

Towards mechanistically predicting animal population abundance and distribution within a real landscape

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Abstract. We present preliminary results concerning a central problem in Ecology with applied implications: to mechanistically predict animal population abundance and distribution within a real landscape. We approach it by combining Resource-Area-Dependence Analysis (RADA) with individual-based modeling (IBM). Common buzzards *Buteo buteo* in lowland UK were used to exemplify it. RADA determined that a buzzard requires, on average, a tree for roosting, 0.56ha of rough-ground and 15ha of grassland (good habitats for small mammals). This information was used to define, in the IBM, virtual animals with realistic resource-related parameters and their values. Rules concerning maximum foraging distances and territorial behavior were then included. The model was run on the 1990 Land Cover Map of Great Britain. Its outputs were: at the individual-level, home-range area, perimeter and proportion of overlap (proxy for territoriality), and, at the population-level, overall range, local density and carrying capacity of the landscape for buzzards. Virtual buzzards' home-ranges and their pattern of overlap were indistinguishable from those of wild buzzards. When compared with two independent field-based estimates, predictions for carrying capacity of 211-226 individuals (100 model runs) suggested buzzards had recovered from previous low levels and reached equilibrium density in the area. As our approach relies on remote sensing for data acquisition, it allows for modeling animals roaming over areas that are huge, dangerous or difficult to access, and for using historical and contemporary datasets and techniques. Future advancements should allow for modeling of social or non-territorial species, and for considering landscape management scenarios in a climate change context.

Palavras-chave: animal ecology, individual-based modelling, remote sensing, ecologia animal, mapeamento, modelagem-baseada em indivíduos, sensoriamento remoto.

1. Introduction

The natural environment from which we, as a species, have emerged, has reached such profound degradation levels that it has been argued that we are at the onset of a new geological era, the Anthropocene (Steffen *et al.* 2011). Among the drivers of such degradation are widespread extinctions of species (Ceballos *et al.* 2015), human cultures and languages (Amano *et al.* 2014), creation of increasingly dysfunctional ecosystems (Scheffer 2015), climate change (IPCC 2013), air, water and soil pollution (Rockström *et al.* 2009), and depletion of mineral resources (Prior *et al.* 2012). Amidst such a daunting scenario, it has been argued that the science of ecology could contribute to reverting the current trend by becoming more predictive and scenario-oriented (Grimm & Railsback 2012; Evans *et al.* 2013). This, the authors argue, requires modeling that takes into account the fact that individuals are the elementary particles of ecological systems, and that system-level

properties, such as population abundance and distribution, or stability and resilience, emerge from interactions among individuals and between them and their environment.

For modeling the abundance and distribution of animal populations within real landscapes, predictive ecology has been advancing through developments in two main fronts: statistical and individual-based models (IBM). Statistical models, under the general umbrella of ‘resource selection functions’, are based on the establishment of relationships between animals’ use of space and resource availability or environmental conditions (Boyce *et al.* 2016). Such models have been allowing for quantitative predictions of animal abundance and distribution within real landscapes and have benefitted from fast improvements in the field of remote sensing, particularly landscape mapping and radio-tracking (Cagnacci *et al.* 2010; Pettorelli *et al.* 2014). Owing to their statistical nature, however, these models do not allow for explicit consideration of the effects of social interactions (ex. territoriality) upon populations and their predictions are limited to landscapes with similar structure to that based on which the model was parameterized (Boyce *et al.* 2016).

In contrast, in individual-based models (IBM), one creates individuals by defining their characteristics and the rules that govern their interactions. Individual success is measured as the achievement of an objective; for example, to reproduce or establish a home-range. As a result of these interactions, the population patterns of abundance and distribution emerge. If model structure is based on ‘first principles’, for example, finding resources such as food or a mate, when projections are made within a different landscape individuals naturally organize themselves in a different way. This is similar to what happens with real animals in a real landscape. It suggests one may be able to extrapolate model projections to situations differing with regards to the distribution of those resources (Grimm & Railsback 2012; Evans *et al.* 2013).

