Linking movement to mortality: a framework for predicting anthropogenic mortality hotspots in wide-ranging animals

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Abstract

Human activities and their impacts are a major source of mortality for wide-ranging animals, yet conservation efforts often remain reactive because it is difficult to predict where mortality is most likely to occur. Approaches to understand and reduce wildlife mortality typically rely on coarse-scale associations between mortality events and landscape features, limiting their ability to identify spatially concentrated high-risk areas and prioritise effective mitigation. We contend that mortality risk arises from interactions between animal space use and human-modified environments, where movements result in spatial overlap with anthropogenic threats. Here, we outline the Movement–Mortality Framework (MMF), a conceptual framework with practical implications that integrates movement ecology, predictive space-use modelling, and spatial threat mapping to predict where anthropogenic mortality is most likely to occur. The MMF combines predicted space use with spatial threat distributions to estimate exposure, identify mortality hotspots and prioritise targeted conservation interventions. We demonstrate this approach using a worked example for the globally Vulnerable Cape Vulture (*Gyps coprotheres*) in South Africa. Predicted exposure was highly spatially concentrated: the highest-risk 1% of the landscape contained 41% and 43% of predicted exposure to powerline collision/electrocution and unintentional poisoning, respectively, while the highest-risk 10% contained 78% and 76%. By linking predictive movement models with spatial threat mapping, the MMF provides a transferable framework for identifying mortality hotspots, supporting evidence-based conservation planning and prioritising targeted mitigation for wide-ranging animals facing anthropogenic threats. **Practical implication:** The MMF provides practitioners with a transferable approach for combining animal space-use predictions with spatial information on anthropogenic threats to identify priority areas for intervention. By targeting locations containing disproportionate levels of predicted exposure, conservation resources can be directed towards areas where mitigation has the greatest potential to reduce anthropogenic mortality.

Keywords

anthropogenic mortality, *conservation planning*, *ecological traps*, *human–wildlife interactions*, *movement ecology*, *mortality risk*, *wildlife mortality*

Data Availability

R code supporting the Cape Vulture worked example can be accessed via Figshare: 10.6084/m9.figshare.33282225. The Cape Vulture population utilisation distribution (PUD) was obtained from Cervantes *et al.* (2023), spatial data on powerline infrastructure were obtained from the World Bank Group (2025), and spatial predictions of unintentional poisoning risk were obtained from Curk *et al.* (2025). Full details of these data sources and their use are provided in the Supporting Information.

Predicting mortality hotspots can be a challenge

Human activities are now a dominant source of mortality for many wide-ranging animals, contributing substantially to population declines across terrestrial, freshwater and marine ecosystems (McCauley *et al*. 2015; Ripple *et al*. 2016; He *et al*. 2019). Anthropogenic threats such as collisions, electrocution, bycatch, poisoning and persecution are among the principal drivers of these population declines. Considerable progress has been made in documenting the causes, patterns and consequences of anthropogenic mortality (e.g., Gantchoff *et al*. 2020; Serratosa *et al*. 2024; Panter *et al*. 2025). However, a fundamental conservation challenge remains: predicting where mortality is most likely to occur (Poulton *et al*. 2024). Without this spatial understanding, conservation interventions may be implemented reactively or across broad areas, limiting the ability to prioritise scarce conservation resources towards locations where interventions are likely to have the greatest benefit (Cattarino *et al*. 2015).

Most approaches used to investigate the spatial drivers of wildlife mortality are retrospective, linking observed mortality events with broad-scale environmental variables to identify landscape correlates of mortality risk (Tintó *et al*. 2010; Hill *et al*. 2019; Murgatroyd et al. 2019). While such approaches provide important insights into the correlates of mortality, they do not explicitly account for how the space use of animals can influence their exposure to anthropogenic threats (Eisaguirre *et al*. 2025). Consequently, they provide limited insights into why mortality is concentrated in some locations but absent from apparently similar landscapes elsewhere.

