2.6)	0.4 (6.1)	0.1 (4.2)
	hen harrier	0 (1.2)	0 (0.3)	0 (0)	0 (0.1)	0 (0.2)	0 (0.3)	0 (0)
	red fox	0.1 (1.6)	0.4 (4.6)	0.3 (13.3)	0.2 (1.8)	1.5 (31.3)	2.4 (34)	1.3 (46.4)
	wildcat	0 (0)	0.6 (7.4)	0.1 (7.5)	0.2 (1.8)	0.3 (6.8)	0.3 (3.9)	0.2 (7.9)
	long-eared owl	0 (0.6)	0.1 (1)	0 (0)	0 (0.1)	0 (0)	0 (0.5)	0 (0)
	badger	0 (0)	0.1 (1.1)	0.1 (5)	0 (0)	0.1 (2)	0.2 (2.6)	0.1 (3.2)
	domestic cat (night)	0.6 (14.3)	0.7 (8.9)	0.5 (23.8)	0.6 (5.3)	0.3 (7)	0.2 (3.1)	0.3 (11.3)
	total	4.0	8.4	1.9	10.7	4.6	6.9	2.9
	total without crow	1.8	5.5	1.5	6.5	2.7	5.8	2.3

Discussion

Response to grassland vole population variations

The general pattern of small mammal population variations observed in our study area confirms earlier observations over the shorter period 1987-1990 [42] for rodents, and the fact well established that *A. terrestris* outcompete *T. europea* for space [52, 73]. *T. europea* at its population peak does not exceed some individuals per hectare, and by distaste and quantity is a negligible prey for most predators [54].

Among the 11 predator species monitored 4 (maybe 6) show a numerical response to the large variations of grassland prey observed over the 20 years of our study. Namely, the common buzzard, the red kite, the wildcat and also the hare, and possibly the kestrel and the hen harrier. However, such response were modulated by population trends on a larger scale. This was the case for the hen harrier and the long-eared owl, with populations decreasing over time in the study area reflecting the general decrease of those species in Franche-Comté and nearby Switzerland [74]. Those variations were also seasonal with generally larger populations in autumn, but in summer for the red

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

kite, corresponding to dispersing birds after reproduction and post-breeding migration. The numerical response of the hare, an herbivore, to grassland vole density variations is more surprising (but see next section). A similar pattern has been observed nearby at a 30 km distance from the study area, from 1976 to 1995, for the capercaillie (*Tetrao urogallus*), in the Massif du Risoux, where the number of fledglings per hen was positively correlated to the cyclic abundance of *A. terrestris* populations [75]. This response was interpreted as being the result of predation switches during the decline phase of the voles, with a predation pressure upon the capercaillie supposed to be relaxed during the high density peak, a phenomenon well documented e.g. in Scandinavian ecosystems [22, 76, 77].

The variations of the population of the other species were independent from grassland vole populations over the study time span.

Interactions within the predator community and with the hare population

A striking feature of the population dynamics observed is the increase of the fox population from the beginning of the study to the autumn 2010, independently from vole populations variations. This increase can be attributed to changes in grassland small mammal control practices by farmers who shifted from late-rodenticide-only to early-integrated control in the early 2000s [32], dividing by more than forty four the quantity of anticoagulant rodenticide used during the 2010-2018 cycles compared to 1996-2000 (Fig. 3a). Massive use of anticoagulant rodenticide is known for its deleterious side-effect on vole predators [8], with sensitivity for canids more than 3 times higher than for felids [78], and this effect has been proven to drastically decrease fox population in the area at the end of the 1990s [26]. Furthermore, Jacquot et al. [7] have shown how fox population has recovered on a regional scale after such a change in rodent control practices. In our study, the predator community shifted from a very low fox density of 0.1 ind.km^{-2} (CI95% 0.01-0.3) foraging in grassland up to a much larger fox abundance of 2.6 ind.km^{-2} (CI95% 2.2-3.2), with a peak at 4.9 ind.km^{-2} in the autumn 2012 (then a stabilization or a slight decrease was observed with an epidemic of sarcoptic mange, still ongoing). This value is one of the highest population densities reported in rural landscapes of Europe [79, 80]. This increase was concomitant with a sudden and dramatic decrease of the hare population during a low density phase of the vole populations, and also with a decrease in the wild and domestic cats. This strongly suggests that those declines might be the consequences of the increase of the fox population, possibly by direct predation or by creating a 'landscape of fear' [81, 82] limiting the distribution of the prey species to shelter-areas where they could not be detected by road-side counts (houses, forest, etc), or both. In Australia, experiments of fox removal showed in one study that cats foraged more in open habitats where foxes were removed [83] and in two others that they were more abundant [84, 85]. Furthermore, in western Poland, hare population responded the same year with 1.7 times higher density to fox removal [86], as well as positively to a sarcoptic mange epidemics depressing the fox population in Scandinavia [22]. We did not observe changes in the spatial distribution of species between the first and the second half of the study, making the 'landscape of fear' hypothesis less likely here, thus suggesting a major role for direct predation.

However the long-term increase of the European badger population since rabies vaccination in the early 1980s is well documented in Europe [87–89], in our study, the sudden increase since summer 2013 stays unexplained.

Except the stability of the carrion crow population at a large number, a striking feature of our system is the change in the predator community structure over the study

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

time span. In the early 2000s, the community was numerically dominated by the common buzzard and domestic and wildcats, and with the increase of the fox population became numerically dominated by the fox itself. However, foxes did not added their number to the other predators and this population increase did not led to an increase in the average number of predators present in the study area. Large variations in vole predator number could be clearly attributed to the temporary increase of the populations of mobile birds of prey (common buzzard, red kite, etc.) in response to grassland vole outbreaks. This stability in the average predator number observed (e.g. in the low density phases of vole populations) suggests compensations among resident species due to predation or competition. Similar compensation has already been suspected in Fennoscandia, where an experimental removal of avian predators in order to understand their role on vole population regulation led to least weasel density increase [90]. In our study, the lack of data about *Mustela* sp. and *Martes* sp. does not permit to know whether those compensations observed in a community subset extend to the whole community of vole predators. Earlier studies in the area and a nearby valley of Switzerland [91, 92] and also in Fennoscandia [93] and northern Spain [15], clearly show that least weasel and stoat abundances follow grassland vole population peaks. Furthermore, small mustelid abundance has been shown to be dampened by fox in north America [94], by generalist predators [93] and by birds of prey [90] in Fennoscandia, but those interactions, possible in our study area, stay unexplored here. Moreover, small mustelids forage in vole galleries and shelter there from bigger predators. The use of rodenticide baits buried in vole galleries as enforced by the regulation [55] might contribute to an additional specific depression of small mustelid populations locally [95, 96].

Impact of predators on grassland vole prey

This study is the first one, to our knowledge, to provide data on the variations of the population densities and daily TFI of a large community of vole predators in a temperate ecosystem in response to large variations of cyclic grassland small mammals over 20 years (four *A. terrestris* population cycles). Several biases are inherent to the methods used (see study limitations above), however, we consider that some robust conclusions can be carefully drawn from this exceptional long-term data set. One additional limitation comes from the fact that the functional response of each species (the dietary variations as a function of available food resources) was not studied parallel to the variations of population densities. This limits the interpretation that can be given to the variations of daily TFI and the evaluation of its impact on prey populations. Thus, here we consider first what we know about predator diet, before discussing their impact on vole prey.

Dietary issues

The carrion crow is mostly opportunistic and feed principally on invertebrate, cereal grain but also small vertebrates, bird eggs, carrion, in various proportions according to place and seasons. At the extreme, vertebrate and eggs in particular can reach 86.6% of dry weight of pellets in winter e.g. in south Spain, and they are often seen to cooperate when killing small vertebrates in pair or small groups, also commonly forcing other birds including raptors to drop prey [61]. Their behaviour has not been systematically studied in our area and the importance of small mammals in the diet is not known yet, however all of the behaviours mentioned above, including scavenging on dead animals, hunting voles and forcing raptors, have been occasionally observed [97]. Thus one can hardly infer conclusions about the impact of a so opportunistic species in this ecosystem e.g.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

on vole regulation. Mechanically, their number however has likely a chronic impact on species vulnerable to predation such as small game and bird nests.

The other species are more specialized on small mammal prey. The detailed diet of the domestic cat is unknown in our area. However in a similarly rural area of the Ardennes, rodents make 55.9% of the dietary items found in 267 domestic cat faeces (6% birds, 36.7% human-linked food), with little difference between outdoor cats (owned by people other than farmers) and farm cats [98]. Rodents (Murids and Cricetids) constitute the main prey of wildcats, and can account for 97% of diet composition [99], while lagomorphs and birds appear generally as alternative prey. However, when the availability of lagomorphs increases, wildcats can substantially shift their diet towards them [100].

In the area, the dietary response of the red fox to variations of grassland vole relative densities differs between *M. arvalis* (no response) and *A. terrestris* (Holling's type III-like) [48]. *M. arvalis* could make up to 60% of prey items in faeces even at very low density (range 0-80% of prey items on the whole range of vole densities), and *A.terrestris* showed a sigmoid increase with quickly a plateau (at 15% of positive intervals of a transect -see material and methods) where it made 40% of diet items in average (range 0-80% of prey items). The description of the dietary response in this context where the two main prey abundances vary among several other alternative food resources is quite complex [21, 46, 47, 101]. The comparisons of multi-species functional response (MSFR) models with empirical data about the red fox and the barn owl showed that switching between prey depends on the proportion of the prey available among other prey (frequency dependence), as commonly thought, but is also dependent on the total amount of prey (density dependence), with non-linear frequency and density dependent interactions [27].