However, obtaining the data for defining realistic model parameters and their values has proven somewhat hard so far. Reasons include the great effort involved in collecting systematic field data over large areas, as well as the theory being in a rather early stage of development when it comes to understanding individuals’ resource requirements (Boyce *et al.* 2016). Owing to this, empirical information for IBMs has been based on assumptions (Rushton *et al.* 1997, 1999; Macdonald & Rushton 2003), estimations after decades of collecting data on small animals ranging over small areas (Goss-Custard *et al.* 1995a,b, 2006; Stillman 2008; Stillman & Goss-Custard 2010), or has come from intensive and costly on-the-ground sampling (Marucco & McIntire 2010; Carter *et al.* 2015). This limits their use, particularly with animals with large ranges in areas that are costly or difficult to access. Examples could be Amazonian manatees *Trichechus inunguis* (Arraut *et al.* 2010, 2016), Jaguars *Panthera onca* (Ramalho & Magnusson 2008) or Harpy eagles *Harpia harpyja* in the Amazon (Aguiar-Silva *et al.* 2014), rhinoceros or elephants in Africa (Valeix *et al.* 2011; Cain *et al.* 2014), or bison *Bison bison* in North America (Plumb *et al.* 2009).

Here we provide one solution to the problem of predicting animal population abundance and distribution within a real landscape. We present Resource-Area-Dependence Analysis (RADA), a statistical analysis that relies on remote sensing information (radio-tracking and mapping) for inferring individuals’ resource requirements. This information is then used to define resource-related parameters and their values in an IBM, where one then programmes rules to govern the interactions. To illustrate the approach, we chose a species for which a comprehensive dataset existed; namely, the common buzzard (*Buteo buteo*) in lowland UK (Kenward *et al.* 2001). Here we provide a synthesis of what we reported in (Arraut *et al.* 2015) and of recent developments that shall be soon submitted as two papers (Arraut *et al. in prep.*; Kenward *et al. in prep.*).

2. Method

2.1 Resource-Area-Dependence Analysis (RADA)

Resource-Area-Dependence Analysis (RADA) involves using the relative variation in the size of home-range cores and of patches of each landscape class contained within them to discover: in which landscape class a resource occurs, how much of it an individual needs on average, and within which home-range core it is usually found (Kenward et al. *in prep.*). The data required are a sample of radio-tracked animals and a thematic map with at least one of its classes containing information regarding the accessibility of the resource to individuals.

First, a subset of the animal population that is hypothesized to present a similar pattern of resource use is defined. This could be, for example, adults, adult females or juveniles. Then, the home-ranges of individuals in this subset are estimated and superimposed on the map. The areas of each map class contained within the sample of home-ranges are plotted independently against the size of the home-ranges within which they occur. In such plots, one expects a point-pattern of dispersion resembling a straight horizontal line – this would imply that each individual adapts the size of its home-range so as to encompass the minimum required amount of that particular resource. The assessment of statistical significance involves testing the regression $\log(a/A)$ against $\log(A)$, with A representing the area of individuals' home-range cores and a the area of a particular map class contained within a home-range core. Significance of observed r and b values is estimated from their position in distributions of 999 randomization values. The distribution is created by selecting home-range outlines at random with replacement from the sample of home-ranges and then randomly placing (rotating and displacing) them on the map within a single convex hull enveloping all of the tracked individuals' ranges. An observed value is considered significantly different from the randomized values, in a two-tailed test, if it is less than 50 (for $P < 0.10$), 25 (for $P < 0.05$) or 5 (for $P < 0.01$) from the top or bottom edges of the distribution of random values, or has no random values beyond it (for $P \leq 0.002$ from one run or $P \leq 0.001$ in both of two runs).

2.2 Empirical Individual-based model (E-IBM)

In the E-IBM, virtual animals are defined based on empirically derived (via RADA) resource-related parameters and values. Additional parameters and rules of interaction are then defined using ancillary information or based on hypotheses. Their precise values may be obtained from the data or determined via calibration. At this stage, one also decides which system-level outputs to measure (see buzzard example below). Overall, it is suggested that model building, from conceptualization to sensitivity and robustness analyses, follows the Pattern-Oriented Modeling approach (Grimm & Railsback 2012), and that its documentation follows the Overview, Design Concepts and Details (ODD) protocol that is used widely in the IBM literature (Grimm *et al.* 2010).

