



Survival and cause-specific mortality of European wildcat (*Felis silvestris*) across Europe

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ABSTRACT

Humans have transformed most landscapes across the globe, forcing other species to adapt in order to persist in increasingly anthropogenic landscapes. Wide-ranging solitary species, such as wild felids, struggle particularly in such landscapes. Conservation planning and management for their long-term persistence critically depends on understanding what determine survival and what are the main mortality risks. We carried out the first study on annual survival and cause-specific mortality of the European wildcat with a large and unique dataset of 211 tracked individuals from 22 study areas across Europe. Furthermore, we tested the effect of environmental and human disturbance variables on the survival probability. Our results show that mortalities were mainly human-caused, with roadkill and poaching representing 57% and 22% of the total annual mortality, respectively. The annual survival probability of wildcat was 0.92 (95% CI = 0.87–0.98) for females and 0.84 (95% CI = 0.75–0.94) for males. Road density strongly impacted wildcat annual survival, whereby an increase in the road density of motorways and primary roads by 1 km/km² in wildcat home-ranges increased mortality risk ninefold. Low-traffic roads, such as secondary and tertiary roads, did not significantly affect wildcat's annual survival. Our results deliver key input parameters for population viability analyses, provide planning-relevant information to maintain subcritical road densities in key wildcat habitats, and identify conditions under which wildcat-proof fences and wildlife crossing structures should be installed to decrease wildcat mortality.

1. Introduction

Humans are changing ecosystems drastically across the globe, with often catastrophic effects on biodiversity (Ripple et al., 2017). While some species show adaptive responses, many others struggle to cope with human pressures (Sih, 2013). Particularly, habitat availability and behavioural plasticity play essential roles in determining whether a species can adapt to, and ultimately survive in, anthropogenic landscapes (Chevin et al., 2010; Sih, 2013). Furthermore, anthropogenic disturbance intensity determines if and to what extent animals alter their behaviour to adapt to the new environment (Wilson et al., 2020). Understanding the relationship between anthropogenic disturbance and species' survival is particularly important as there is increasing evidence of critical thresholds in adaptability (Chevin et al., 2010). Beyond such thresholds animals cannot cope with the rate of disturbance, which consequently leads to increased mortality and reduced reproduction (Chevin et al., 2010).

Fitness metrics (i.e. survival and reproduction) are powerful indicators for assessing the impact of anthropogenic disturbances on wildlife of conservation concern (Kight and Swaddle, 2007). The spatial variation in individual survival is driven by local resource-related differences of habitat quality and the mortality risk posed by humans, natural predators, parasites and competitors (DeCesare et al., 2014; Gaillard et al., 2010). In the case of naturally rare, wide-ranging species with low reproduction rates, small reductions in individual survival, especially in adult females, can have serious consequences for population persistence (Benson et al., 2020; Goodrich et al., 2008; Vickers et al., 2015). Therefore, management for the survival of threatened species hinges critically on information on the primary causes of mortality and a solid understanding of factors influencing individual survival across sexes and age-classes (Benson et al., 2020; Goodrich et al., 2008).

One of the most direct effects of anthropogenic disturbance is the fragmentation of natural habitats into smaller and more isolated patches, separated by a matrix of human-transformed land cover (Haddad et al., 2015). This human-transformed matrix consists of habitats unsuitable for many species, but importantly also of anthropogenic structures, such as roads, railways, fences or buildings, that pose barriers to movement and can increase mortality (Borda-de-Água et al., 2017; Haddad et al., 2015; Riley et al., 2003). Roads are particularly important in this context. Expansion of the global road network is a key driver of habitat fragmentation, especially in industrialised and densely-populated areas such as Europe, and roads negatively affect wildlife populations by hampering movement and increasing mortality risk (Coffin, 2007).

Felids are typically solitary species with large area requirements, which makes them struggle particularly with adapting to fragmented

anthropogenic landscapes (Riley et al., 2003; Vickers et al., 2015). Their high mobility increases the likelihood of road crossings and encounters with anthropogenic structures that increase mortality (Haines et al., 2005; Vickers et al., 2015), especially in areas with high road density (Poessel et al., 2014; Westekemper et al., 2021). Roadkill indeed represents the main source of mortality for various felid species (e.g. Ferreras et al., 1992; Haines et al., 2005; Vickers et al., 2015) and higher road densities within individuals' home-ranges are associated to increased mortality risk (Blackburn et al., 2021). Combined with intrinsic traits that make wild felids vulnerable, such as their low reproductive rates, roads and associated vehicular traffic can lead to marked population declines (Fahrig and Rytwinski, 2009). A second major cause of mortality for wild felids is poaching (i.e. illegal killing of animals), which often precludes their coexistence with humans (Goodrich et al., 2008; He et al., 2004; Heurich et al., 2018). Although 47% of the world's felids are currently facing high extinction risk, i.e. vulnerable or endangered on IUCN's (2021) Red List of Threatened Species, the relative importance of these factors often remains unclear. It is thus urgent to identify factors affecting the long-term population persistence of felids in anthropogenic landscapes.

The European wildcat (*Felis silvestris*), hereafter 'wildcat', is a small and elusive felid species protected by the Bern Convention and the EU Habitats Directive. It experienced a significant contraction of its historical range due to habitat fragmentation and extensive trapping and poaching. After legal protection, human persecution declined and over the subsequent decades the Central European and Italian metapopulations of wildcats have slowly recovered (Anile et al., 2017; Klar et al., 2009). In contrast, the Scottish and Iberian metapopulations continue to decline (Gil-Sánchez et al., 2020; Lozano and Malo, 2012). Habitat fragmentation, low prey availability, hybridisation with domestic cats and mortality caused by humans are still major threats for the species today (Anile et al., 2019; Klar et al., 2009; Lozano and Malo, 2012). What remains unclear are the factors that lead to population increase, stability or decline across most individual wildcat subpopulations. Estimation of fitness metrics such as annual survival is badly needed to support demographic analyses of local populations.