Impact of predation on vole population dynamics

In our study area [33, 34], the population of the main prey species varied between 0 and about 1000 ind.ha^{-1} on a scale of tens of km^2, an amplitude 5-100 times larger than those observed on a similar scale e.g. in the Greenland Arctic with *D. groenlandicus* (0-10 ind.ha^{-1}) [14], in Revinge area, Sweden with *M. agrestis* (5-10 ind.ha^{-1}) [93], in Messarges area, France with *M. arvalis* (5-120 ind.ha^{-1}) [21], or in the Kielder forest, Scotland with *M. agrestis* (20-250 ind.ha^{-1}) [102]. A similar amplitude has been reported locally for *M. arvalis* in alfalfa semi-permanent plots of some ha in an intensive agriculture matrix of ploughed fields of western France (50-1500 ind.ha^{-1}) [103]. Abundance estimates of other studies were not expressed as densities, however one can reasonably assume that in crop field landscapes of Spain [104] and north-eastern and central Europe [4, 105], *M. arvalis* can reach also densities exceeding by far 1000 ind.ha^{-1} locally in grassy field margins and semi-permanent leguminous or grassland plots, but those densities are limited to a small fraction of farmland in large matrices of suboptimal habitats such as ploughed fields [44]. In our study area, two species, *A. terrestris* and *M. arvalis* had large fluctuations of similar amplitude against only one in the other systems, population surges extending on large areas of tens of km^2 of highly productive and connective grassland. This ecosystem offered periodically (permanently on a large scale) an incredible biomass of several tens of kg.ha^{-1} of voles easy to access in grassland, to a large number of predator species. Here, we will try to understand in such system whether there are periods in vole population fluctuations when predation can be a key-factor controlling vole densities. At its maximum during the autumn 2008, the TFI was 10.7 kg.km^{-2}.day^{-1}, hence , with an average weight of 80 g.vole^{-1} [54], the equivalent of 134 montane water voles.km^{-2}.day^{-1}. With a carrying capacity of 1000 water voles.ha^{-1} and a predator diet made of an unrealistic 100% water vole at high density of voles (a food intake figure totally unlikely considering predator diets not

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

exclusively based on voles even when specialized, see e.g. the carrion crow's, the fox's, etc.), above 78 voles.ha^{-1}, this community would not be able to decrease the vole population during its growth phase (for simulations, see `https://zaaj.univ-fcomte.fr/spip.php?article114&lang=en` and `https://github.com/pgiraudoux/shinyPred/tree/master/shinyPred_en` for the code). At densities of voles exceeding some tens voles.ha^{-1}, predators alone do not appear to be capable of instigating a population crash in our area. By contrast, daily TFI at a low or medium water vole densities can considerably slow down the population increase. For instance, with a population of 2 vole.ha^{-1} at the beginning of the reproduction season, and a conservative 50% of voles in the diet for the lowest TFI (1.9 kg.km^{-2}.day^{-1}, hence 12 voles.km^{-2}.day^{-1} in spring 2007), voles would be 27 ind.ha^{-1} at the end of the year instead of 91 ind.ha^{-1} without predation. Some parameters configuration based on observed TFI at low density can even lead to vole extinction (e.g. autumn 1999 and 2010). Hence, to summarize, in our study area, the increase of predator populations due to mobile predators during the growth and high density phase of a grassland vole cycle, however responsible for consuming several ten thousands of voles.km^{-2}.year^{-1} and for reducing the vole population dramatically, was likely not enough to trigger alone the decline of vole populations. However, predators during the low density phase were enough to considerably slow down the growth phase or even to extinct vole populations locally.

Furthermore, our study documents the fact that domestic cat populations could reach much higher densities of 2.4-9.1 ind.km^{-2} up to more than 18 ind.km^{-2} around villages within a 250-500 m radius, except in the winter nights when they likely prefer to stay warmly at home. In south-central Sweden, Hansson [106] observed that domestic cats, supplied with continuous alternate food, were able to dampen the population fluctuations of the field vole, compared to more or less cat-free areas. In villages at some kilometers of our study area, Delattre et al. [35, 45] reported a systematically decreasing abundance of common vole colonies around villages near our study area during similar fluctuations of vole abundance, within an area extending 300 to 400 m from the village edge, this gradient persisting throughout a complete vole population fluctuation. They subsequently hypothesized that this lower density of voles might be the result of cat predation around villages. This figure and our estimates indicate that the combination of domestic cat density and diet, added to the density and diet of the other predators, is enough to explain this effect.

The specific distribution of domestic cats, close to villages, can also cause spatial heterogeneity in predation pressure. For instance, during the small mammal low density phases, their proportion varied between 5.9% (autumn 2010) and 23.4% (spring 2007) of the total number of predators counted. In areas far from villages (e.g. $>$ 500 m) where domestic cats were rare or absent, in reality, the real density of vole predators could be locally lower than the numbers given in Tab. 4 (e.g. 33.5 versus 43.7 ind.km^{-2} in spring 2007) or differences be small as in the autumn 2010 (19.7 versus 20.9 ind.km^{-2}).

Conclusion

Overall, our results indicate that in such ecosystem with large variations of grassland prey, the structure of the predator community can change over the long term without changing its overall variations over a rodent cycle, and its TFI variation pattern. Although an unknown remains about the role of small and medium mustelid populations, the higher predator densities observed during the grassland rodent peak was mostly due to mobile birds of prey which followed the rodent population increase. However, resident predators alone during the low density phase of grassland rodent populations were capable to slow-down the increase or even to extinct rodent populations locally, but the whole predator community alone was unable to explain the

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

population decrease observed after a high density peak. In such system, the carrion crow was numerically the largest population with the largest TFI, but its impacts in the ecosystem could not be clearly assessed due to its diet eclecticism. After a shift in rodent control practices and a much more moderate usage of anticoagulant rodenticides, the red fox population recovered and then stabilized at much larger densities, which likely impacted negatively hare, wildcat and domestic cat populations. The domestic cat population was aggregated close to buildings, with a 400 m buffer where vole population is generally lower.

From an applied viewpoint, our results strongly suggest that, in such a highly productive and connective grassland system favourable to grassland voles, any means aiming at increasing the populations of predators during the low density phase (e.g. hedgerow networks, roosts, cats around villages, etc.) should lead to a better control of grassland small mammal populations (slowing down the increase phase) [107]. However, the impacts of a management with large densities of cats around human settlement on other wildlife [108, 109] and pathogen organism transmission (e.g. *Toxoplasma gondi*) [110, 111] should be considered. Moreover, in such systems and due to unavoidable prey switches some populations like the European hare can be caught in a predation sink and can sustain at low density only. Management options aiming at increasing these vulnerable populations by culling predators (e.g. the red fox, etc.) would conflict with the interests of other stakeholders interested in small mammal pest control. The prohibiting costs and manpower for culling a large number of predators on the long term and the ethical concern of such management should prevent this approach most often shown to be unsuccessful [112, 113] and not accepted socially [29]. Other ways including adaptive hunting plans and demand, modification of habitats and landscapes favouring other equilibriums in the community should be looked for, which implies evidence-based and constructive dialogue about management targets and options between all stakeholders of such socio-ecosystems [114].

References

1. Krebs CJ. Population fluctuations in rodents. The University of Chicago Press; 2013.

2. Villette P. Spatial and Temporal Characteristics of Bacterial Parasite Communities in Outbreaking Fossorial Water Vole (Arvicola terrestris) Populations: Static Uniformity or Dynamic Heterogeneity? Université de Franche-Comté; 2018.

3. Huitu O, Kiljunen N, Korpimäki E, Koskela E, Mappes T, Pietiäinen H, et al. Density-dependent vole damage in silviculture and associated economic losses at a nationwide scale. Forest Ecology and Management. 2009;258(7):1219–1224. doi:10.1016/j.foreco.2009.06.013.

4. Jacob J, Imholt C, Caminero-Saldaña C, Couval G, Giraudoux P, Herrero-Cófreces S, et al. Europe-wide outbreaks of common voles in 2019. Journal of Pest Science. 2020;doi:10.1007/s10340-020-01200-2.

5. Delibes-Mateos M, Smith AT, Slobodchikoff CN, Swenson JE. The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. Biological Conservation. 2011;144(5):1335–1346. doi:10.1016/j.biocon.2011.02.012.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

6. Giraudoux P, Villette P, Quéré JP, Damange JP, Delattre P. Weather influences M. arvalis reproduction but not population dynamics in a 17-year time series. Scientific Reports. 2019;9(1):13942. doi:10.1038/s41598-019-50438-z.

7. Jacquot M, Coeurdassier M, Couval G, Renaude R, Pleydell D, Truchetet D, et al. Using long-term monitoring of red fox populations to assess changes in rodent control practices. Journal of Applied Ecology. 2013;50(6):1406–1414. doi:10.1111/1365-2664.12151.

8. Coeurdassier M, Riols R, Decors A, Mionnet A, David F, Quintaine T, et al. Unintentional wildlife poisoning and proposals for sustainable management of rodents. Conserv Biol. 2014;28(2):315–21. doi:10.1111/cobi.12230.

9. Andersson M, Erlinge S. Influence of predation on rodent populations. Oikos. 1977;29:591–597.

10. Korpimaki E, Norrdahl K. Experimental reduction of predators reverses the crash phase of small-rodent cycles. Ecology. 1998;79(7):2448–2455. doi:10.1890/0012-9658(1998)079[2448:EROPRT]2.0.CO;2.

11. Korpimaki E, Norrdahl K, Klemola T, Pettersen T, Stenseth NC. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. Proceedings of the Royal Society B-Biological Sciences. 2002;269(1495):991–997. doi:10.1098/rspb.2002.1972.

12. Graham IM, Lambin X. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. Journal of Animal Ecology. 2002;71(6):946–956.

13. Oli MK. Population cycles of small rodents are caused by specialist predators: or are they? Trends in Ecology and Evolution. 2003;18(3):105–107. doi:10.1016/S0169-5347(03)00005-3.

14. Gilg O, Sittler B, Sabard B, Hurstel A, Sane R, Delattre P, et al. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos. 2006;113(2):193–216. doi:10.1111/j.2006.0030-1299.14125.x.

15. Mougeot F, Lambin X, Rodríguez-Pastor R, Romairone J, Luque-Larena JJ. Numerical response of a mammalian specialist predator to multiple prey dynamics in Mediterranean farmlands. Ecology. 2019;100(9):e02776. doi:10.1002/ecy.2776.

16. Gilg O, Hanski I, Sittler B. Cyclic dynamics in a simple vertebrate predator-prey community. Science. 2003;302(5646):866–868. doi:10.1126/science.1087509.

17. Hanski I, Henttonen H. In: Population cycles of small rodents in Fennoscandia. Oxford University Press; 2002. p. 44–68.

18. Lambin X, Bretagnolle V, Yoccoz NG. Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? Journal of Animal Ecology. 2006;75(2):340–349. doi:10.1111/j.1365-2656.2006.01051.x.