2.3 Example: common buzzard in lowland UK

Seventy-two common buzzards were monitored in Dorset during October 1990-94, shortly after their main autumn dispersal period (Walls and Kenward 1995). From these, 114 seasonal home-ranges were estimated using standard samples of 30 locations (Kenward 2001). Mapping data came from the 25x25-m resolution Land Cover Map of Great Britain (LCMGB), which was developed by supervised likelihood classifications of combined winter and summer Landsat Thematic Mapper scenes imaged in November 1989 and July 1990 (Fuller et al. 1994a,b).

Establishing a territory meant finding the required areas of each resource-containing map class within the maximum travel distances from the site where the virtual buzzard initially settled (this was a pixel of the woodland map class chosen randomly). If the required resources were not accessible from the settling site, the individual would mark that site as

‘used’ (so that other individuals would not try settling on it) and then emigrate/die (no distinction). A model run would end when there were no potential settling sites left.

Model outputs were the size and perimeter of buzzard home-ranges, as estimated with Minimum Convex Polygons (MCP) from 25%-100% at 5% intervals, the proportion of each individual’s 85% MCP contours that overlapped with at least one other adult non-sibling, total population range, population density locally (within 2x3km quadrants) and carrying capacity of the landscape for buzzards. The choice of 85% MCP for the overlap output was based on results obtained for the territorial pattern of wild buzzards (Walls & Kenward 2001). Outputs were computed per run and results were based on 100 runs.

3. Results and Discussion

When applied to the common buzzard case, RADA showed that on average each wild individual needed 0.54ha (0.35-0.82ha) within its inner home-range core, 15ha of meadow within its outermost core, and a tree for roosting. To illustrate actual RADA outputs, Table 1 shows results for the analysis involving meadow. Correlations obtained using independent home-range estimation algorithms consistently pointed towards the need for meadow within the outermost cores, suggesting results were biologically meaningful, as opposed to algorithm-dependent. In addition, values for *r* ranging from -0.17 to -0.20 for the most significant results suggest there exists variation in meadow patch quality or in individuals’ resource requirements. The explanation might be that buzzards are better at killing rabbits (*Oryctolagus cuniculus*), an important prey (Hodder 2000), when these are roaming over larger grassland areas; in small patches rabbits have better chance of escaping into the undergrowth of adjacent tree- or bush-dominated patches. Considering the 99% Kernel results, mean minimum meadow requirements per buzzard was 15ha (details of this calculation are reported in (Arraut et al. *in prep.*; Arraut et al. 2015)).

Following the methodology explained above, initial parameters in the IBM were: ‘roosting site’ = 0.0625ha of woodland (= 1 pixel), ‘area of required rough-ground’ = 0.56ha, and ‘area of required meadow’ = 15ha. We then calibrated maximum travel distances for finding rough-ground or meadow by comparison with radio-tracking data on wild animals. Calibrated values were: 150m for rough-ground and 1200m for meadow.

Tabela 1. Matrix of correlation coefficients for proportion of meadow for 114 common buzzards in southern England. Significance levels, by randomization, are $P \leq 0.05$ (pale gray), $P \leq 0.01$ (dark gray) and $P \leq 0.002$ (black). Abbreviations for home-range estimation methods correspond to: Ellipse = Jennrich-Turner Ellipse, Kernel = Kernel Density Estimator, MCP = Minimum Convex Polygon, HM = Harmonic mean.

Estimator	Percentage inclusion of density distribution or locations														
	30%	35%	40%	45%	50%	55%	60%	65%	70%	75%	80%	85%	90%	95%	99%/1
Ellipse	0.01	-0.01	-0.02	-0.02	-0.02	-0.03	-0.04	-0.05	-0.05	-0.08	-0.10	-0.12	-0.15	-0.16	-0.18
Kernel	-0.11	-0.09	-0.10	-0.11	-0.14	-0.10	-0.14	-0.15	-0.15	-0.16	-0.17	-0.17	-0.17	-0.18	-0.20
MCP	-0.05	-0.09	-0.01	-0.05	-0.06	-0.03	-0.02	-0.04	-0.06	-0.05	-0.05	0.00	-0.08	-0.09	-0.14
HM	-0.05	-0.05	-0.08	-0.13	-0.13	-0.14	-0.14	-0.13	-0.12	-0.12	-0.11	-0.10	-0.70	-0.80	-0.11

A comparison of the percentage overlap of the predicted population range on the range of the sampled buzzards yielded 97.2% coincidence, indicating the model’s omission error was low (red areas in Figure 1). Though commission error is difficult to determine objectively in this case, it was noticed that the two areas where buzzards were predicted to occur, but had not been tracked, were in areas where sampling had been unsystematic or absent: the one to the

southwest lies within a restricted-access military range whereas the one to the east is a large bog with no road access.