Animal space use is shaped by the distribution of resources, environmental conditions, energetic requirements, experience and social information. In human-modified landscapes, these factors can direct animals towards areas that also contain anthropogenic threats. For example, roads may provide carrion that attracts scavengers while simultaneously increasing the risk of vehicle collisions (Singh *et al*. 2024). Fishery discards can attract seabirds to areas of elevated bycatch risk (Bicknell *et al*. 2013), grouse moors may provide favourable foraging opportunities for raptors while simultaneously exposing them to persecution (Redpath *et al*. 2002), and renewable energy infrastructure may intersect with the preferred landscape features of soaring birds (Murgatroyd *et al*. 2021). Where attractive resources and anthropogenic threats overlap, behaviours associated with resource use may increase exposure to anthropogenic threats and consequently elevate mortality risk.

Because exposure to anthropogenic threats depends partly on where and how animals use landscapes, mortality risk can be understood as spatially mediated by animal movement and space use (Eisaguirre *et al*. 2025). Integrating movement and mortality processes therefore offers a route from documenting where animals die towards predicting where mortality risk is spatially concentrated, with potential to inform proactive conservation planning and targeted mitigation (Eisaguirre *et al*. 2025).

Advances in GPS telemetry have greatly improved our understanding of animal movement and habitat use, but these data are still only occasionally integrated directly with mortality risk within broader mechanistic frameworks. Movement-informed predictive approaches have been applied to characterise spatial variation in mortality risk associated with wind-energy infrastructure (Murgatroyd *et al*. 2021), powerlines (Pay *et al*. 2025), vehicle collisions (Bénard *et al*. 2024), and poisoning (Peters *et al*. 2023). Together with evidence that anthropogenic mortality is highly spatially aggregated, with disproportionate numbers of deaths occurring within relatively small areas or at a small subset of infrastructure (Guil *et al*. 2011; Klaassen *et al*. 2013; Sebastián-González *et al*. 2018; May *et al*. 2020), these studies suggest that mortality is not randomly distributed across landscapes, but rather that it reflects where animal space use overlaps with anthropogenic threats (Gauld *et al*. 2022). However, these applications have largely been developed independently for individual threats and lack a broader conceptual framework that can be applied consistently across multiple anthropogenic mortality sources. More generally, movement models predict where animals are likely to occur, whereas mortality studies focus on where deaths have already been detected, with limited integration between the two.

Building on these advances, here we present the Movement–Mortality Framework (MMF), a conceptual framework that links predicted space use with anthropogenic threats to identify where mortality hotspots are most likely to occur across human-dominated landscapes. The MMF integrates movement ecology, predictive space-use modelling and spatial threat mapping to identify locations where animal space use overlaps with anthropogenic threats. We demonstrate the framework using a worked example for the globally Vulnerable Cape Vulture (*Gyps coprotheres*) (BirdLife International 2026) in South Africa. This example illustrates how movement-informed mortality predictions can support more effective conservation planning, targeted mitigation and evidence-based policy for wide-ranging animals.

The Movement–Mortality Framework (MMF): a behavioural framework for predicting anthropogenic mortality hotspots

Within the MMF (Fig. 1), a mortality hotspot is defined as *a spatially explicit area where the overlap between animal space use and anthropogenic threats produces a disproportionately high probability of mortality relative to the surrounding landscape*. Rather than replacing existing knowledge of the causes and spatial patterns of anthropogenic mortality, the MMF builds upon this information to predict where mortality is most likely to occur. Accurate prediction of mortality hotspots also requires information on where individuals are likely to occur, derived from telemetry, breeding locations, occupancy models or species distribution models, because movement-mediated exposure can only occur where animals are present (Fig. 1).