19. Lidicker WZ. Landscape approaches in mammalian ecology and conservation. University of Minnesota Press; 1995.

20. Lidicker WZ. A food web / landscape interaction model for microtine rodent density cycles. Oikos. 2000;91:435–445.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

21. Dupuy G, Giraudoux P, Delattre P. Numerical and dietary responses of a predator community in a temperate zone of Europe. Ecography. 2009;32(2):277–290. doi:10.1111/j.1600-0587.2008.04930.x.

22. Lindström ER, Andren H, Angelstam P, Cederlund G, Hornfeldt B, Jaderberg L, et al. Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. Ecology. 1994;75(4):1042–1049.

23. Bergerud A. Prey Switching in a Simple Ecosystem. Scientific American. 1983;249(6):130–. doi:10.1038/scientificamerican1283-130.

24. Luque-Larena JJ, Mougeot F, Arroyo B, Vidal MD, Rodríguez-Pastor R, Escudero R, et al. Irruptive mammal host populations shape tularemia epidemiology. PLoS Pathogens. 2017;13(11). doi:10.1371/journal.ppat.1006622.

25. Viel JF, Giraudoux P, Abrial V, Bresson-Hadni S. Water vole (Arvicola terrestris scherman) density as risk factor for human alveolar echinococcosis. Am J Trop Med Hyg. 1999;61(4):559–565.

26. Raoul F, Michelat D, Ordinaire M, Decote Y, Aubert M, Delattre P, et al. Echinococcus multilocularis: secondary poisoning of fox population during a vole outbreak reduces environmental contamination in a high endemicity area. International Journal For Parasitology. 2003;33(9):945–954.

27. Baudrot V, Perasso A, Fritsch C, Giraudoux P, Raoul F. The adaptation of generalist predators' diet in a multi-prey context: insights from new functional responses. Ecology. 2016;97(7):1832–1841. doi:10.1890/15-0427.1.

28. Woodroffe R, Redpath SM. When the hunter becomes the hunted. Science. 2015;348(6241):1312–1314. doi:10.1126/science.aaa8465.

29. Delibes-Mateos M, Mougeot F, Arroyo B, Lambin X. Hunted predators: Charisma confounds. Science. 2015;349(6254):1294–1294. doi:10.1126/science.349.6254.1294-a.

30. Ríos-Saldaña CA, Delibes-Mateos M, Ferreira CC. Are fieldwork studies being relegated to second place in conservation science? Global Ecology and Conservation. 2018;14:e00389. doi:10.1016/j.gecco.2018.e00389.

31. Lindenmayer D, Likens J, Haywood A, Miezis L. Adaptive monitoring in the real world: proof of concept. Trends in ecology and evolution. 2011;26(12):641–646. doi:10.1016/j.tree.2011.08.002.

32. Giraudoux P, Couval G, Levret A, Mougin D, Delavelle A. Suivi à long terme d'une zone de pullulation cyclique de campagnols terrestres: le contrôle raisonné des populations est possible! Fourrages. 2017;230:169–176.

33. Giraudoux P, Delattre P, Habert M, Quere JP, Deblay S, Defaut R, et al. Population dynamics of fossorial water vole (Arvicola terrestris scherman): a land usage and landscape perspective. Agriculture Ecosystems and Environment. 1997;66:47–60.

34. Berthier K, Piry S, Cosson JF, Giraudoux P, Foltete JC, Defaut R, et al. Dispersal, landscape and travelling waves in cyclic vole populations. Ecology Letters. 2014;17(1):53–64. doi:10.1111/ele.12207.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

35. Delattre P, Giraudoux P, Baudry J, Quere JP, Fichet E. Effect of landscape structure on Common Vole (Microtus arvalis) distribution and abundance at several space scales. Landscape Ecology. 1996;11(5):279–288.

36. Duhamel R, Quéré JP, Delattre P, Giraudoux P. Landscape effects on the population dynamics of the fossorial form of the water vole (Arvicola terrestris sherman). Landscape Ecology. 2000;15:89–98.

37. Morilhat C, Bernard N, Bournais C, Meyer C, Lamboley C, Giraudoux P. Responses of Arvicola terrestris scherman populations to agricultural practices, and to Talpa europaea abundance in eastern France. Agriculture Ecosystems and Environment. 2007;122(3):392–398. doi:10.1016/j.agee.2007.02.005.

38. Morilhat C, Bernard N, Foltete JC, Giraudoux P. Neighbourhood landscape effect on population kinetics of the fossorial water vole (Arvicola terrestris scherman). Landscape Ecology. 2008;23(5):569–579. doi:10.1007/s10980-008-9216-9.

39. Foltete JC, Giraudoux P. A graph-based approach to investigating the influence of the landscape on population spread processes. Ecological Indicators. 2012;18:684–692. doi:10.1016/j.ecolind.2012.01.011.

40. Foltete JC, Couval G, Fontanierc M, Vuidel G, Giraudoux P. A graph-based approach to defend agro-ecological systems against water vole outbreaks. Ecological Indicators. 2016;71:87–98. doi:10.1016/j.ecolind.2016.06.033.

41. Berny PJ, Buronfosse T, Buronfosse F, Lamarque F, Lorgue G. Field evidence of secondary poisoning of foxes (Vulpes vulpes) and buzzards (Buteo buteo) by bromadiolone, a 4-year survey. Chemosphere. 1997;35(8):1817–1829.

42. Giraudoux P, Delattre P, Quere JP, Damange JP. Structure and kinetics of rodent populations in a region under agricultural land abandonment. Acta Oecologica. 1994;15(4):385–400.

43. Raoul F, Defaut R, Michelat D, Montadert M, Pépin D, Quéré JP, et al. Landscape effects on the populations dynamics of small mammal communities: a preliminary analysis of prey-resource variations. Rev Ecol (Terre Vie). 2001;56:339–352.

44. Delattre P, Giraudoux P, Baudry J, Truchetet D, Musard P, Toussaint M, et al. Land use patterns and types of common vole (Microtus arvalis) population kinetics. Agriculture, Ecosystems and Environment. 1992;39:153–169.

45. Delattre P, De Sousa B, Fichet E, Quéré JP, Giraudoux P. Vole outbreaks in a landscape context: evidence from a six year study of Microtus arvalis. Landscape Ecology. 1999;14:401–412.

46. Giraudoux P. Utilisation de l'espace par les hôtes du ténia multiloculaire (Echinococcus multilocularis) : conséquences épidémiologiques. Université de Bourgogne; 1991. Available from: `https://tel.archives-ouvertes.fr/tel-00522886`.

47. Weber JM, Aubry S. Predation by foxes, Vulpes vulpes, on the fossorial form of the water vole, Arvicola terrestris scherman, in western Switzerland. Journal of Zoology, London. 1993;229:553–559.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

48. Raoul F, Deplazes P, Rieffel D, Lambert JC, Giraudoux P. Predator dietary response to prey density variation and consequences for cestode transmission. Oecologia. 2010;164:129–139.

49. von Döhren P, Haase D. Ecosystem disservices research: A review of the state of the art with a focus on cities. Ecological Indicators. 2015;52:490–497. doi:10.1016/j.ecolind.2014.12.027.

50. Delattre P, Giraudoux P, Damange JP, Quere JP. Recherche d'un indicateur de la cinétique démographique des populations du Campagnol des champs (Microtus arvalis). Revue d'Ecologie (Terre Vie). 1990;45:375–384.

51. Quéré JP, Raoul F, Giraudoux P, Delattre P. An index method applicable at landscape scale to estimate relative population densities of the common vole (Microtus arvalis). Revue d'Ecologie (Terre et Vie). 2000;55:25–32.

52. Giraudoux P, Pradier B, Delattre P, Deblay S, Salvi D, Defaut R. Estimation of water vole abundance by using surface indices. Acta theriologica. 1995;40(1):77–96.

53. Légifrance. Arrêté du 31 mars 2014 portant reconnaissance des organismes à vocation sanitaire dans le domaine animal ou végétal; 2014. Available from: `https://www.legifrance.gouv.fr/affichTexte.do?cidTexte=JORFTEXT000028811750&dateTexte=20191231`.

54. Quéré J, Le Louarn H. Les rongeurs de France. Faunistique et Biologie. Versailles: Editions QUAE; 2011.

55. Legifrance. Arrêté du 14 mai 2014 relatif au contrôle des populations de campagnols nuisibles aux cultures ainsi qu'aux conditions d'emploi des produits phytopharmaceutiques contenant de la bromadiolone; 2014. Available from: `https://www.legifrance.gouv.fr/affichTexte.do?cidTexte=JORFTEXT000029039908`.

56. Crocker D, Hart A, Gurney J, McCoy C, Central Science Laboratory. Project PN0908: methods for estimating daily food intake of wild birds and mammals. Department for Environment, Food and Rural Affairs; 2002. Available from: `http://sciencesearch.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&Completed=0&ProjectID=6619`.

57. Henri C, Lafontaine L, Mouches A. In: Le Blaireau (Meles meles Linnaeus, 1758). SFEPM; 1988. p. 35.

58. Artois M. In: Le Renard roux (Vulpes vulpes Linnaeus, 1758). SFEPM; 1989. p. 90.

59. Artois M, Duchene MJ, Pericard JM, Xemar V. In: Le Chat domestique errant ou Haret (Felis catus, Linnaeus 1758). SFEPM; 2001. p. 50.

60. Stahl P, Léger F. In: Le Chat sauvage d'Europe (Felis silvestris Schreber, 1777). SFEPM; 1992. p. 50.

61. Cramp S. Handbook of the Birds of Europe, the Middle East and North Africa. Oxford University Press; 1994.

62. R Core Team. R: A Language and Environment for Statistical Computing; 2019. Available from: `https://www.R-project.org/`.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

63. Miller DL, Rexstad E, Thomas L, Marshall L, Laake JL. Distance Sampling in R. Journal of Statistical Software. 2019;89(1):1–28. doi:10.18637/jss.v089.i01.

64. Giraudoux P. pgirmess: Spatial Analysis and Data Mining for Field Ecologists; 2018. Available from: `https://CRAN.R-project.org/package=pgirmess`.

65. Bivand R, Keitt T, Rowlingson B. rgdal: Bindings for the 'Geospatial' Data Abstraction Library; 2019. Available from: `https://CRAN.R-project.org/package=rgdal`.

66. Bivand R, Rundel C. rgeos: Interface to Geometry Engine - Open Source ('GEOS'); 2019. Available from: `https://CRAN.R-project.org/package=rgeos`.