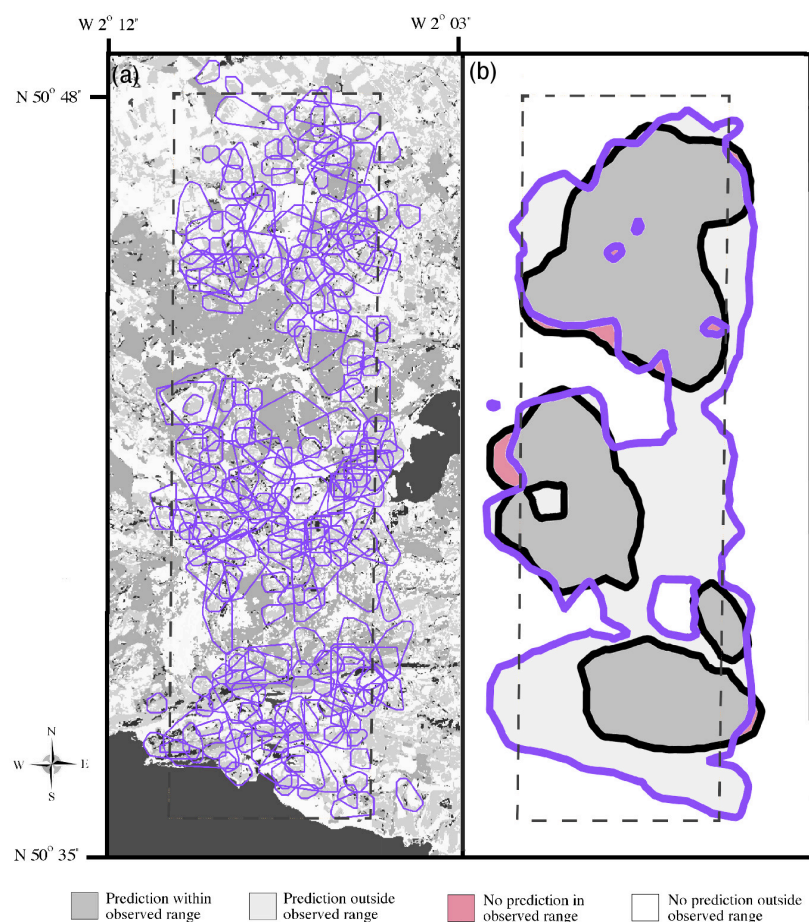


Figure 1 – Predictions for buzzard population at carrying capacity: (a) 85% MCP home-ranges (N=223), (b) spatial distribution (purple polygons) superimposed on areas occupied by wild buzzards (black polygons).

The model predicted that the carrying capacity of the study region for buzzards would be reached at 211-226 individuals (Table 2). This range fell well within the ranges obtained by two independent field-based estimates from the mid 1990s (Table 2). This suggests that after undergoing a dramatic population collapse in the 1950s, owing to a decline in the rabbit population following the introduction of the myxoma virus by UK authorities, by the mid 1990s buzzards in the study area had recovered to their equilibrium density.

Table 2 – Comparisons between Buzzard-IBM calculations for abundance at carrying capacity after 100 model runs and independent estimates from Transect and Mark-Resighting (M-R) surveys made between 1990 and 1998 (Kenward *et al.* 2000).

	M1	Transect	M-R
Abundance	219	256	250
95% CI	218-219	152-435	82-417
Variation	211-226	-	-

To our knowledge, the Buzzard IBM presented here is the first to mechanistically predict the carrying capacity of a real landscape for a real animal population. This kind of modeling may allow for assessing the status of populations within conservation areas or multi-functional landscapes. Comparison of model predictions with data on wild animals could clarify, for example, whether a population is at or below carrying capacity. This might be particularly relevant for vulnerable or endangered species, for which the maximization of abundance within available refuges is often desirable. Moreover, we suspect that the overcoming of some challenges concerning the structure of the model presented here will facilitate the creation of models for other species that, like buzzards, are solitary and territorial. This could be the case with, for example, Amazonian manatees, Harpy eagles or jaguars. Expanding the potential use of this approach will require, among other things, understanding the effect on RADA results of variation in patch quality, as well as developing the basic model structure for animals that use space in ways that are more complicated than buzzards. African lions *Panthera leo*, which are social and territorial (Packer *et al.* 2005), and several species of large herbivores, which are social but non-territorial, are but a few examples.