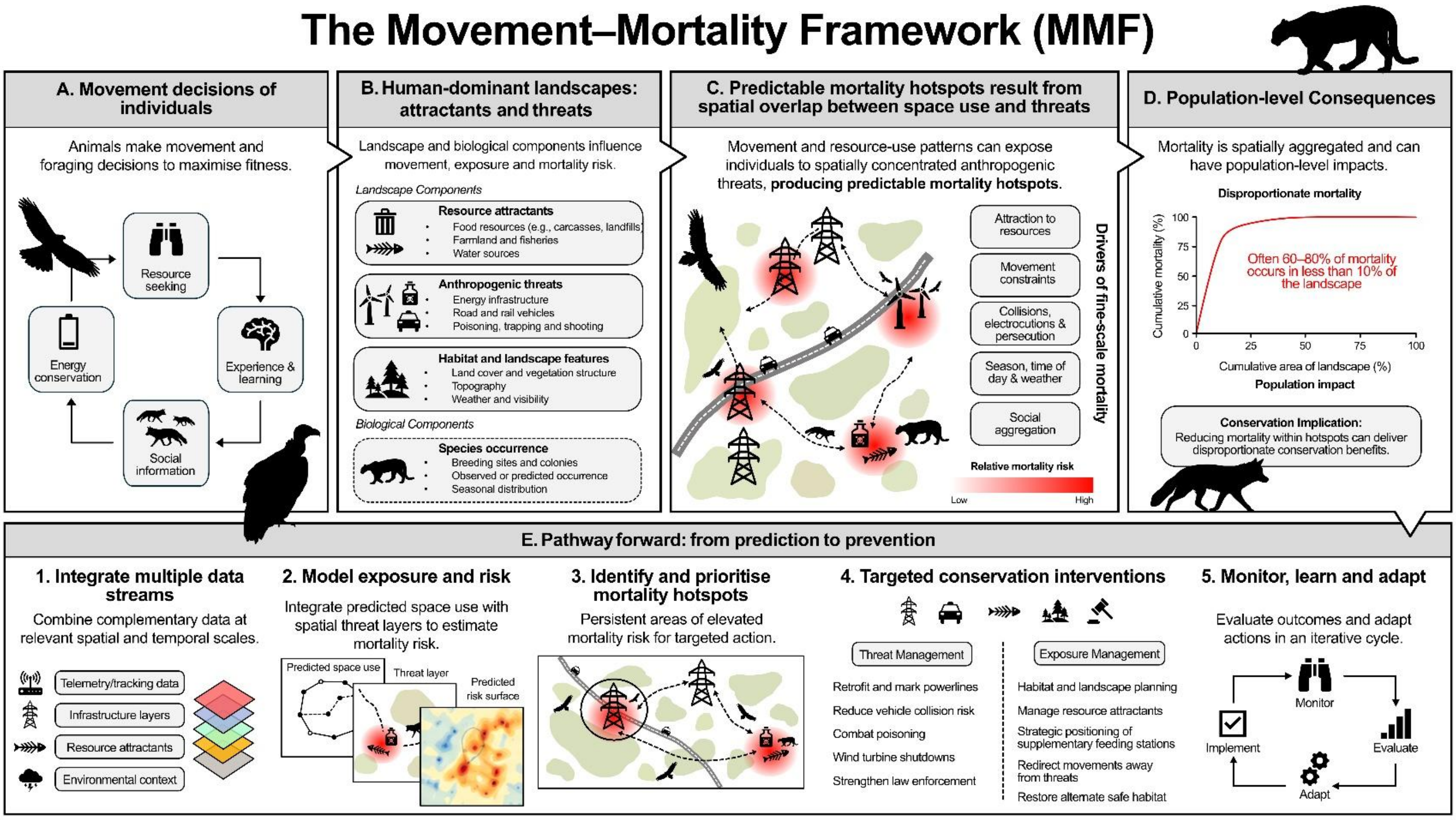

Figure 1. The Movement–Mortality Framework (MMF), a mechanistic conceptual framework linking animal movement and anthropogenic threats to the spatial prediction and prevention of mortality. The framework integrates individual movement processes (A) with landscape and biological components influencing animal occurrence and threat exposure (B) to predict spatially concentrated mortality risk (C) and its potential population-level consequences (D). The MMF is operationalised through an iterative pathway from prediction to prevention (E), integrating complementary data streams to model exposure and risk, identify mortality hotspots, target interventions towards threats and/or exposure, and monitor outcomes to support adaptive conservation.