67. QGIS Development Team. QGIS Geographic Information System; 2009. Available from: `http://qgis.osgeo.org`.

68. Efron B, Tibshirani RJ. An Introduction to the Bootstrap. Monographs on Statistics and Applied Probability. Chapman and Hall/CRC; 1994. Available from: `https://www.crcpress.com/An-Introduction-to-the-Bootstrap/Efron-Tibshirani/p/book/9780412042317`.

69. Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press; 2001.

70. Buckland ST, Rexstad EA, Marques TA, Oedekoven CS. Distance Sampling: Methods and Applications. Methods in Statistical Ecology. Springer International Publishing; 2015. Available from: `http://link.springer.com/10.1007/978-3-319-19219-2`.

71. Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, et al. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology. 2010;47(1):5–14. doi:10.1111/j.1365-2664.2009.01737.x.

72. Burnham KP, Anderson DR. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. Springer; 2002.

73. Delattre P, Clarac R, Melis JP, Pleydell DRJ, Giraudoux P. How moles contribute to colonization success of water voles in grassland: implications for control. Journal of Applied Ecology. 2006;43(2):353–359. doi:10.1111/j.1365-2664.2006.01134.x.

74. LPO Franche-Comté (collectif). Les oiseaux de Franche-Comté. Répartition, tendances et conservation. Biotope; 2018.

75. Leclercq B, Desbrosses R, Giraudoux P. Cycles démographiques du campagnol terrestre (Arvicola terrestris), et reproduction et cinétique des Tetraonidae du massif du Risoux, Jura, France. Gibier et Faune Sauvage. 1997;14:31–47.

76. Angelstam P, Lindström E, Widén P. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. Ecography. 1985;8(4):285–298. doi:10.1111/j.1600-0587.1985.tb01181.x.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

77. Marcström V, Kenward RE, Engren E. The impact of predation on boreal tetraonids during vole cycles: an experimental study. Journal of Animal Ecology. 1988;57:859–872.

78. Erickson WA, Urban DJ. Potential risks of nine rodenticides to birds and non target mammals: a comparative approach. US Environmental Protection Agency, Office of Prevention, Pesticides and Toxic Substances; 2004. Available from: `http://www.fluoridealert.org/pesticides/EPA-HQ-OPP-2006-0955-0005.pdf`.

79. Ruette S, Lieury N, Albaret M, Arnauduc JP, Devillard S. Evolution des populations de renards en France. Analyse des suivis réalisés par comptage nocturne (2004-2013). Faune sauvage. 2015;306:1–6.

80. Demirbas Y. Density of European Hare and Red Fox in Different Habitats of Kirikkale Province (Central Anatolia), with a Low Level in Hare Number and an Expected Correlation in Spring. Acta Zoologica Bulgarica. 2015;67:515–520.

81. Laundre JW, Hernandez L, Ripple WJ. The Landscape of Fear: Ecological Implications of Being Afraid. The Open Ecology Journal. 2010;3(1).

82. Bleicher SS. The landscape of fear conceptual framework: definition and review of current applications and misuses. PeerJ. 2017;5:e3772. doi:10.7717/peerj.3772.

83. Molsher R, Newsome AE, Newsome TM, Dickman CR. Mesopredator Management: Effects of Red Fox Control on the Abundance, Diet and Use of Space by Feral Cats. PLoS ONE. 2017;12(1). doi:10.1371/journal.pone.0168460.

84. Read J, Bowen Z. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildlife Research. 2001;28(2):195–203. doi:10.1071/wr99065.

85. Marlow NJ, Thomas ND, Williams AAE, Macmahon B, Lawson J, Hitchen Y, et al. Cats (Felis catus) are more abundant and are the dominant predator of woylies (Bettongia penicillata) after sustained fox (Vulpes vulpes) control. Australian Journal of Zoology. 2015;63(1):18–27. doi:10.1071/ZO14024.

86. Panek M, Kamieniarz R, Bresiński W. The effect of experimental removal of red foxes Vulpes vulpes on spring density of brown hares Lepus europaeus in western Poland. Acta Theriologica. 2006;51(2):187–193. doi:10.1007/BF03192670.

87. Macdonald DW, Newman C. Population dynamics of badgers (Meles meles) in Oxfordshire, U.K.: numbers, density and cohort life histories, and a possible role of climate change in population growth. Journal of Zoology. 2002;256(1):121–138. doi:10.1017/S0952836902000158.

88. Holmala K, Kauhala K. Ecology of wildlife rabies in Europe. Mammal Review. 2006;36(1):17–36. doi:10.1111/j.1365-2907.2006.00078.x.

89. Sobrino R, Acevedo P, Escudero MA, Marco J, Gortázar C. Carnivore population trends in Spanish agrosystems after the reduction in food availability due to rabbit decline by rabbit haemorrhagic disease and improved waste management. European Journal of Wildlife Research. 2009;55(2):161–165. doi:10.1007/s10344-008-0230-7.

90. Norrdahl K, Korpimaki E. Effects of predator removal on vertebrate prey populations: Birds of prey and small mammals. Oecologia. 1995;103(2):241–248.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

91. Delattre P. Density of weasel (Mustela nivalis L.) and stoat (Mustela erminea L.) in relation to water wole abundance. Acta Zoologica Fennica. 1983;174:221–222.

92. Debrot S, Mermod C. The spatial and temporal distribution pattern of the stoat (Mustela erminea L.). Oecologia. 1983;59(1):69–73. doi:10.1007/BF00388075.

93. Erlinge S. Demography and Dynamics of a Stoat Mustela erminea Population in a Diverse Community of Vertebrates. Journal of Animal Ecology. 1983;52(3):705–726. doi:10.2307/4449.

94. Latham RM. The fox as a factor in the control of weasel populations. Journal of Wildlife Management. 1952;16(4):516–517.

95. Fernandez-de-Simon J, Coeurdassier M, Couval G, Fourel I, Giraudoux P. Do bromadiolone treatments to control grassland water voles (Arvicola scherman) affect small mustelid abundance? Pest Management Science. 2019;75(4):900–907. doi:10.1002/ps.5194.

96. Baudrot V, Fernandez-de Simon J, Coeurdassier M, Couval G, Giraudoux P, Lambin X. Trophic transfer of pesticides: the fine line between predator-prey regulation and pesticide-pest regulation. Journal of Applied Ecology. 2020;n/a(n/a). doi:10.1111/1365-2664.13578.

97. Montaz J, Jacquot M, Coeurdassier M. Scavenging of rodent carcasses following simulated mortality due to field applications of anticoagulant rodenticide. Ecotoxicology. 2014;23(9):1671–1680. doi:10.1007/s10646-014-1306-7.

98. Forin-Wiart MA. Identification des facteurs de variation de la prédation exercée par les chats domestiques (Felis silvestris catus) en milieu rural. Reims; 2014. Available from: `http://www.theses.fr/2014REIMS032`.

99. Condé B, Nguyen-Thi-Thu-Cuc, Vaillant F, Schauenberg P. Le régime alimentaire du chat forestier (F. silvestris Schr.) en France. Mammalia. 1972;36(1):112–119. doi:10.1515/mamm.1972.36.1.112.

100. Malo AF, Lozano J, Huertas DL, Virgós E. A change of diet from rodents to rabbits (Oryctolagus cuniculus). Is the wildcat (Felis silvestris) a specialist predator? Journal of Zoology. 2004;263(4):401–407. doi:10.1017/S0952836904005448.

101. Bernard N, Michelat D, Raoul F, Quere JP, Delattre P, Giraudoux P. Dietary response of Barn Owls (Tyto alba) to large variations in populations of common voles (Microtus arvalis) and European water voles (Arvicola terrestris). Canadian Journal of Zoology. 2010;88(4):416–426.

102. Lambin X, Petty S, Mackinnon JL. Cyclic dynamics in field vole populations and generalist predation. Journal Of Animal Ecology. 2000;69:106–118. doi:10.1046/j.1365-2656.2000.00380.x.

103. Pinot A, Barraquand F, Tedesco E, Lecoustre V, Bretagnolle V, Gauffre B. Density-dependent reproduction causes winter crashes in a common vole population. Population Ecology. 2016;58(3):395–405. doi:10.1007/s10144-016-0552-3.

104. Rodriguez-Pastor R, Jose Luque-Larena J, Lambin X, Mougeot F. "Living on the edge": The role of field margins for common vole (Microtus arvalis) populations in recently colonised Mediterranean farmland. Agriculture Ecosystems and Environment. 2016;231:206–217. doi:10.1016/j.agee.2016.06.041.

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

105. Jacob J, Ktadlec E. In: Rodent outbreaks in Europe: dynamics and damage. international rice research institute ed. Singleton G., Belmain S., Brown P., Hardy B.; 2010. p. 207–224.

106. Hansson L. The domestic cat as a possible modifier of vole dynamics. Mammalia. 1988;52(2):159–164. doi:10.1515/mamm.1988.52.2.159.

107. Paz A, Jareno D, Arroyo L, Vinuela J, Arroyo B, Mougeot F, et al. Avian predators as a biological control system of common vole (Microtus arvalis) populations in north-western Spain: experimental set-up and preliminary results. Pest Management Science. 2013;69(3):444–450. doi:10.1002/ps.3289.

108. Woods M, Mcdonald R, Ris S. Predation of wildlife by domestic cats Felis catus in Great Britain. Mammal Review Blackwell Science. 2003;33:174–188. doi:10.1046/j.1365-2907.2003.00017.x.

109. Loss SR, Will T, Marra PP. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications. 2013;4(1):1–8. doi:10.1038/ncomms2380.

110. Lélu M, Langlais M, Poulle ML, Gilot-Fromont E. Transmission dynamics of Toxoplasma gondii along an urban–rural gradient. Theoretical Population Biology. 2010;78(2):139–147. doi:10.1016/j.tpb.2010.05.005.

111. Gotteland C, Gilot-Fromont E, Aubert D, Poulle ML, Dupuis E, Dardé ML, et al. Spatial distribution of Toxoplasma gondii oocysts in soil in a rural area: Influence of cats and land use. Veterinary Parasitology. 2014;205(3):629–637. doi:10.1016/j.vetpar.2014.08.003.

112. Morters MK, Restif O, Hampson K, Cleaveland S, Wood JLN, Conlan AJK. Evidence-based control of canine rabies: a critical review of population density reduction. Journal of Animal Ecology. 2014; p. 6–14. doi:10.1111/j.1365-2656.2012.02033.x@10.1111/(ISSN)1365-2656.OAWEEK2014.