To the best of our knowledge, annual survival rates of the European wildcat have never been reported. Records of longevity shows that the wildcat can have a relatively long lifespan (up to 10 years in the wild; Anile et al., 2020) despite its small body mass, which often results in lower longevity (Healy et al., 2014). However, longevity in the wild also depends on several local factors (e.g. absence of natural predators and widespread refuges; Anile et al., 2020), and it has been found to be correlated with mortality such that species experiencing low mortality rates invest more in long-term survival (Healy et al., 2014). However, human-caused mortality plays a central role in this picture, often causing critical drops in survival (Andrén et al., 2006).

Overall, the impact of the different human-caused mortalities on wildcat survival is unclear. For example, roadkill represented an important source of mortality for wildcats along German motorways as well as other smaller roads with lower traffic intensity (Klar et al., 2009). However, these estimates are derived from the collection of carcasses along road segments and cannot be compared to other mortality causes. Likewise, wildcats show sex-specific responses to anthropogenic disturbance, with females avoiding areas near roads more than males (Jerosch et al., 2018; Oliveira et al., 2018). Indeed, females typically exploit smaller home-ranges in habitats with high natural vegetation cover and low human-disturbance for raising offspring, while males exploit larger home-ranges even outside the natural vegetation, which provides them access to multiple females (Beugin et al., 2016; Oliveira et al., 2018). This behaviour could mean males face higher mortality risk by increasing the probability of road crossings, as in other felid species (Poessel et al., 2014; Schwab and Zandbergen, 2011). However, potential differences in wildcats' mortality risk between sexes depending on home-range characteristics have never been tested. Regarding poaching, estimates based on the collection of carcasses for parasite surveys (Falsone et al., 2014) and during population monitoring activities (personal observation) suggest that human persecution still occurs,

but evidence of illegally-killed wildcats is scarce and does not allow for reliable estimations (Lozano and Malo, 2012).

The wildcat is a species of conservation concern, especially in the highly developed countries of Central and Western Europe, characterised by high human population density and substantial habitat fragmentation. Understanding the extent of different anthropogenic sources of mortality and how these affect the survival of wildcats is therefore a matter of urgency for wildcat conservation. To address this research gap, we analysed a large dataset of telemetry data from 211 tracked wildcats across Europe to estimate the annual survival of the species. We hypothesized i) roadkill to be the most important source of mortality for the wildcat and ii) a higher risk-taking propensity of males. Hence, we predicted a drop in the annual survival with increasing road density within the home-range and a significantly lower annual survival for males as a consequence of the higher risk taken in anthropogenic landscapes.