Importantly, the MMF identifies opportunities to reduce mortality either by mitigating anthropogenic threats directly or by managing animal exposure through habitat and landscape interventions. Where resource attractants and anthropogenic threats spatially coincide, movement decisions that are otherwise adaptive, can result in elevated mortality risk. For instance, predictable scavenging areas used by White-backed Vultures (*Gyps africanus*) may also overlap with high poisoning risk areas (Monadjem *et al*. 2018). The location and intensity of mortality hotspots will vary with resource availability, environmental conditions, species distribution and species-specific movement ecology, reflecting dynamic interactions between behaviour and anthropogenic threats. Integrating movement data with spatial threat mapping can identify these high-risk areas and support targeted mitigation (Peters *et al*. 2023; Curk *et al*. 2025).

From prediction to mitigation: a pathway for identifying and reducing mortality risk

Building spatially explicit models of risk based on the MMF, rely on 1) robust predictive space use models, 2) reliable information on species' distribution, 3) reliable information on causes of anthropogenic mortality, and 4) high-resolution anthropogenic threat layers (Fig. 1). Rather than reacting to observed mortality events (e.g. sites of electrocutions, collisions or persecutions) for conservation management actions, such models allow conservation practitioners to anticipate where mortality is most likely to occur and proactively prioritise conservation mitigations at these locations. This can be useful for the conservation of declining species, but also when preparing for species reintroductions (Brink et al. 2020; Hunter-Ayad *et al*. 2020; Lee et al. 2024).

To illustrate this framework, we applied the MMF to the globally Vulnerable Cape Vulture in South Africa (Fig. 2). We used the population utilisation distribution (PUD) developed by Cervantes *et al*. (2023), which combines a space use model with data on colony distribution and colony size data to predict population space use. Two of the main threats to this species have been identified to be poisoning, and powerline collisions and electrocutions (Boshoff *et al*. 2011; Phipps *et al*. 2013). We combined the PUD with national datasets describing powerline (transmission) infrastructure (World Bank Group 2025) and unintentional poisoning risk (reproduced from Curk *et al*. 2025). By integrating predicted space use with the spatial distribution of each threat, we generated spatially explicit predicted exposure surfaces identifying where Cape Vultures are most likely to encounter each mortality source (Fig. 2).