113. Comte S, Umhang G, Raton V, Raoul F, Giraudoux P, Combes B, et al. Echinococcus multilocularis management by fox culling: An inappropriate paradigm. Prev Vet Med. 2017;147:178–185. doi:10.1016/j.prevetmed.2017.09.010.

114. Bretagnolle V, Benoit M, Bonnefond M, Breton V, Church J, Gaba S, et al. Action-orientated research and framework: insights from the French long-term social-ecological research network. Ecology and Society. 2019;24(3). doi:10.5751/ES-10989-240310.

Acknowledgements

This article is dedicated to Régis Defaut, who deceased in 2008 and has been at the initiative and the true core of the ZELAC, a farmer group experimenting on environmentally-friendly control of *A. terrestris* populations in the study area, including the road side counts and transects used in this study since 1999. Special thanks to Denis Truchetet and Philippe Guillemard, from the Ministry of Agriculture, who have provided support since the beginning, to Jean-Marie Curtil from the *Chambre Interdépartementale d'Agriculture Doubs - Territoire de Belfort* and Raphaël Bouquet who have provided data on the evolution of grass and milk production, to Clementine Fristch and Francis Raoul for helpful references about food intakes, to the *Maison des*

bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

sciences de l'homme et de l'environnement Claude Nicolas Ledoux, who provided technical assistance to get IGN data, and to the innumerable FREDON technicians, students and volunteers who participated to the road-side counts for their technical assistance. Legal authorization for night road-side counts has been provided by the *Direction Départementale des Territoires du Doubs*. This research has been carried out in the *Zone atelier Arc jurassien* `https://zaaj.univ-fcomte.fr` and received financial support from the Ministry of Agriculture and from the *Région de Franche-Comté*.

Author contributions statement

PG conceived the study with Régis Defaut, designed the sampling plan and the data base. GC organized the transects and road side counts since 2006, AL collected transect and road-side count data, managed the data base since 2014 and georeferenced the observations. PG, AL, MC, GC participated to the road-side counts. EA provided critical insights about cat ecology. PG analyzed the data and wrote the MS. All authors discussed the results and reviewed the MS.

Supporting information captions

S1 kml file. Location of the study area (can be dropped in a Google Earth window or read from a GIS)

S2 Excel file. Road side counts (sheet 1) and list of species observed (sheet 2)

S3 Excel file. Small mammal data

S4 Word file. Detection functions of diurnal road side counts

S5 Word file. Detection functions of nocturnal road side counts

S6 Excel file. Data for computing theoretical daily food intakes

S7 Word file. Variations in biomass by species.

S8 Word file. Variations in theoretical daily food intake by species.

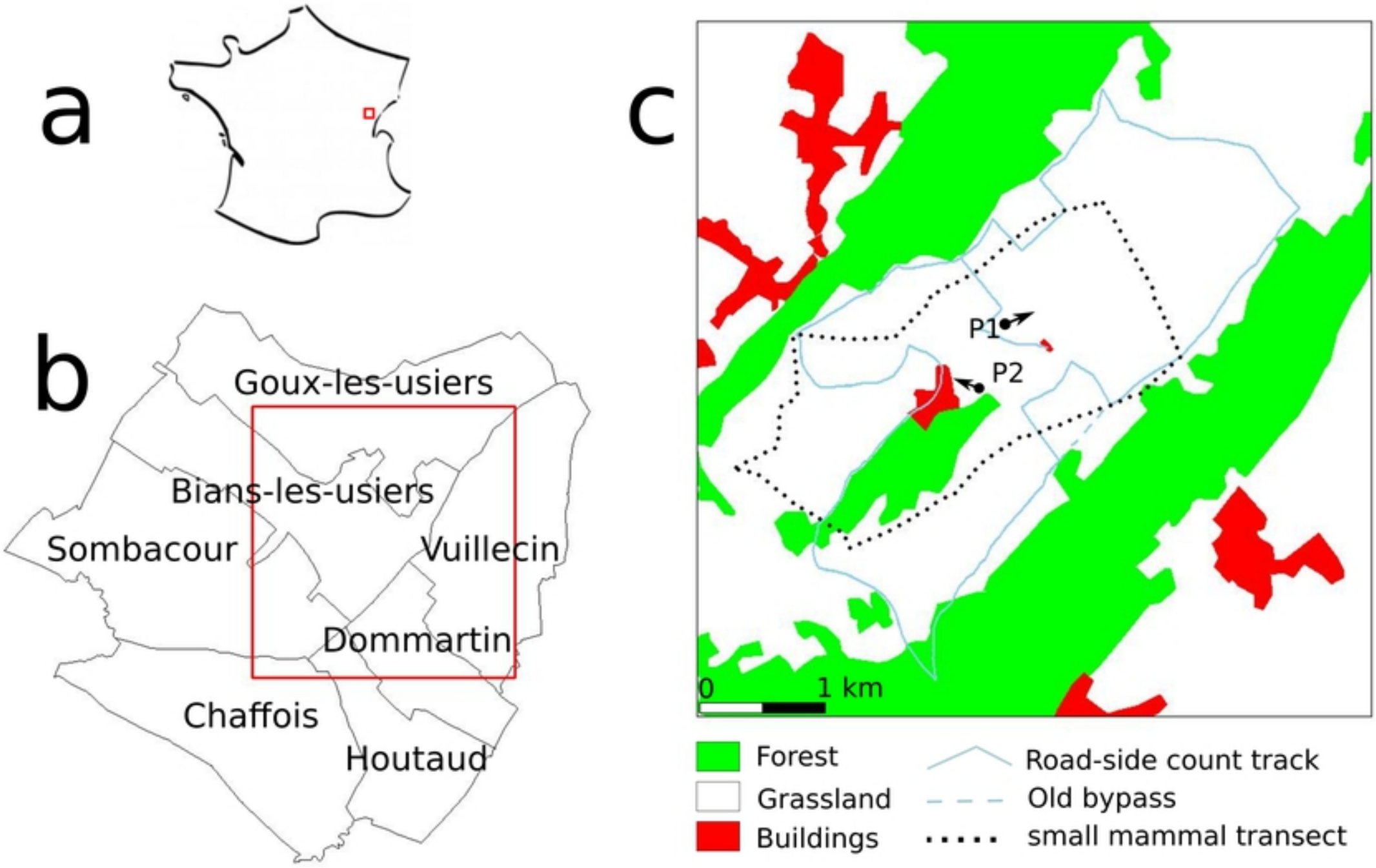
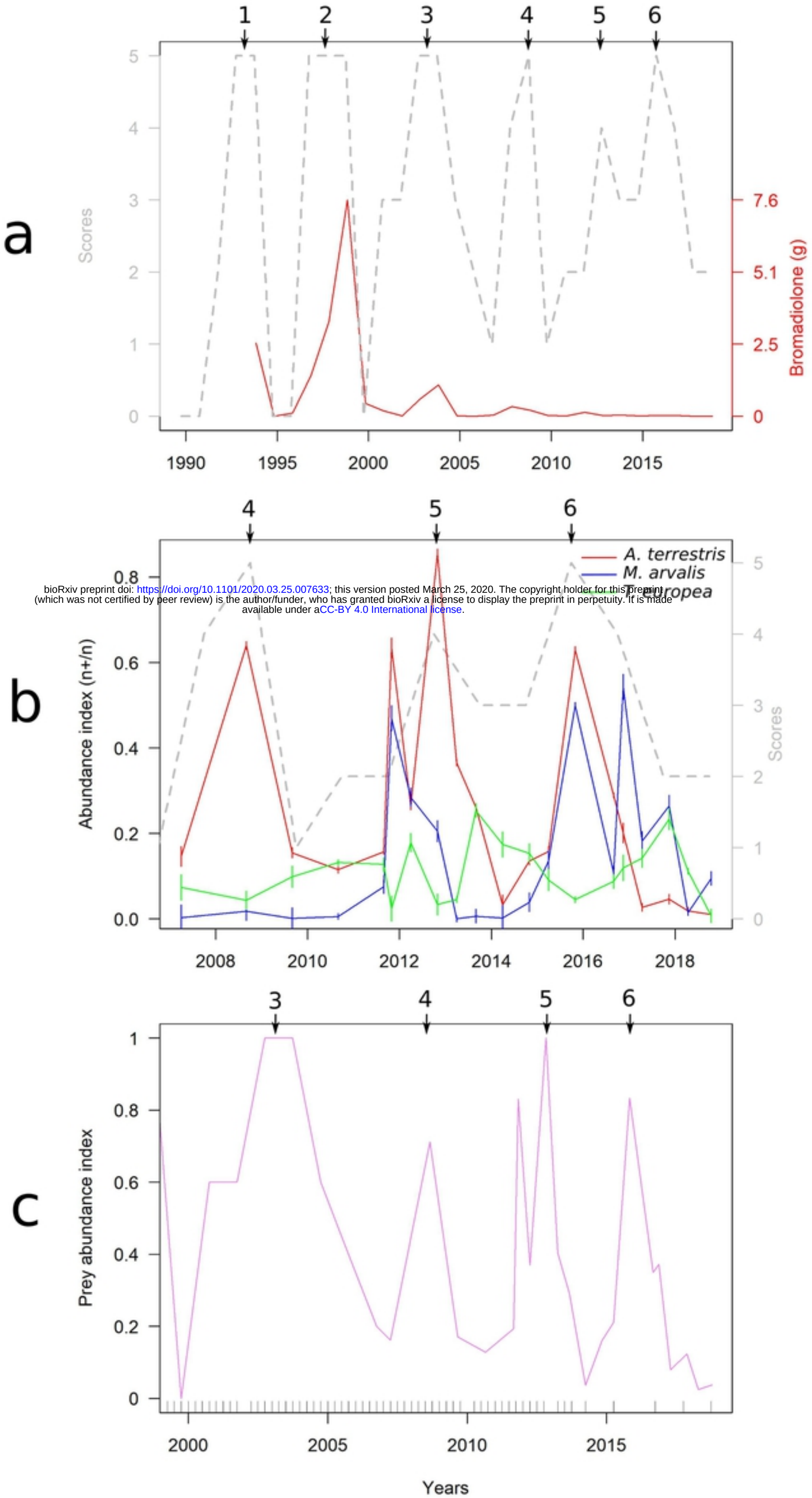

a
b
Goux-les-usiers
Bians-les-usiers
Sombacour
Vuillecin
Dommartin
Chaffois
Houtaud
c
P1
P2
0
1 km
Forest
Grassland
Buildings
Road-side count track
Old bypass
small mammal transect