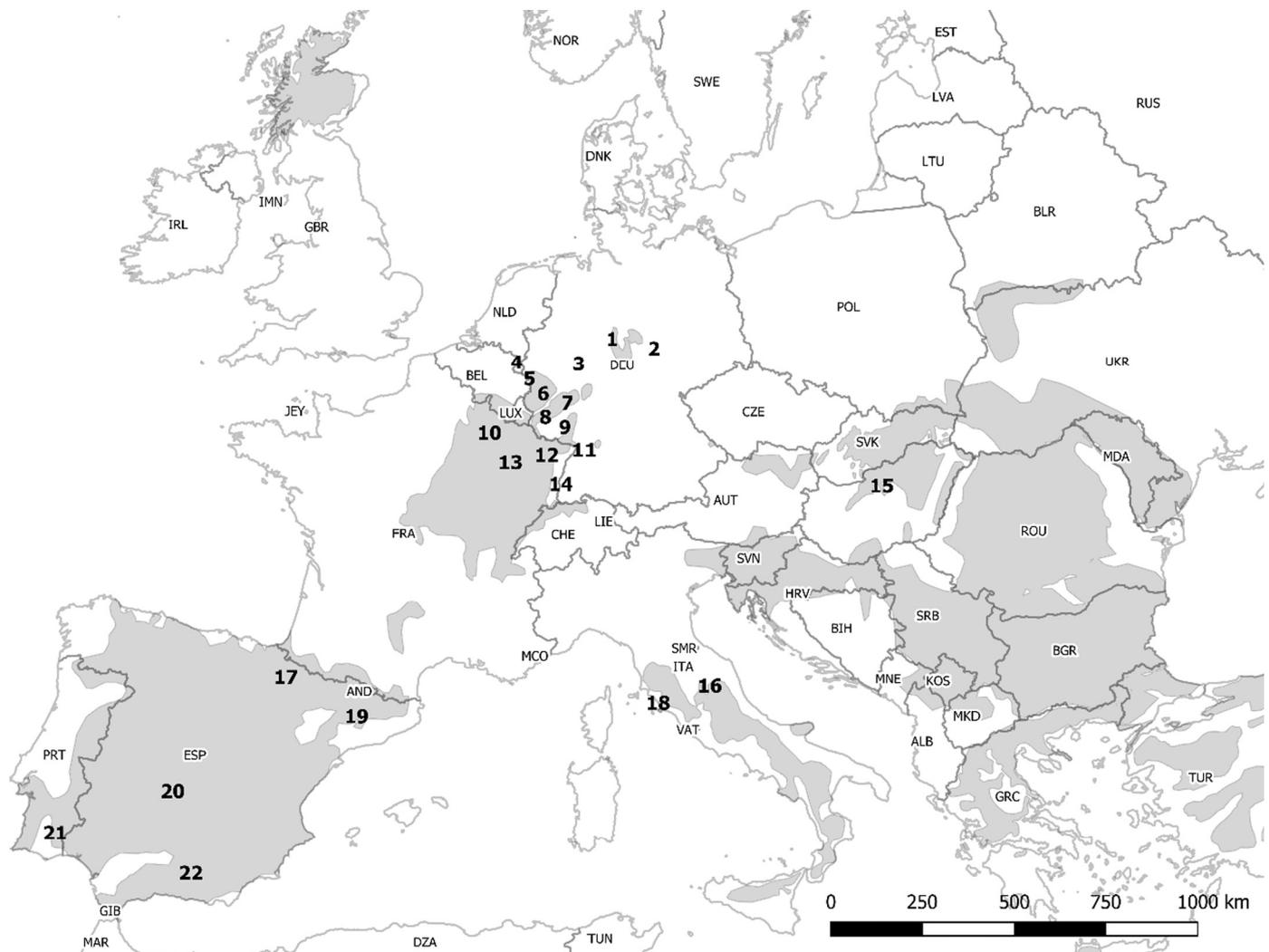


Fig. 1. Locations of the 22 study areas within the distribution range of the European wildcat adapted from the IUCN Red List of Threatened Species (version 2015.2) (<https://www.iucnredlist.org/>) and numbered from the North to the South: 1 - Solling; 2 - Golden Aue; 3 - Rothaar Mountains; 4 - Vijlenerbos; 5 - Eifel; 6 - Eifel/Moselle Mountains; 7 - Soonwald; 8 - Moselle Mountains/Hunsrueck/Haardtswald; 9 - Pfälzerwald; 10 - Argonne Ardennaise; 11 - Bienwald forest; 12 - Northern Vosges; 13 - Lorraine; 14 - Rheinauen Kaiserstuhl; 15 - Gödöllő Hills; 16 - Paradiso di Pianciano Estate; 17 - Izagaondoa Valley; 18 - Maremma Regional Park; 19 - Lleida region; 20 - Cabañeros National Park; 21 - Gudiana Valley Natural Park; 22 - Sierra Arana.

2. Materials and methods

2.1. Data collection and study areas

Our study was based on data provided by the collaborative EURO-WILDCAT project (<https://eurowildcat.org/>) and external research groups. We collected data from 211 individuals in 22 study areas, distributed in 7 countries across Europe (Fig. 1; Appendix A, Table A1). Most wildcats were genetically identified, with only few exceptions where the classification was based on phenotypical characteristics of the coat pattern (Kitchener et al., 2005; Ragni and Possenti, 1996). No hybrids were included in the analysis. Overall, our dataset contained 63,069 radio-tracking days (mean = 244.45 days \pm 152.30 standard deviation). The sex ratio was balanced (females = 109, males = 102), while age was skewed towards adults, with 79.07% adults (>2 years) and 20.93% subadults (1–2 years). We excluded juveniles (<1 year) from the analyses because the sample size was too small to estimate their survival (5.9%). We categorised mortality causes into “roadkill”, “poaching”, “mowing”, “disease” and “unknown”.

2.2. Environmental and human disturbance variables

Wildcat home-ranges were the spatial unit of our analysis because the home-range represents the portion of the landscape that affects the survival of individuals (see Appendix A for details on the home-range estimation). We reclassified the Corine Land Cover (CLC) map (Büttner, 2014) at a spatial resolution of 100 m (<https://www.copernicus.eu>) into 13 classes assumed to be ecologically relevant from the perspective of wildcats (Appendix A, Table A2), and we calculated the proportion of each class within the individual home-range. We followed Russo et al. (2020) and used different CLC inventories for each individual depending on the year of monitoring, specifically: the 1990 CLC inventory for home-ranges from 1990 to 1998; the 2000 CLC inventory for home-ranges from 1999 to 2003; the 2006 CLC inventory for home-ranges from 2004 to 2009; the 2012 CLC inventory for home-ranges from 2010 to 2014; the 2018 CLC inventory for home-ranges from 2015 to 2018. To capture the effect of forest configuration, we segmented the forest class in a binary CLC forest/non-forest map into three forest fragmentation classes: core forest (forest pixels not bordering other non-forest), edge forest (forest pixels bordering non-forest), and non-forest, using Morphological Spatial Pattern Analysis (Vogt et al., 2007). We then calculated the share of each fragmentation class per home-range. As measures of topography, we included average elevation (m) and slope (degrees) per home-range, derived from the ‘Shuttle Radar Topography Mission’ (<http://srtm.csi.cgiar.org/>) (Jarvis et al., 2008). We downloaded ‘OpenStreetMap’ road data from ‘Geofabrik’ (2018) and considered paved and public roads that represent a significant risk for the species, namely: motorways (i.e. major divided highways); primary (i.e. national roads often link larger towns); secondary (i.e. regional roads often link towns); tertiary (i.e. local roads often link smaller towns and villages). This classification is also related to traffic intensity, with motorways and primary roads being the busiest. In the absence of actual data on traffic intensity, we followed Pinto et al. (2018) and reclassified motorways and primary roads as high-traffic roads, and secondary and tertiary roads as low-traffic roads. Trunk roads were not present in any of the wildcats’ home-ranges. We calculated the density of each road class within home-ranges by dividing the length of roads (km) in the home-range by the home-range area itself (km²). Five individuals from the study areas “Eifel/Moselle Mountains” were not included in the spatial analysis because they were monitored during A60 motorway construction (i.e. zero traffic) (Klar et al., 2009; personal communication). Furthermore, to obtain unbiased results, seven individuals from the same study area and one individual from “Golden Aue” were removed from the spatial analysis because they were monitored after implementation of wildcat-proof fencing, which was never surmounted by wildcats, thus preventing access to the motorway

(Klar et al., 2009; personal communication). Collinearity between variables and summary of the covariates is shown in Appendix A.

2.3. Survival analysis

To investigate the most important sources of mortality, we estimated cause-specific mortality rates by means of the weighted empirical cumulative distribution function presented by Geskus (2011), which allows for right-censored and left-truncated data. In such a framework, individuals that sustain a competing event (i.e. died from a cause different from the cause of interest) remain in the risk set with a weight depending on the censoring and truncation distribution. As we aimed to study the cumulative incidence function for all the causes of death, a reweighted dataset was built for each of the five mortality causes with the help of the function ‘crprep’, implemented in the R package “mstate” (de Wreede et al., 2011). We then fitted five different models, one for each mortality cause, with the function ‘survfit’ in the R package survival (Therneau, 2015) as shown in Geskus (2011).