Yet another potential use of this modeling approach concerns scenario-oriented landscape management. As virtual individuals adapt their use of space to the local distribution of resources, predictions for landscapes with similar composition but different structure should, in principle, be valid. Such landscapes could reflect, for example, alternative management scenarios that take into account agricultural production and climate change. This would allow policy to be better tailored to particular conservation outcomes, analogously to what has been happening in the scenario-driven climate change arena (IPCC 2013). The development this approach to the point where it can be reliably used in scenario-oriented modeling is an on-going research.

4. Conclusions

Our results illustrate the potential of the RADA-IBM approach for modeling the abundance and distribution of a real animal within a real landscape. The use of remote sensing for deriving the empirical data indicates its applicability to animals that roam over areas that are large, dangerous or difficult to access from the ground. It also suggests that developments in our modeling approach will be closely linked to progresses in the field of remote sensing. This is an on-going research and further steps will aim at making it applicable to social or non-territorial species, as well as in scenario-oriented landscape management.

Acknowledgements

We thank Dr. Evlyn Novo for a useful revision.

Bibliographical References

- Aguiar-Silva, F.H.; Sanaiotti, T.M.; Luz, B.B.. Food Habits of the Harpy Eagle, a Top Predator from the Amazonian Rainforest Canopy. **Journal of Raptor Research**, 48, 24–35, 2014.
- Amano, T.; Sandel, B.; Eager, H.; Bulteau, E.; Svenning, J.-C.; Dalsgaard, B.; Rahbek, C.; Davies, R.G.; Sutherland, W.J. Global distribution and drivers of language extinction risk. **Proceedings. Biological sciences / The Royal Society**, 281, 20141574, 2014.
- Arraut, E.M.; Arraut, J.L.; Marmontel, M.; Mantovani, J.E.; Novo, E.M.L.M. (2016). Bottlenecks in the migration routes of Amazonian manatees and the threat of hydroelectric dams. *Acta Amazônica (in print)*.
- Arraut, E.M.; Macdonald, D.W.; Kenward, R.E. In the wake of buzzards: from modelling to conservation and management in a changing landscape. In: Macdonald, D. W.; Feber, R. (Org.). **Wilife Conservation on Farmland Vol. 2**, Oxford, Oxford University Press, 2015.

cap. 10, p.203–222..

Arraut, E.M.; Marmontel, M.; Mantovani, J.E.; Novo, E.M.L.M.; Macdonald, D.W.; Kenward, R.E. The lesser of two evils: seasonal migrations of Amazonian manatees in the Western Amazon. **Journal of Zoology**, 280, 247–256, 2010.

Arraut, E.M.; Walls, S.S.; Macdonald, D.W.; Kenward, R.E. Mechanistically modeling of distribution and abundance of real animals in real landscapes: the common buzzard example (*in prep.* **Ecology**).

Boyce, M.S.; Johnson, C.J.; Merrill, E.H.; Nielsen, S.E.; Solberg, E.J.; van Moorter, B. REVIEW: Can habitat selection predict abundance? (L. Börger, Ed.). **Journal of Animal Ecology**, 85, 11–20, 2016.

Cagnacci, F.; Boitani, L.; Powell, R.A.; Boyce, M.S. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. **Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences**, 365, 2157–62, 2010.

Cain, B.; Wandera, A.B.; Shawcross, S.G.; Edwin Harris, W.; Stevens-Wood, B.; Kemp, S.J.; Okita-Ouma, B.; Watts, P.C. Sex-Biased Inbreeding Effects on Reproductive Success and Home Range Size of the Critically Endangered Black Rhinoceros. **Conservation Biology**, 28, 594–603., 2014.

Ceballos, G.; Ehrlich, P.R.; Barnosky, A.D.; García, A.; Pringle, R.M.; Palmer, T.M. Accelerated modern human – induced species losses: entering the sixth mass extinction. **Sciences Advances**, 1, 1–5, 2015.