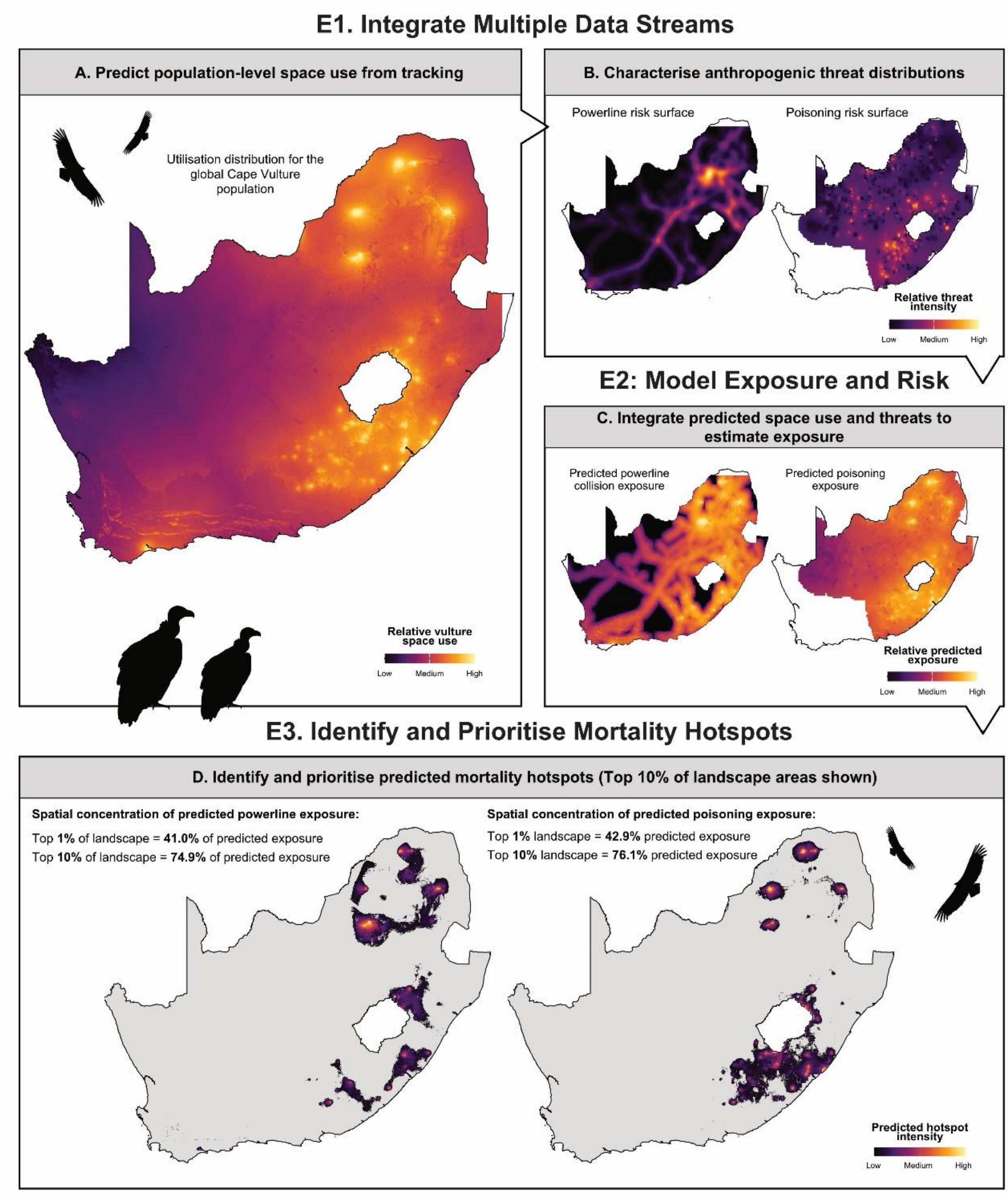

Figure 2. Illustration of steps E1–E3 of the Movement–Mortality Framework (MMF; Fig. 1) using Cape Vultures (*Gyps coprotheres*) in South Africa. E1 – Integrate multiple data streams: (A) A space use model is combined with colony size and distribution to estimate the population utilisation distribution (PUD) of the globally Vulnerable Cape Vulture population (reproduced from Cervantes *et al.* 2023), representing predicted space use across the landscape, and (B) spatial distributions of two important anthropogenic threats are represented as continuous threat surfaces for powerline infrastructure (World Bank Group 2025) and unintentional poisoning (Curk *et al.* 2025). E2 – Model exposure and risk: (C) predicted space use is integrated with each threat layer to estimate relative exposure, identifying areas where vultures are most likely to encounter each potential mortality source. E3 – Identify and prioritise

mortality hotspots: (D) predicted mortality hotspots are identified by prioritising the highest-exposure areas of the landscape. The highest-risk 10% of the landscape is shown spatially.

Predicted exposure was highly spatially aggregated for both threats (Fig. 2D). The highest-risk 1% of the landscape contained 41% of predicted exposure to powerline collision/electrocution and 43% of predicted exposure to unintentional poisoning, while the highest-risk 10% contained 78% and 76%, respectively (Fig. 3). However, this degree of spatial concentration partly reflects the ecology of our worked example, the colonial Cape Vulture, for which movements are spatially structured around breeding and roosting sites. Exposure may be less strongly concentrated in territorial or more evenly distributed species, and the proportion of landscape requiring mitigation will therefore depend on species-specific movement ecology and space use. This worked example demonstrates how movement-informed risk modelling can identify spatially restricted priority areas where targeted mitigation may yield disproportionately large conservation benefits. Although this example illustrates the predictive capability of the MMF, the accuracy of mortality predictions will depend on the quality of movement and species distribution data, the correct identification and spatial representation of key threats, and the assumption that predicted exposure is a reliable proxy for mortality risk.