We implemented semi-parametric Cox proportional-hazards models to test the effects of covariates, particularly the variables road density and sex, on survival time (Cox, 1972). As we considered spatial variables, this analysis was based only on individuals who met the criteria for home-range calculation. We chose an annual recurrent timescale (1 May–30 April) in which individuals enter the model in a staggered manner (Pollock et al., 1989) in the day and month of the release with GPS or VHF transmitter. An individual is right-censored if the death does not occur before the end of the monitoring or if it is still monitored until the end of the recurrent timescale (30 April). In the latter case, the individual re-enters on the first of May. The risk sets will then include all individuals alive on the day and month of death regardless of the study year (Fieberg and DelGiudice, 2009). In our case, this gives larger and consistent risk sets over time despite the wide timespan of the survey (28.7 years).

We first ran mixed-effect models with ‘study area’ and ‘animal ID’ as random-effects with the R package “coxme” (Therneau, 2019) and tested significance of the random effects (i.e. if a variance parameter is equal to zero) with a Likelihood Ratio Test (LRT). If random-effects were non-significant, we simplified to fixed-effect models (i.e. no random effects) in the “survival” package (Therneau, 2015). Some individuals had multiple observations in the dataset because they were monitored in multiple calendar years with different home-ranges or changed from subadults to adults (Benson et al., 2020). Thus, we clustered observations by ‘animal ID’ in the model fit to account for correlations (Fieberg and DelGiudice, 2009; Therneau and Grambsch, 2000) and to enable robust “sandwich” SE estimates. As dictated by the low number of mortality events ($n = 15$), typical of rare and elusive species that live in low population densities, we tested no more than two variables simultaneously to avoid overfitting models (Benson et al., 2020; Fieberg and DelGiudice, 2009; Peduzzi et al., 1995). All continuous variables used in the models were scaled. We used ‘Akaike’s Information Criteria’ for small sample sizes (AICc) for model selection and applied Analysis of Variance (ANOVA) to ascertain the significance of covariates in the most supported models. We provided predictions of annual survival and 95% confidence intervals in relation to the road density of high-traffic roads based on the coefficients of the most highly ranked Cox model with the function ‘Predict’ in the R package rms (Harrell, 2020). We estimated sex- and age-specific annual survival rates of all individuals adjusted for the Cox proportional hazards-model covariates by means of the function ‘survfit’ in the “survival” package (Therneau, 2015). Model diagnostics and a Bayesian model alternative fitting all variables at the same time are shown in Appendix A.

Finally, we tested if our estimates were in line with the maximum longevity of the wildcat by inspecting available data on longevity of 156 carnivores and 30 felid species from the AnAge database (de Magalhães and Costa, 2009). Only data on longevity in captivity are available for such a large number of species. We limited the dataset to carnivore

species with “acceptable” or “high” data quality (Lemaître et al., 2014). We ran two linear models (i.e. one accounting for all carnivores in the database, one only accounting for felid species) to test the effect of adult weight (which is available for more species in the database than the body mass), on the maximum longevity, in the manner of Lemaître et al. (2014) who used data on all mammal species.

3. Results

Female home-range sizes ranged from 0.69 km² to 53.04 km² (mean = 4.63 km² ± 0.44 SE), while male home-range sizes ranged from 0.68 km² to 54.81 km² (mean = 14.79 km² ± 0.93 SE). Similar densities of high-traffic roads were found in females' (mean = 0.07 km/km² ± 0.02 SE) and males' (mean = 0.07 km/km² ± 0.01 SE) home-ranges, while lower densities of low-traffic roads were found in females' home-ranges (mean = 0.22 km/km² ± 0.04 SE) compared to males' home-ranges (mean = 0.35 km/km² ± 0.03 SE) (Fig. 2; Appendix A, Table A3).

Of 211 tracked individuals, a total of 24 mortality events were recorded. 83.25% of the wildcat annual mortality was caused by humans, with roadkill being the most frequent cause (Table 1; Appendix B, Fig. B1). Roadkill occurred in every region included in the study. Seven females and six males died in vehicle collisions, from which six were subadults and seven were adults.

Altogether, 162 individuals (90 females, 72 males; 15 mortality events) met the prerequisites for home-range calculation and were included in our Cox models to test for the effect of covariates on annual wildcat survival. The random-effects of ‘study area’ and ‘animal ID’ were not significant (top ranked model: LogLik = 0.02, df = 1, P = 0.89) so we performed fixed-effect Cox models only. The most important variable affecting the survival of wildcats was the density of high-traffic roads (i.e. motorways and primary roads) within the home-range, which was included in all four best-performing models with $\Delta AICc < 2$ (Table 2). The ANOVA of the selected models showed that density of high-traffic

Table 1

Summary of cause-specific mortality with the percentage for each cause. Annual mortality rates (AMR) of each cause are reported, with standard errors (SE) and percentages (%) of the total annual mortality rate. Mowing = agricultural activity that involves the use of machinery for cutting grass.

Causes of mortality	N. of events recorded	% of total events	AMR	SE of AMR	% of AMR
Roadkill	13	54.17%	0.079	0.022	56.68%
Poaching	5	20.83%	0.031	0.014	22.31%
Disease	3	12.50%	0.012	0.007	8.67%
Unknown	2	8.33%	0.011	0.008	8.08%
Mowing	1	4.17%	0.006	0.006	4.26%
Sum	24	100%	0.140	0.057	100%

roads was the only statistically significant variable (Wald test $\chi^2 = 15.78$, df = 1, P = 0.00007). The exclusion of either sex ($\chi^2 = 2.88$, df = 1, P = 0.09), density of low-traffic roads ($\chi^2 = 1.64$, df = 1, P = 0.20) or age class ($\chi^2 = 1.02$, df = 1, P = 0.31), did not significantly decrease the variance explained. According to the model with only the density of high-traffic roads as an explanatory variable (Appendix B, Table B1), an increase in the road density by 1 km/km² increases the hazard rate by a factor of 8.89 ± 0.55 robust SE. High-traffic roads also had on average the lowest density in wildcat home-ranges (0.07 ± 0.02 km/km²; Fig. 2; Appendix A, Table A3). Predictions of annual survival under different road density conditions based on this coefficient are provided in Appendix B, Table B2.