Evans, M.R.; Bithell, M.; Cornell, S.J.; Dall, S.R.X.; Díaz, S.; Emmott, S.; Ernande, B.; Grimm, V.; Hodgson, D.J.; Lewis, S.L.; Mace, G.M.; Morecroft, M.; Moustakas, A.; Murphy, E.; Newbold, T.; Norris, K.J.; Petchey, O.; Smith, M.; Travis, J.M.J.; Benton, T.G. Predictive systems ecology. **Proceedings. Biological sciences / The Royal Society**, 280, 20131452, 2013.

Grimm, V.; Berger, U.; DeAngelis, D.L.; Polhill, J.G.; Giske, J.; Railsback, S.F. The ODD protocol: A review and first update. **Ecological Modelling**, 221, 2760–2768, 2010.

Grimm, V.; Railsback, S.F. Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. **Philosophical Transactions of the Royal Society B: Biological Sciences**, 367, 298–310, 2012.

Hodder, K.H. **The common buzzard in lowland UK: relationships between food availability, habitat use and demography**. 2000. 183 p. PhD Thesis, Southampton University. 2000.

IPCC. **5th Assessment Report of the Intergovernmental Panel on Climate Change**, 2013.

Kenward, R.E.; Arraut, E.M.; Robertson, P.A.; Fuller, R.M.; Walls, S.S.; Casey, N.M.; Aebischer, N.J. Resource-Area-Dependence Analysis: towards inferring the role of resources in structuring animals’ home ranges (*in prep.* **Ecological Monographs**).

Kenward, R.; Walls, S.S.; Hodder, K.H. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. **Journal of Animal Ecology**, 70, 1–13, 2001.

Packer, C.; Hilborn, R.; Mosser, A.; Kissui, B.; Borner, M.; Hopcraft, G.; Wilmshurst, J.; Mduma, S.; Sinclair, A.R.E. Ecological change, group territoriality, and population dynamics in Serengeti lions. **Science**, 307, 390–3, 2005.

Pettorelli, N.; Laurance, W.F.; O’Brien, T.G.; Wegmann, M.; Nagendra, H.; Turner, W. Satellite remote sensing for applied ecologists: opportunities and challenges (E.J. Milner-Gulland, Ed.). **Journal of Applied Ecology**, 51, 839–848, 2014.

Plumb, G.E.; White, P.J.; Coughenour, M.B.; Wallen, R.L. Carrying capacity, migration, and dispersal in Yellowstone bison. **Biological Conservation**, 142, 2377–2387, 2009.

Prior, T.; Giurco, D.; Mudd, G.; Mason, L.; Behrisch, J. Resource depletion, peak minerals and the implications for sustainable resource management. **Global Environmental Change**,

22, 577–587, 2012.

Ramalho, E.E.; Magnusson, W.E. Uso do habitat por onça-pintada (*Panthera onca*) no entorno de lagos de várzea, Reserva de Desenvolvimento Sustentável Mamirauá, AM, Brasil. **Uakari**, 4, 33–39, 2008.

Rockström, J.; Steffen, W.; Noone, K.; Persson, A.; Chapin, F.S.; Lambin, E.F.; Lenton, T.M.; Scheffer, M.; Folke, C.; Schellnhuber, H.J.; Nykvist, B.; De Wit, C.A.; Hughes, T.; Van Der Leeuw, S.; Rodhe, H.; Sörlin, S.; Snyder, P.K.; Costanza, R.; Svedin, U.; Falkenmark, M.; Karlberg, L.; Corell, R.W.; Fabry, V.J.; Hansen, J.; Walker, B.; Liverman, D.; Richardson, K.; Crutzen, P.; Foley, J.A. A safe operating space for humanity. **Nature**, 461, 472–475, 2009.

Scheffer, M. Creating a safe operating space for iconic ecosystems. **Science**, 347, 1317–1319, 2015.

Steffen, W.; Grinevald, J.; Crutzen, P.; McNeill, J. The Anthropocene: conceptual and historical perspectives. **Philosophical transactions. Series A, Mathematical, physical, and engineering sciences**, 369, 842–67, 2011.

Valeix, M.; Fritz, H.; Sabatier, R.; Murindagomo, F.; Cumming, D.; Duncan, P. Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. **Biological Conservation**, 144, 902–912, 2011.

Walls, S.S.; Kenward, R.E. Spatial consequences of relatedness and age in buzzards. **Animal Behaviour**, 61, 1069–1078, 2001.