Figure 1

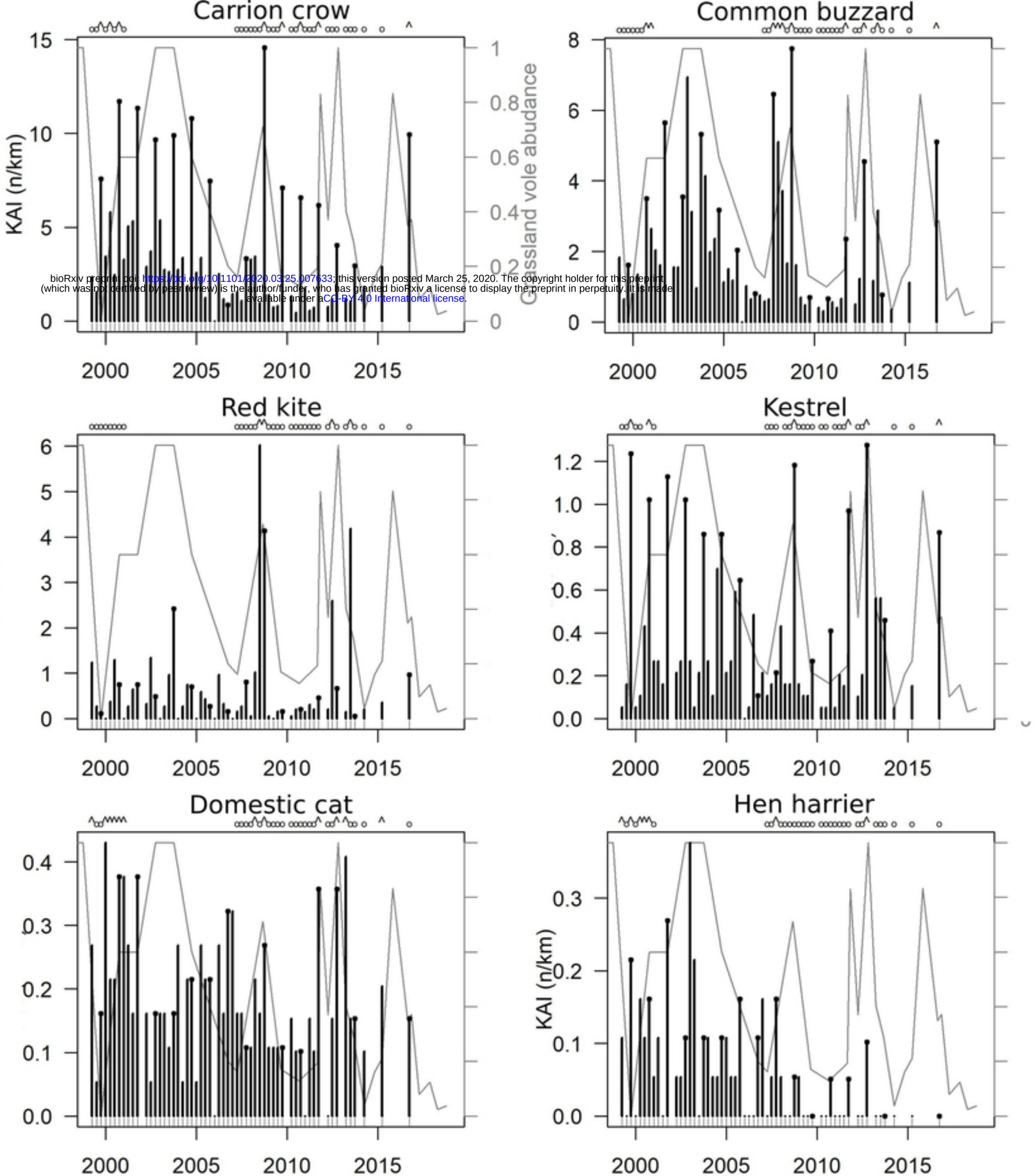
bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Figure 2



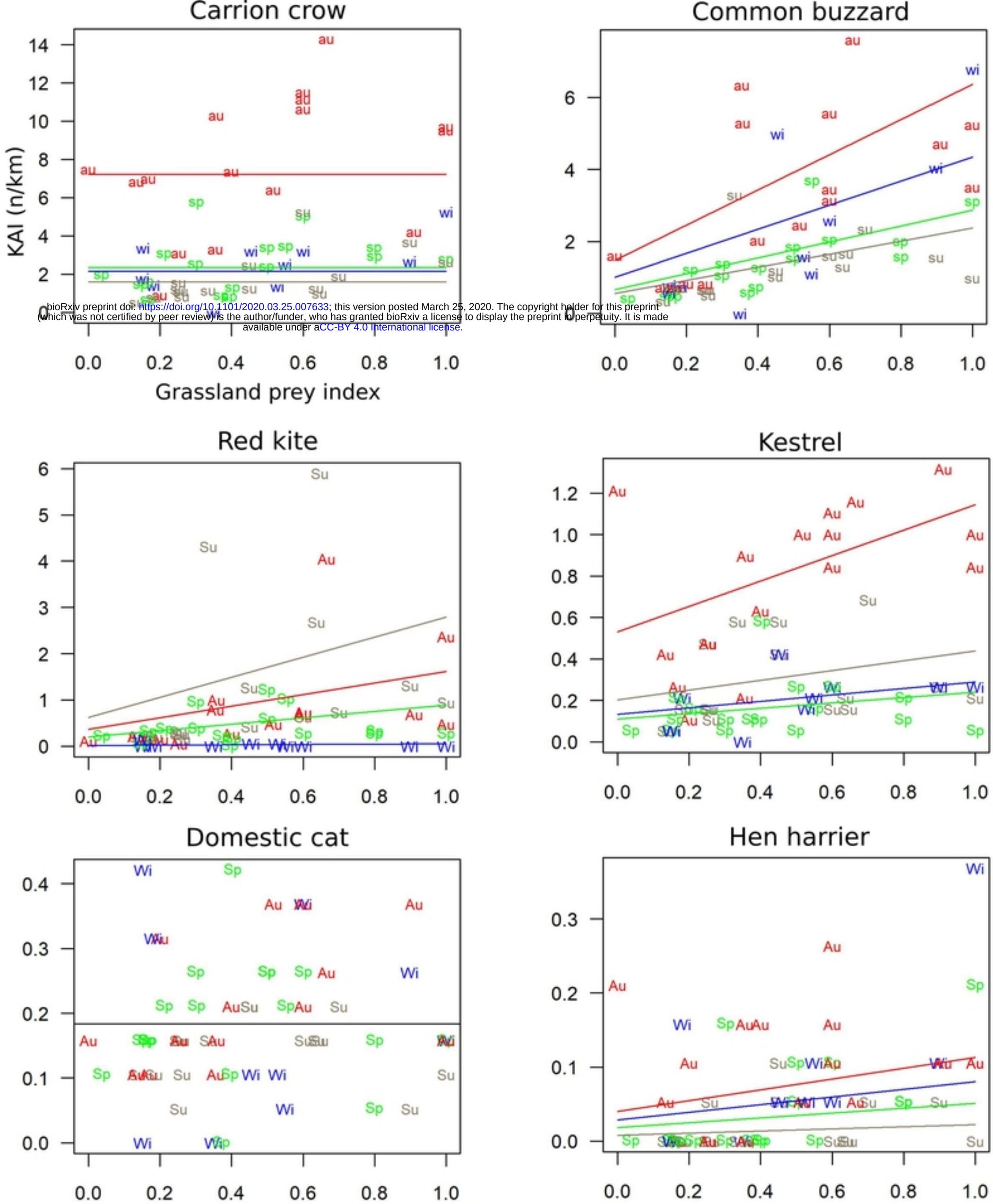
bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Figure 3



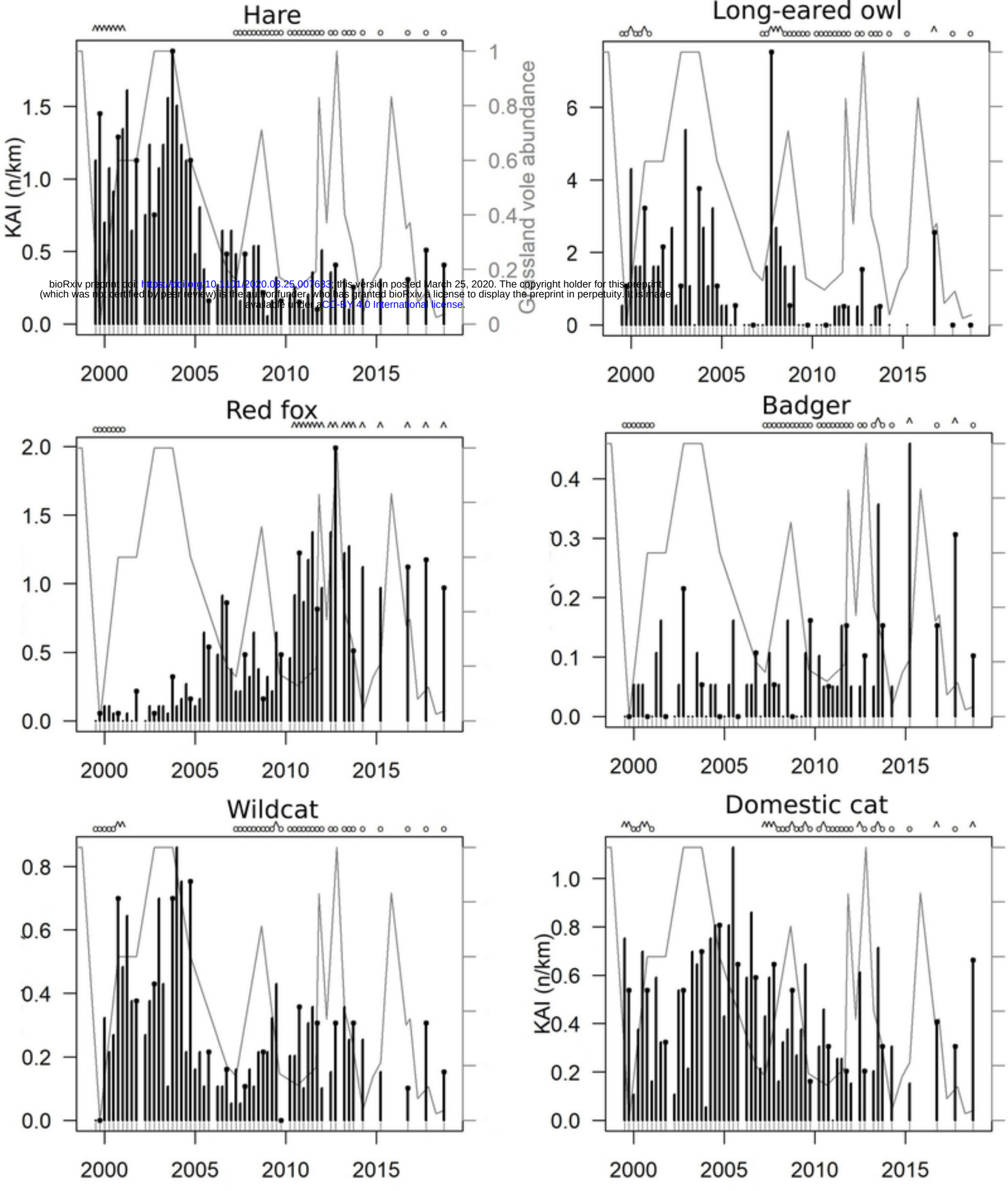
bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Figure 4