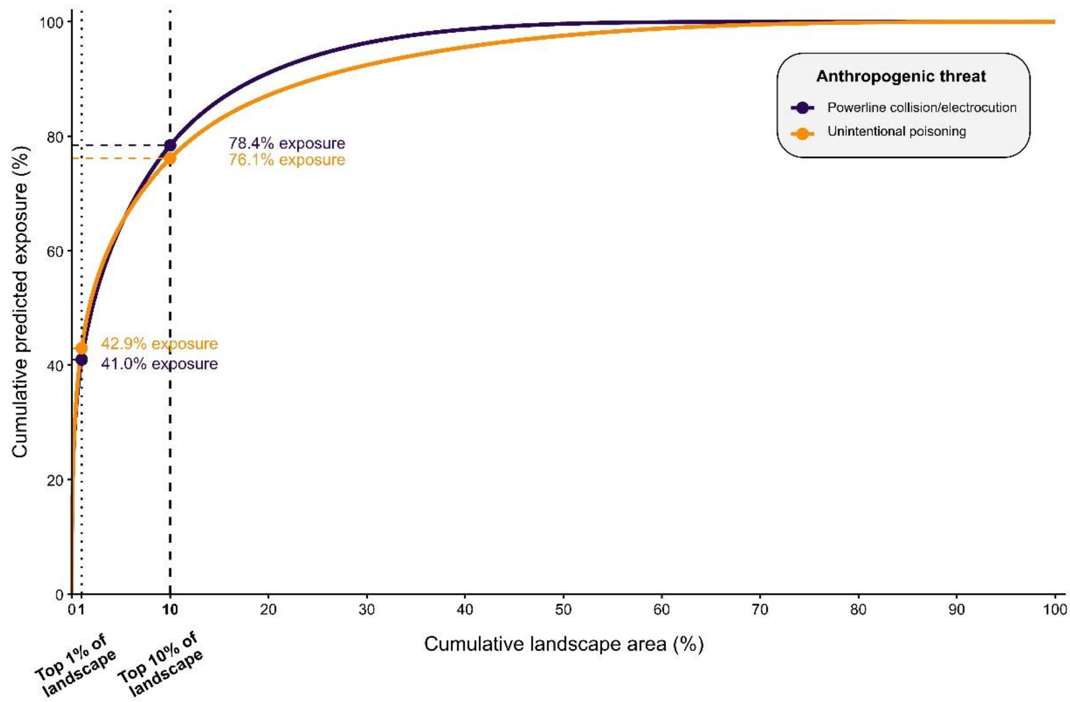

Figure 3. Cumulative predicted exposure of Cape Vultures (*Gyps coprotheres*) to powerline collision/electrocution and unintentional poisoning in the South African worked example, after ranking landscape cells from highest to lowest predicted exposure. The highest-risk 1% of the landscape contains 41.0% and 42.9% of total predicted exposure to powerline collision/electrocution and unintentional poisoning, respectively, while the highest-risk 10% contains 78.4% and 76.1%. These patterns illustrate the strong spatial aggregation of predicted exposure and the potential for spatial prioritisation of targeted conservation interventions.

Because anthropogenic mortality is often concentrated within relatively small areas (Poulton *et al*. 2024), identifying mortality hotspots enables conservation actions to be spatially prioritised. For example, wildlife overpasses, underpasses and exclusion fencing along the Trans-Canada Highway in Banff National Park reduced wildlife–vehicle collisions by approximately 80% while restoring connectivity for large mammals (Clevenger *et al*. 2002). Likewise, hazardous powerlines can be prioritised for retrofitting, wind turbines can be curtailed during periods of elevated collision risk (Lehman *et al*. 2007), and poisoning prevention programmes targeted within predicted high-risk areas (Brink et al. 2020).