The mean annual survival of all individuals adjusted for the most highly ranked Cox model covariates (i.e. at the mean road density of high-traffic roads) was 0.90 ± 0.03 SE (95% CI = 0.85–0.95). The mean annual survival was higher for females (0.92 ± 0.03 SE; 95% CI = 0.87–0.98) than for males (0.84 ± 0.05 SE; 95% CI = 0.75–0.94), while it was 0.85 ± 0.07 SE (95% CI = 0.72–1.00) for subadults and 0.90 ± 0.03 SE (95% CI = 0.84–0.96) for adults. The annual survival was 0.90 ± 0.06 SE (95% CI = 0.79–1.00) for subadult females and 0.93 ± 0.03 SE

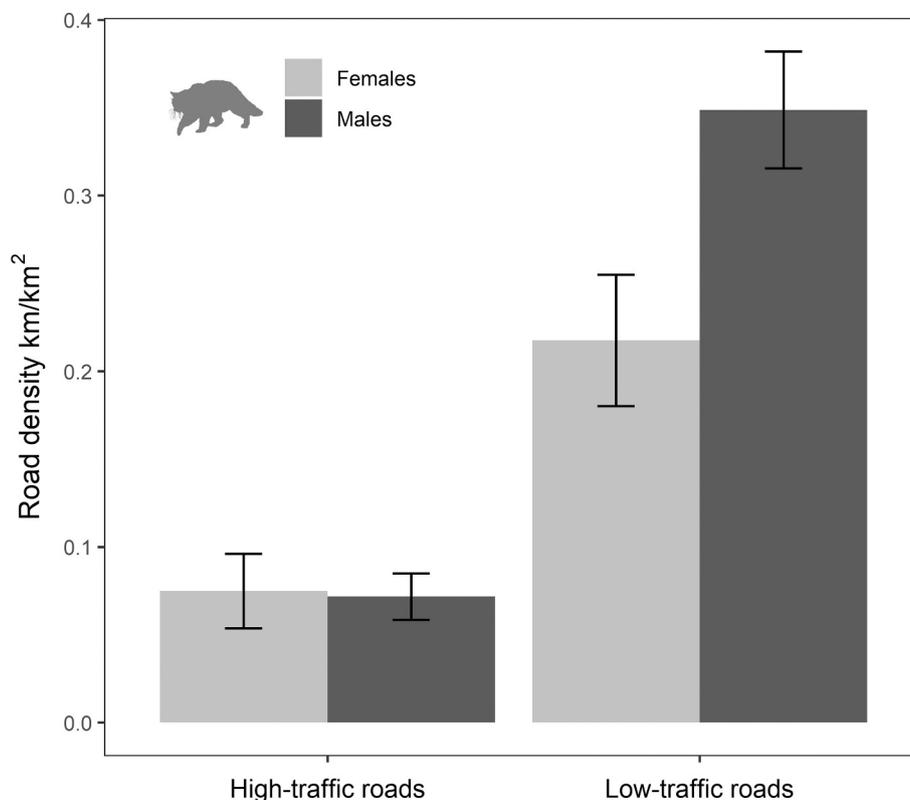


Fig. 2. Average densities with SE of high-traffic (i.e. motorways and primary roads) and low-traffic roads (i.e. secondary and tertiary roads) in female and male wildcat home-ranges. Females had lower densities of low-traffic roads in their home-ranges, while no difference on high-traffic roads were found.

Table 2

Cox model selection based on AICc. Names of columns: K = number of model parameters; AICc = Akaike information criterion for small sample sizes; Δ AICc = Delta AICc; W = AICc Weight.

Models	K	AICc	Δ AICc	W
High-traffic roads density + Sex	2	141.57	0.00	0.24
High-traffic roads density	1	142.32	0.75	0.17
High-traffic roads density + Low-traffic roads density	2	142.78	1.20	0.13
High-traffic roads density + Age	2	143.46	1.89	0.09
Coniferous forest + Sex	2	145.51	3.94	0.03
Sex	1	145.58	4.01	0.03
NULL	0	145.82	4.25	0.03
Agricultural fields + Sex	2	146.02	4.45	0.03
Sex + Area	2	146.14	4.57	0.02
Latitude	1	146.74	5.17	0.02
Pastures + Sex	2	146.74	5.17	0.02
Grasslands + Sex	2	147.07	5.50	0.02
Sex + Age	2	147.17	5.60	0.01
Scrublands + Sex	2	147.19	5.62	0.01
Low-traffic roads density	1	147.26	5.68	0.01
Age	1	147.30	5.73	0.01
Elevation + Sex	2	147.31	5.74	0.01
Low-traffic roads density + Sex	2	147.36	5.78	0.01
Mixed forest + Sex	2	147.36	5.79	0.01
Human infrastructures + Sex	2	147.37	5.80	0.01
Slope + Sex	2	147.59	6.02	0.01
Broadleaf forest + Sex	2	147.60	6.02	0.01
Forest edges + Sex	2	147.60	6.03	0.01
Area	1	147.78	6.20	0.01
Low-traffic roads density + Age	2	148.86	7.29	0.01

(95% CI = 0.87–0.99) for adult females, while it was 0.79 ± 0.1 SE (95% CI = 0.62–1.00) for subadult males and 0.85 ± 0.05 SE (95% CI = 0.76–0.96) for adult males (Fig. 3). Confidence intervals overlapped throughout, suggesting that differences in annual survival probabilities among sexes and age classes could not be discriminated with certainty given the current sample size and therefore we interpret these differences cautiously.

All model assumptions were met and no influential outlying observations were detected. The Bayesian model alternative confirmed high-traffic road density as the only variable affecting annual survival, though with a less pronounced effect (Appendix B). The maximum longevity of the wildcat in captivity (19 years) proved to be well predicted by adult weight (Appendix B, Fig. B6).

4. Discussion

Understanding the factors influencing the survival of species of conservation concern in anthropogenic landscapes is critical for identifying effective conservation measures, and thus for ensuring their long-term survival. Using a large and unique telemetry dataset, we assessed, for the first time, annual survival and cause-specific mortality of the European wildcat. Although our results reveal a relatively high annual survival probability, we found that 83% of the annual mortality of the wildcat was caused by humans, with roadkill being the most important cause of mortality. The risk of mortality increases by a factor of nine if the density of highly-trafficked roads in an individual's home-range increased by 1 km/km^2 .