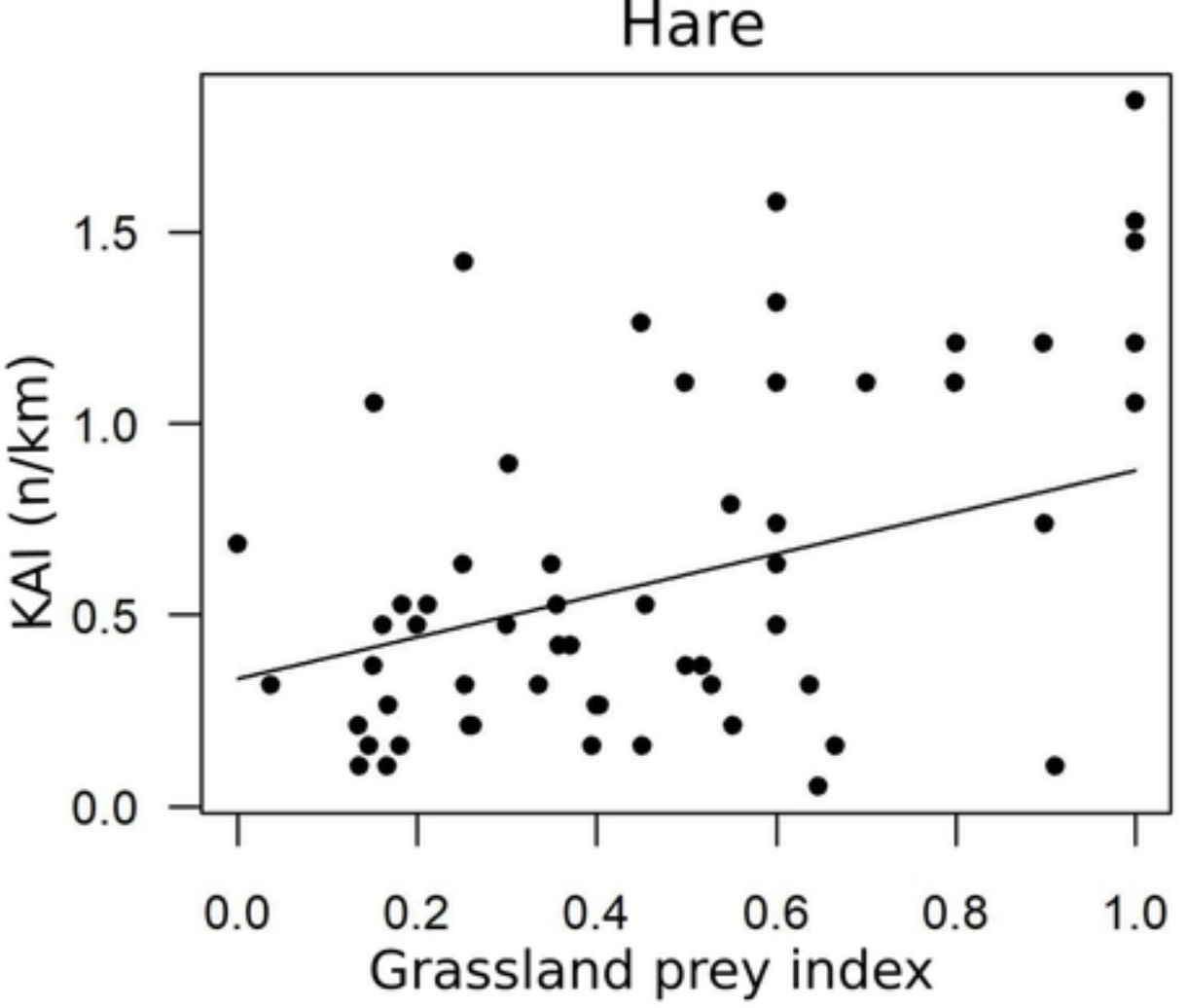
bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

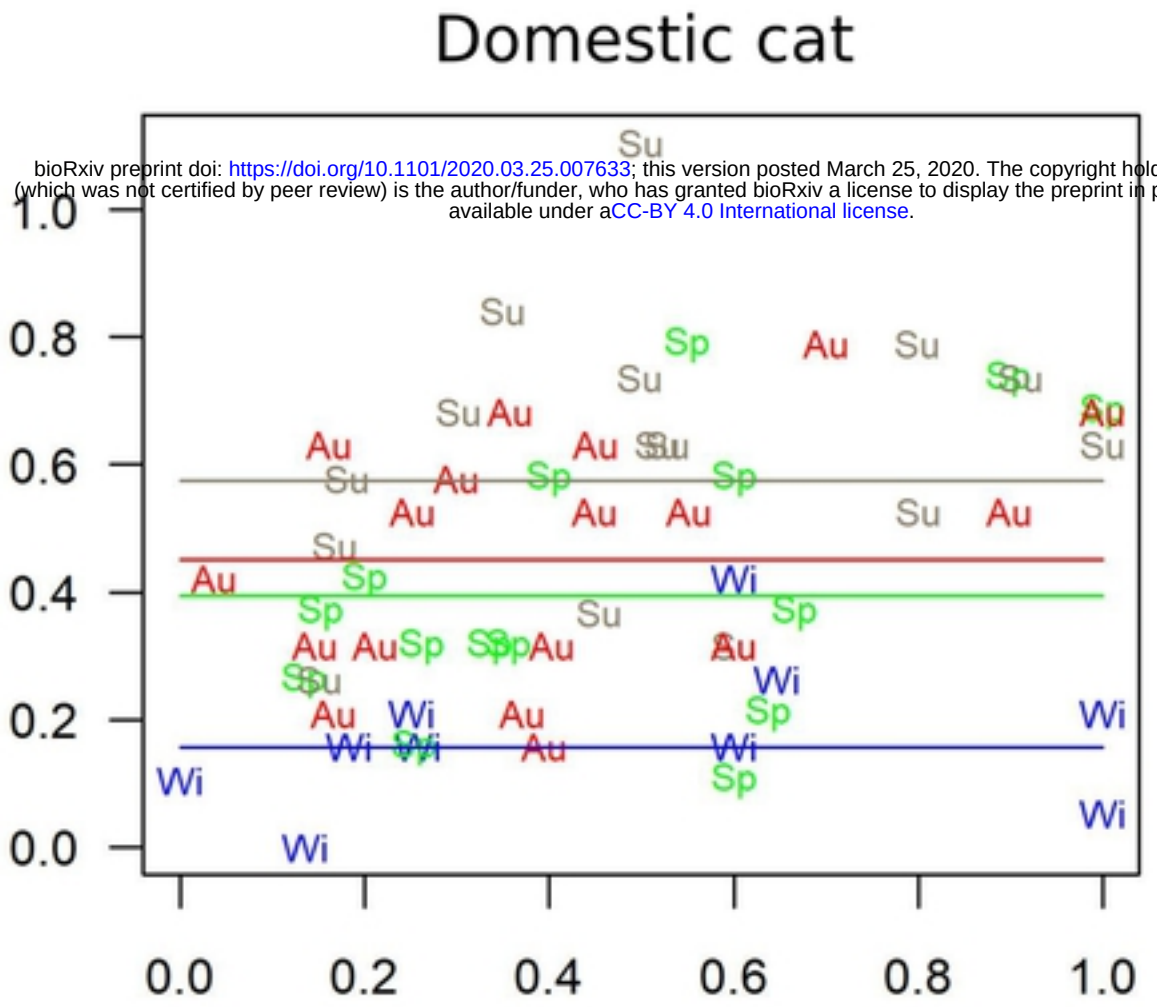
Figure 5



bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under a CC-BY 4.0 International license.