Conservation policy and practice

Framing anthropogenic mortality as a behaviourally mediated and spatially predictable process provides a mechanistic basis for moving beyond reactive assessments of mortality in wide-ranging animals towards proactive and spatially targeted conservation action. The principles underlying the MMF should be broadly applicable to most wide-ranging species that repeatedly move through landscapes containing anthropogenic threats. Such, movement-informed approaches have already been used to predict bycatch risk in marine predators (Clay *et al*. 2019), collision risk around wind energy infrastructure (Curk *et al*. 2025; Pay *et al*. 2025), road mortality in large carnivores (Bencin *et al*. 2019), vessel-strike risk for whales (Nisi *et al*. 2024), and poisoning risk for scavengers (Peters *et al*. 2023). By identifying where mortality is most likely to occur, conservation interventions such as wildlife crossing structures, powerline retrofitting, turbine curtailment and poisoning prevention can be prioritised where they are expected to deliver the greatest conservation benefit. Continued advances in movement ecology, remote sensing, species distribution modelling and high-resolution environmental mapping are transforming our ability to predict space use by animal populations. Coupling these approaches with explicit analyses of anthropogenic threats offers considerable opportunities for improving conservation planning.

Conclusion

Anthropogenic mortality is often spatially predictable because it reflects interactions between animal movement and anthropogenic threats. By linking predictive movement models with spatial threat mapping, the Movement–Mortality Framework provides a transferable approach for identifying where mortality is most likely to occur and where conservation interventions are likely to have the greatest impact. As movement ecology and spatial modelling advance, approaches such as the MMF can help shift conservation from simply documenting patterns and causes of mortality towards anticipating and preventing it.

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Supplementary Information for

“Linking movement to mortality: a framework for predicting anthropogenic mortality hotspots in wide-ranging animals”

Supplementary Methods

Illustrative application of the Movement–Mortality Framework using Cape Vultures

To illustrate the Movement–Mortality Framework (MMF), we applied the workflow to the globally Vulnerable Cape Vulture (*Gyps coprotheres*) across South Africa using population-level movement and anthropogenic threat datasets. This example is intended as a proof-of-concept demonstrating how population-level movement data can be integrated with spatial threat layers to identify areas of elevated mortality exposure. It should therefore be interpreted as an illustrative application rather than a fully parameterised mortality risk model. All analyses were conducted in R version 4.4.1 (R Core Team 2024).

Population utilisation distribution

Population-level movement data were represented using a population utilisation distribution (PUD), generated by Cervantes *et al*. (2023), from 68 Cape Vultures tracked using GPS telemetry across South Africa over approximately two decades. Cervantes *et al*. (2023) fitted step-selection models to describe habitat selection and movement behaviour before simulating steady-state utilisation distributions around core breeding colonies. Colony-specific utilisation distributions were subsequently weighted by estimated colony size to produce a PUD representing the expected spatial distribution of the global Cape Vulture population. The PUD represents the relative probability of space use across the species' range and was supplied as a continuous raster surface. The raster was cropped and masked to the South African national boundary using administrative boundaries obtained from the World Bank Global Administrative Areas database (World Bank Group 2026).

Because utilisation distributions are strongly right-skewed, we log-transformed the PUD values for visualisation in the figures. However, all analyses were conducted using the original raster values. To estimate the proportion of time that the global population was expected to spend within each raster cell, the utilisation distribution was normalised by dividing each cell by the sum of all raster values:

$$P_i = \frac{UD_i}{\sum UD}$$

where P_i represents the relative probability of use of raster cell i.