Overall, human-caused mortality accounted for most of the wildcat annual mortality in our dataset, reaching 83%. High mortalities caused by humans are often found in carnivores because landscape transformation and constant human presence forces them to live in high-risk areas. Similar values of human-caused mortality have been reported in other felid species such as the Amur tiger (*Panthera tigris altaica*) (83%; Goodrich et al., 2008) and the cougar (*Puma concolor*) (65%; Vickers et al., 2015) and for mesocarnivores such as the red fox (*Vulpes vulpes*) and the corsac fox (*Vulpes corsac*) (60%; Murdoch et al., 2010). While this highlights a clear conservation need for the wildcat and other

carnivores, it also provides concrete starting points for interventions – as anthropogenic mortality can indeed be addressed relatively directly in contrast to other pressures, such as from climate change.

Roadkills represented more than 50% of wildcat mortality across Europe. This finding corroborates the assumption that roadkill is the main source of mortality for the European wildcat (Westekemper et al., 2021). Our results are consistent with the high percentage of roadkills found by Falsone et al. (2014) despite the different methodologies used, thereby confirming the reliability of both studies. Our results are based on telemetry data, which provide unbiased estimates of cause-specific mortality rates by assuming that all the causes of mortality for a tracked animal have the same probability of occurring (Naef-Daenzer et al., 2017). The percentage of roadkills of the total mortality reported in our study is among the highest recorded for felid species in anthropogenic landscapes. For example, Haines et al. (2005) showed that roadkills accounted for 45% of ocelot (*Leopardus pardalis*) mortality in Texas, while it accounted for 28% of the cougar mortality in southern California (Vickers et al., 2015). Furthermore, with 13 roadkills out of 211 (6.2%) total tracked wildcats in our study, we found at a broader scale a similar pattern shown by Klar et al. (2009), who found one roadkill out of 12 (8.3%) tracked wildcats.

The effects of different road classes on wildcat's survival patterns varied considerably, with high-traffic roads (i.e. motorways and primary roads) showing a strong negative effect on annual survival. Based on Fig. 2, these road types occurred at lower densities in wildcat home-ranges in comparison with secondary and tertiary roads, suggesting either an avoidance in second-order habitat selection or extinction of wildcat populations in areas with a high density of motorways and primary roads due to high mortality. Although denser in wildcats' home-ranges and usually more widespread across the landscape (Blackburn et al., 2021; Westekemper et al., 2021), low-traffic roads did not significantly affect the survival in our study. This pattern can be explained by intrinsic properties of roads such as traffic intensity, roadway width and vehicular speed that make motorways and primary roads more hazardous to cross. For the same reason, high-traffic roads might discourage wildcats from crossing, as reported for badgers (Clarke et al., 1998). For example, in Germany wildcats crossed highly trafficked motorways and primary roads (2500–10,000 vehicles/day) less frequently than expected by chance, while observed and random road-crossing rates for less-trafficked local roads (200–300 vehicles/day) were equal (Klar et al., 2009). Even so, Klar et al. (2009) found 30–40% of the wildcats living along the motorway were killed each year, confirming that wildcat does cross high-traffic roads leading to high mortality. On the other hand, even roads with lower traffic intensity but more widespread across the landscape have been found to severely hinder genetic connectivity between wildcats' populations in Germany (Westekemper et al., 2021). Further studies on wildcat movement behaviour are needed to clarify the barrier effect of different road types and the mortality associated with crossings attempts.

An increase in the density of high-traffic roads in the home-range by 1 km/km^2 increases the risk of mortality ninefold. Klar et al. (2009) showed that road-crossings of high-traffic roads takes a heavy toll on wildcats, but the direct link between survival and the density of such roads was so far unknown. We enhance the current knowledge by showing how high-traffic roads density within individuals' home-ranges shapes wildcats' survival. According to our predictions (Appendix B, Table B2), annual survival probability of wildcats would decrease from 0.91 without roads to 0.88 with a density of high-traffic roads of 0.16 km/km^2 (i.e. the average high-traffic roads density in our study areas) in the home-range. For the highest value of high-traffic road density found in our study areas (0.67 km/km^2), annual survival drops to 0.67. However, the uncertainty of these estimates increases with increasing road density because of the low number of home-ranges with a very high density of high-traffic roads. To better understand the impact of very high road densities and potential thresholds for the survival of the species, telemetry studies focused on such areas are needed.