Figure 6





bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633; this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

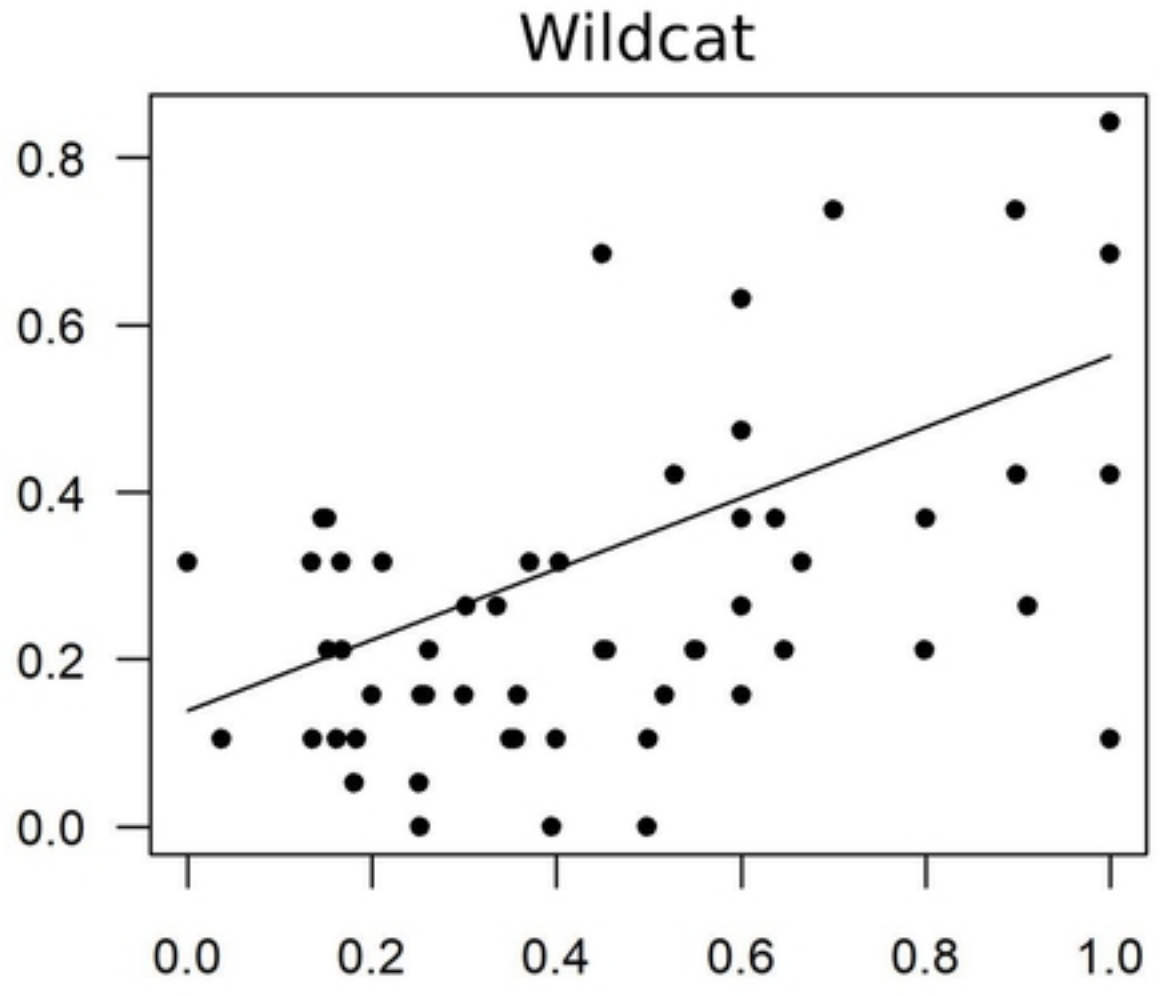


Figure 7

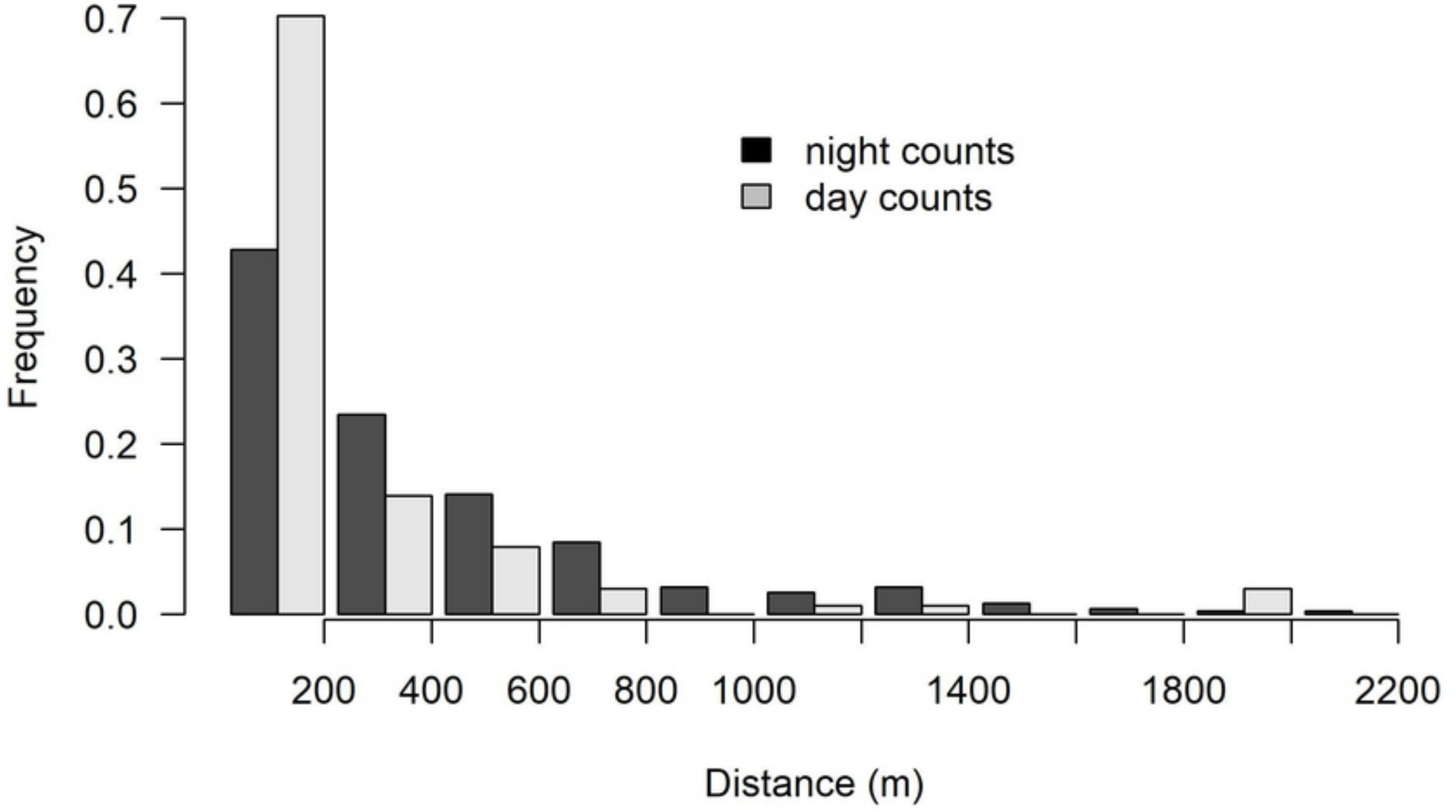
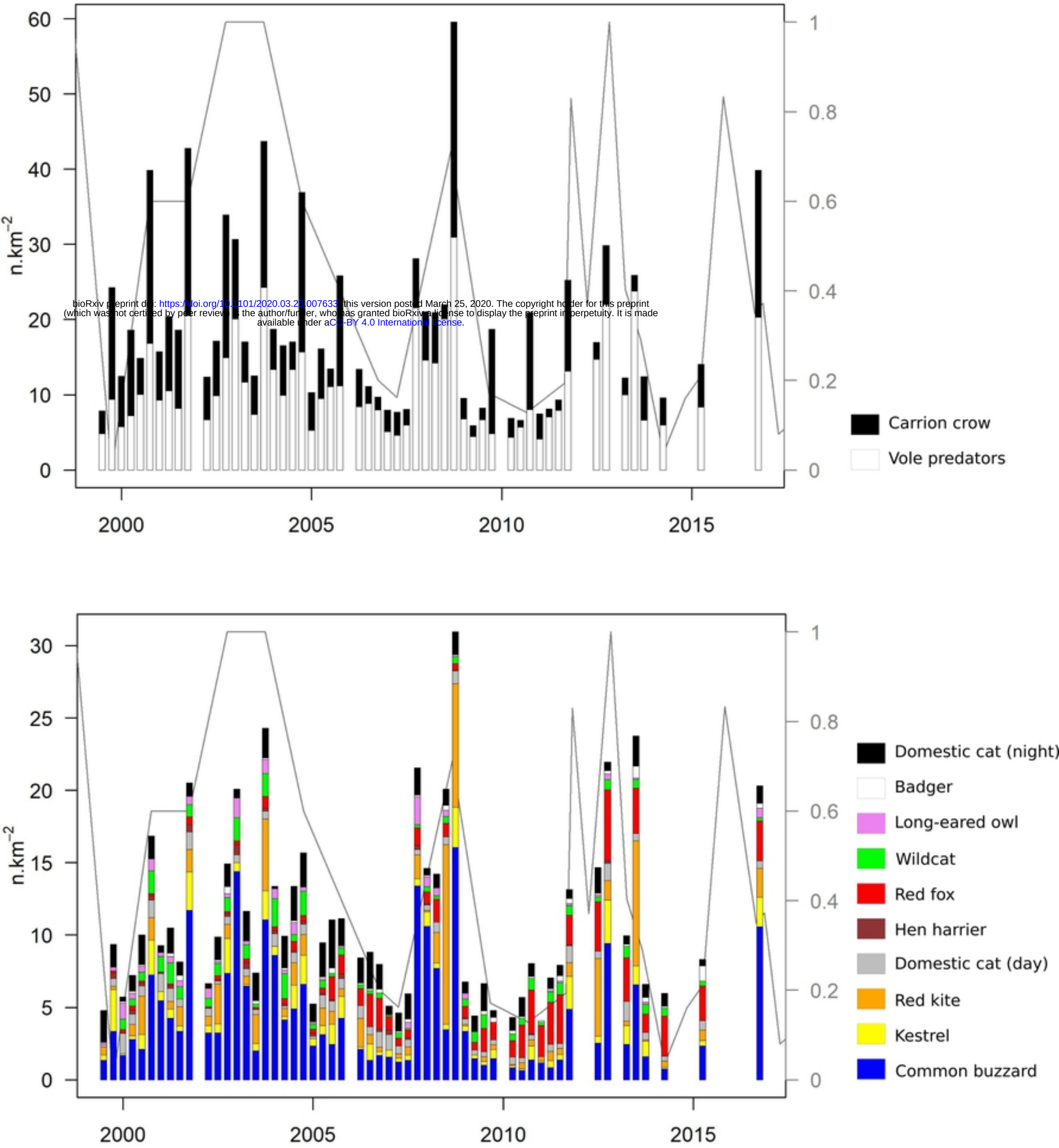

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Frequency
night counts
day counts
200
400
600
800
1000
1400
1800
2200
Distance (m)

Figure 8



bioRxiv preprint doi: https://doi.org/10.1101/2020.03.25.007633 this version posted March 25, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Figure 9