Powerline infrastructure data

Transmission and distribution line data were obtained from the World Bank Group EnergyData repository (World Bank Group 2025), comprising a March 2017 extract of OpenStreetMap transmission infrastructure across South Africa. The dataset includes the national transmission network and many lower-voltage transmission and distribution lines (down to 44 and 88 kV), providing comprehensive spatial coverage of electricity infrastructure. The powerline vector dataset was clipped to the South African boundary before being rasterised to the same spatial resolution and extent as the Cape Vulture PUD using the rasterize() function in the 'terra' package (Hijmans 2025).

Rather than treating transmission lines as binary features, we estimated a continuous powerline density surface by applying a Gaussian kernel using the focal() function also in the 'terra' package. A smoothing distance of 0.15 decimal degrees (approximately 16–17 km at South African latitudes) was used to represent the declining influence of powerline infrastructure with increasing distance while producing a continuous hazard surface suitable for illustration. The resulting density raster was linearly rescaled between 0 and 1. All transmission and distribution lines were treated as equivalent hazard features for illustrative purposes. Consequently, variation in line voltage, conductor configuration, pylon design, and species-specific collision or electrocution susceptibility was not incorporated.

Poisoning data

A national unintentional poisoning raster layer was used to represent the spatial distribution of poisoning risk across South Africa (see Curk *et al*. 2025). Using the resample() function in the 'terra' package, we resampled the poisoning raster to match the resolution and grid alignment of the PUD using bilinear interpolation before being linearly rescaled between 0 and 1.

Predicted exposure surfaces

Predicted exposure to each mortality source was estimated by combining the probability of space use with the corresponding hazard layer according to

$$E_i = P_i \times H_i$$

where E_i is the predicted exposure within raster cell i, P_i is the relative probability of use derived from the utilisation distribution, and H_i is the relative hazard intensity.

Separate exposure surfaces were generated for powerline infrastructure and poisoning. These exposure surfaces identify locations where high vulture use spatially coincides with elevated anthropogenic threats.

Identification of mortality hotspots

To illustrate how the MMF can prioritise conservation management interventions, predicted mortality hotspots were defined as the 10% of raster cells with the highest predicted exposure values for each threat.

For each exposure surface, the 90th percentile exposure value was calculated, and all cells exceeding this threshold were classified as hotspot cells. We then quantified the proportion of total predicted exposure contained within these hotspot cells:

$$\frac{\sum E_{\mathrm{hotspot}}}{\sum E_{\mathrm{total}}} \times 100$$

where $\sum E_{\mathrm{hotspot}}$ represents the summed exposure within hotspot cells and $\sum E_{\mathrm{total}}$ represents total predicted exposure across the landscape.

To evaluate the degree of spatial aggregation, the observed proportion of exposure contained within hotspot cells was compared with the expectation under a random spatial distribution, in which the highest 10% of the landscape would be expected to contain approximately 10% of total exposure. Enrichment was therefore calculated as:

$$\frac{\text{Observed exposure captured}}{\text{Expected exposure captured}}$$

Values substantially greater than 1 indicate that predicted mortality exposure is concentrated within a relatively small proportion of the landscape, identifying areas where targeted mitigation is expected to deliver disproportionate conservation benefits.

Spatial aggregation of predicted exposure

To quantify the degree to which predicted mortality exposure was spatially concentrated, cumulative exposure curves were constructed separately for powerline infrastructure and unintentional poisoning. For each predicted exposure surface, raster cells were ranked from highest to lowest predicted exposure. The cumulative proportion of total landscape area and cumulative proportion of total predicted exposure were then calculated by progressively summing raster cells in descending order of predicted exposure.

To illustrate the concentration of predicted exposure within the landscape at different levels of spatial prioritisation, the proportions of total predicted exposure contained within the highest-risk 1% and 10% of the landscape were calculated for each threat. These were determined from the cumulative exposure curves after the upper 1% and 10% of ranked landscape area had been included. Under a random spatial distribution of exposure, these areas would be expected to contain approximately 1% and 10% of total predicted exposure, respectively. Greater concentrations indicate increasing spatial aggregation of predicted exposure and identify opportunities for spatially targeted conservation interventions.

Supplementary References

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