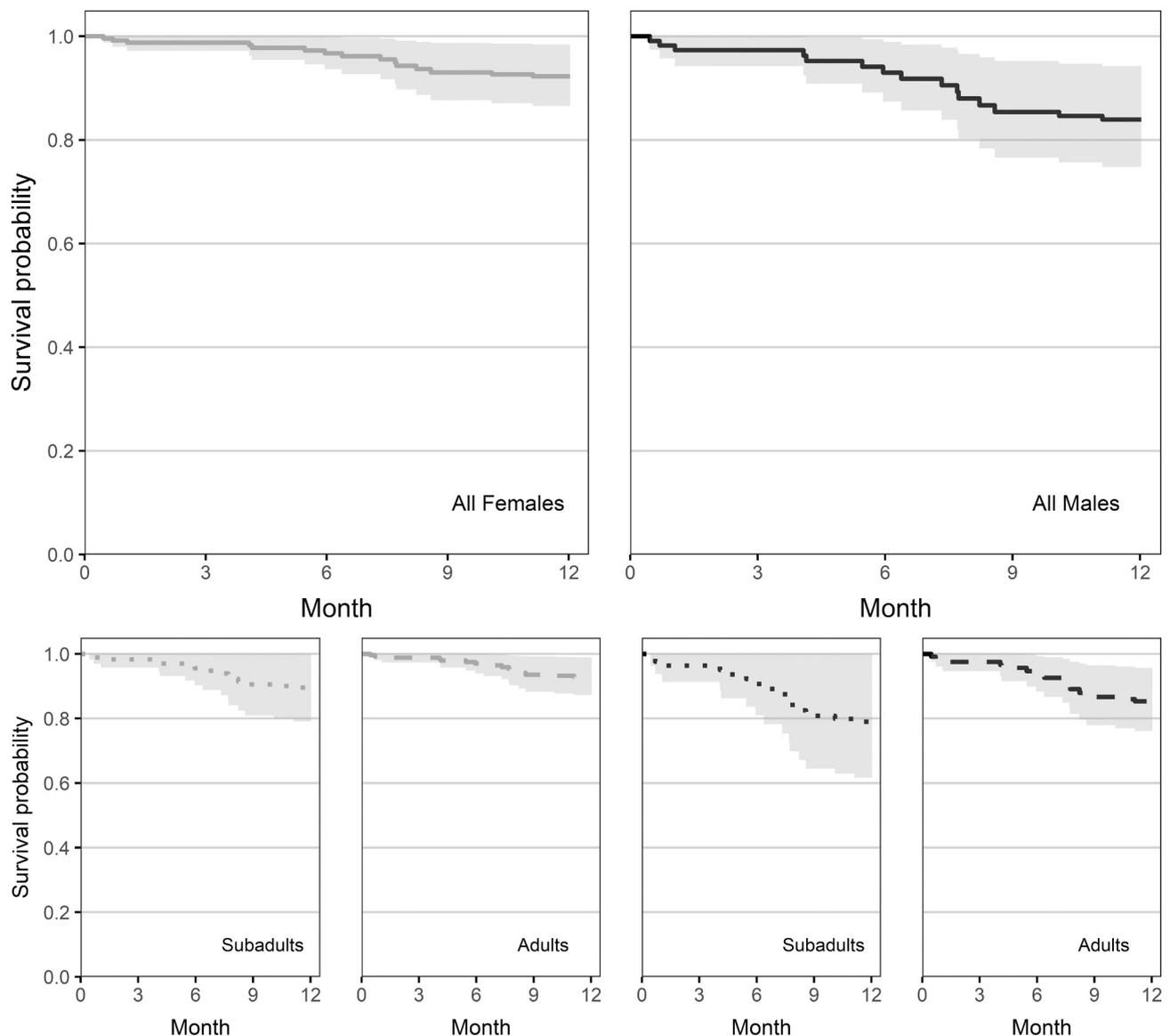


Fig. 3. Adjusted annual survival curves based on Cox model estimations. Survival curves of females and males of all age classes are shown in the upper part of the figure. In the lower part, survival curves of subadults and adults are displayed underneath their respective sex. On average, females had a higher annual survival probability than males. Subadults of both sexes had a lower annual survival in comparison to adults. Please note that all confidence intervals overlap, therefore preventing a clear separation of the different estimations.

The second most important cause of mortality in our study was poaching. However, the extent of this mortality cause was lower than for larger felids, such as the Amur tiger or the Eurasian lynx (*Lynx lynx*) (Goodrich et al., 2008; Heurich et al., 2018). An explanation for this result could be the different diets of wildcats and larger felids. While the wildcat mainly preys on rodents and rabbits (Germain et al., 2009; Lozano et al., 2006), larger felids prey also on livestock and high-profile game species. In comparison, conflicts with wildcats are generally minor and occur primarily in Mediterranean areas, where the European rabbit (*Oryctolagus cuniculus*) is an important small game species (Lozano and Malo, 2012). In addition, cases of accidental killing due to confusion with domestic cats can occur in areas where the latter can be shot legally. Since the majority of data used here derived from Central Europe, the effect of poaching might be underestimated. We found the same percentage of poached wildcat in Portugal and Northeastern Spain, with one individual poached out of six monitored (16%), while in Northeastern France, 3 out of 16 monitored wildcats were poached (19%). Data on poaching is scarce and notoriously difficult to obtain because poachers tend to conceal their activities so that the cause of mortality

remains unknown (Heurich et al., 2018; Liberg et al., 2012). With a low temporal resolution of tracking data, which is the case for most of the data in our study, cases of poaching might go undetected. Therefore, our results might be a conservative estimate, but even if we assume unknown causes of death are all attributed to poaching, the percentage of mortality due to poaching would only increase to 29% and would still be lower than the mortality due to roadkills. Besides poaching, accidental poisoning (Lozano and Malo, 2012) or natural causes of death such as disease (e.g. Fromont et al., 2000) and intra-guild predation from larger carnivores (Nájera et al., 2019) are plausible explanations of the low amount of unknown mortality found in this study. A temporally and spatially detailed GPS tracking with mortality sensors and immediate autopsy once death is confirmed would be able to shed more light on unknown and hidden mortality causes.

We found a high value of annual survival probability for the European wildcat relative to its body mass. Life-history theories typically predict that larger species tend to live longer than smaller species (Healy et al., 2014). However, many species live longer than expected by their body size if the mortality owing to natural or anthropogenic causes is

low (Healy et al., 2014). We found that wildcat adult body weight well predicted its maximum longevity in captivity, therefore, we cannot conclude that this felid has a disproportionately high longevity than predicted by its size. Yet, the annual survival probability is considered a more precise life-history parameter than the maximum longevity, and the two estimates are not necessarily correlated (Krementz et al., 1989). Estimates of the annual survival probability strictly depend on the overall number of death events, no matter the cause. Despite the high human-related mortality, our study shows relatively low wildcat mortality owing to natural and unknown causes, which might explain the relatively high annual survival probability. Annual survival rates similar to wildcat's have been reported for resident ocelots in Texas (0.9) (Haines et al., 2005) and for bobcat (*Lynx rufus*) in Southern Illinois (0.8) (Nielsen and Woolf, 2002). Mortality causes of resident ocelots were distributed among human-caused, natural and unknown mortality, while bobcats mostly died from human-caused mortality. Vickers et al. (2015) found a much lower annual survival probability of cougars (0.6), with most of the mortalities related to humans and a substantial number of mortalities due to natural or unknown causes. In summary, a species suffering from high human-related mortality but a low mortality due to natural causes, is likely to experience higher annual survival probabilities than species experiencing high mortality from both sources. Despite the wildcat's relatively high annual survival found in our study, the disproportionately high percentage of human-related mortality reported here should not be ignored and emphasizes the importance of long-term monitoring to assess local population development.

We found a lower annual survival in males than females, but this difference was not significant. In accordance with previous studies (Anile et al., 2017; Oliveira et al., 2018), we found on average males maintained larger home-ranges than females and tolerated higher densities of low-traffic roads in the home-range, although no differences in the density of high-traffic roads could be revealed. The difference in annual survival probability of females' and males' was reported to be not significant in several felid species, such as Iberian lynx (*Lynx pardinus*; Ferreras et al., 1992), ocelot (Haines et al., 2005) and cougar (Vickers et al., 2015), although exceptions exist (Goodrich et al., 2008). Vickers et al. (2015) found a low cougar survival probability (<0.6) that did not differ between sexes. Roadkill was the most important cause of mortality and it affected both sexes equally. Although we also found road mortality impacted both sexes equally, the annual survival probability of females and males was relatively high. This is encouraging because survival of females is a crucial demographic parameter (Benson et al., 2020; Riley et al., 2003) that can determine the reproductive success of the entire population (Riley et al., 2003). In the absence of reproductive parameters of local populations, we cannot confirm any positive trend. We suggest focusing further study on the investigation of reproductive parameters of wildcat populations to better understand their demography.

5. Conclusions and management implications

Our study provides the first estimate of European wildcat annual survival and reveals roadkill as the most important cause of mortality for this species in Europe. This was possible due to an extensive collaboration between wildcat researchers bringing together telemetry data collected across Europe. Although data on road traffic intensity is not available at the European scale, our approach considers at least differences among road classes (Pinto et al., 2018), and highlights the direct link between the density of high-traffic roads and the annual survival probability of individuals. We thereby provided new insights into the basic ecology of the species, but further studies are needed to ascertain whether density of high-traffic and low-traffic roads affect movement behaviour, habitat selection and occurrence of the wildcat. In particular, we recommend further study to focus on the movement behaviour of wildcats living in areas with different conditions of road density and traffic intensity and to compare spatiotemporal differences of road-

crossings and road-kills. In addition, further research is needed to estimate important demographic parameters such as population growth rates.

Europe is characterised by the highest road density found anywhere in the world and the road network is continuously expanding and the traffic intensity is increasing. Consequently, roadless areas become sparser (Meijer et al., 2018). With increasing road densities in areas inhabited by the European wildcat, the encouraging values of annual survival probability might drop. We believe the annual survival we document provides a major contribution to demographic models allowing the prediction of population dynamics and viability for specific areas. Furthermore, we strongly suggest accounting for the density of high-traffic roads and to adjust the survival values in such models accordingly. In terms of practical management, we suggest the need for measures that limit the expansion of motorways and primary roads in areas where wildcat populations reside. Where such limitations are not feasible, conservation planners and wildlife managers in areas inhabited by wildcats should consider fencing sections of motorways and primary roads with wildcat-proof fences in combination with viaducts and overpasses to decrease mortality from roadkills and to avoid isolation of subpopulations. For instance, Klar et al. (2009) showed that wildcat mortality on motorway sections was reduced by 83% after fencing. Finally, other aspects of wildcat ecology such as landscape-wide connectivity (Westekemper et al., 2021) should be considered to identify areas and types of roads requiring urgent management actions.

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Data accessibility

Part of the raw data is available through the EUROWILDCAT platform. Access to the EUROWILDCAT database is obtained subject to the terms of use and after contacting the persons in charge (see <https://eurowildcat.org/contacts/>).

CRediT authorship contribution statement

Matteo Luca Bastianelli: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Joseph Premier:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Mathias Herrmann:** Investigation, Data curation, Writing – review & editing. **Stefano Anile:** Investigation, Data curation, Writing – review & editing. **Pedro Monterroso:** Investigation, Data curation, Writing – review & editing. **Tobias Kuemmerle:** Formal analysis, Writing – review & editing. **Carsten F. Dormann:** Writing – review & editing, Validation. **Sabrina Streif:** Investigation, Data

curation, Writing – review & editing. **Saskia Jerosch**: Investigation, Data curation, Writing – review & editing. **Malte Götz**: Investigation, Data curation, Writing – review & editing. **Olaf Simon**: Investigation, Data curation, Writing – review & editing. **Marcos Moleón**: Investigation, Data curation, Writing – review & editing. **José María Gil-Sánchez**: Investigation, Data curation, Writing – review & editing. **Zsolt Biró**: Investigation, Data curation, Writing – review & editing. **Jasja Dekker**: Investigation, Data curation, Writing – review & editing. **Analena Severon**: Investigation, Data curation, Writing – review & editing. **Axel Krannich**: Investigation, Data curation, Writing – review & editing. **Karsten Hupe**: Investigation, Data curation, Writing – review & editing. **Estelle Germain**: Investigation, Data curation, Writing – review & editing. **Dominique Pontier**: Investigation, Data curation, Writing – review & editing. **René Janssen**: Investigation, Data curation, Writing – review & editing. **Pablo Ferreras**: Investigation, Data curation, Writing – review & editing. **Francisco Díaz-Ruiz**: Investigation, Data curation, Writing – review & editing. **José María López-Martín**: Investigation, Data curation, Writing – review & editing. **Fermín Urra**: Investigation, Data curation, Writing – review & editing. **Lolita Bizzarri**: Investigation, Data curation, Writing – review & editing. **Elena Bertos-Martín**: Investigation, Data curation, Writing – review & editing. **Markus Dietz**: Investigation, Data curation, Writing – review & editing. **Manfred Trinzen**: Investigation, Data curation, Writing – review & editing. **Elena Ballesteros-Duperón**: Investigation, Data curation, Writing – review & editing. **José Miguel Barea-Azcón**: Investigation, Data curation, Writing – review & editing. **Andrea Sforzi**: Investigation, Data curation, Writing – review & editing. **Marie-Lazarine Poulle**: Investigation, Data curation, Writing – review & editing. **Marco Heurich**: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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