



Invited reply

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Crying wolf: limitations of predator–prey studies need not preclude their salient messages

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A rapidly growing body of the literature reveals the important roles apex predators play in shaping the composition and functioning of ecological communities worldwide [1,2]. The principal effects of apex predators—namely herbivore and mesopredator population suppression—are often evident following their removal from environments, or their reintroduction, including rewilding initiatives [3,4]. What remains less clear, however, is to what extent humans versus other apex predators affect ecosystems, how both interact across gradients of anthropogenic pressure and how such interactions can be affected by underlying bottom-up processes. Such questions are critical to answer in the Anthropocene [5], where effective management of ecosystems and conservation of biodiversity requires a better understanding of how top-down and bottom-up processes vary according to anthropogenic influences.

Our work in Romania, which spanned natural to modified agricultural landscapes, and where humans and a diverse predator community coexist, suggests that apex predators are particularly important in suppressing herbivores, but that human influence is more prominent across the ecosystem, affecting species at multiple trophic levels [6]. Kuijper *et al.* [7] provide a critical response to some of the limitations and interpretations of our study. We thank Kuijper *et al.* [7] for responding to our work, and also for reaffirming the need for increased recognition of the importance of studying predator–prey interactions within human-dominated landscapes. Kuijper *et al.*'s [7] primary concerns with our study are: (i) inappropriate bottom-up data; (ii) unsuitable camera trap design to answer our study's aims; (iii) that top-down and bottom-up processes are not examined at appropriate spatial scales; (iv) the high wolf densities we reported and our inability to examine human impacts on wolves; and (v) that human drivers on wolf densities were not included in our models.

The predator–prey literature is replete with active debate about how and what we can and cannot discern regarding predators' effects on ecosystems [8–10], and hence how this might affect applications, including managing overabundant populations and invasive species, and undertaking species reintroductions and rewilding [11]. Not sufficiently acknowledged by Kuijper *et al.* [7] and other similarly critical responses to field-based predator–prey studies (e.g. [12]), however, is that virtually all these studies have limitations resulting from the necessity to work at large geographical extents and in complex human–natural systems with often rare and cryptic fauna. Therefore, we certainly need to be careful not only when assessing the importance of these limitations, but also not be hasty in dismissing studies and hence potentially overlooking important messages they might still provide. We address Kuijper *et al.*'s [7] concerns below, and as part of this aim to promote more considered discussion regarding the challenges of undertaking predator–prey studies and interpreting their results and significance.

Criticism 1: Kuijper *et al.* [7] raise concerns whether our data (e.g. land cover) used to characterize bottom-up processes are appropriate, including the scale at which habitat features are measured and hence used in statistical models. While it is always preferable not to rely on proxy variables and instead have direct empirical measures of both fine- and large-scale habitat variation, we argue that the land cover map we used (Corine Land Cover 2006 [6]) was indeed an appropriate proxy for assessing bottom-up factors. This is because the productivity of forest and pasture differ substantially in our study system, and there is ample empirical evidence that forest and pasture extent are indeed important bottom-up drivers of apex predator, mesopredator and herbivore distributions [6], and the thematic detail of our land cover map captures these important aspects of resource availability well.

In regard to Kuijper *et al.*'s [7] concerns about how variation in the spatial grain of analysis of habitat may affect the ability to recognize habitat heterogeneity [13], in our study this potential issue appears negligible. An *ad hoc* comparison of the Corine 2006 forest layer with a woody vegetation layer that we derived from SPOT 5 satellite data (scenes from 2010; $10 \times 10 \text{ m}^2$ resolution) revealed that only 3.3% of the inner forest might be open. This means that broad-scale patchiness (such as larger openings in the canopy) is captured well by the Corine data (at a minimum mapping unit of 25 ha), notably well below the average home range of species reported on in our study [14,15]. Kuijper *et al.* [7] are therefore incorrect to conclude that no appropriate bottom-up controls were included in our models. Importantly, we do not question that other factors may influence species' distributions, as, for example, human-mediated bottom-up factors (supplemental feeding) are almost certain to affect deer populations (as discussed in [6]). This does not, however (as claimed by Kuijper *et al.*'s [7] critique), invalidate other suitable bottom-up factors.

Criticism 2: Kuijper *et al.* [7] suggest our camera trapping design was unsuitable to answer our study's aims, asserting it was not randomized, and question our decision to place cameras close to paths in the forest, but not also away from paths, and deeper within the forest. Our design did in fact employ a randomized approach to camera placement across the landscape (within grid cells), with cameras being placed at the closest appropriate place to the randomly selected point and according to logistical constraints (ease of access and time taken to deploy and retrieve cameras). Ideally, we would have liked to deploy cameras off and on paths and across as much of the available habitat as possible, but the disadvantages of placing cameras along paths were considered against other potential problems. A desire to maximize our sample sizes (species detections) was weighed against our available resources, and resulted in optimizing our design to maximize species encounter rates. Species in our study are wide ranging and often use paths, hence placing cameras on or near paths (within randomly selected grid cells) is a sensible way to survey to maximize detection (albeit with having to accept a trade-off of potentially inflated estimates of some species' detections). Moreover, given the high sampling effort of our study (more than 3000 camera days), the placement of cameras near trails is unlikely to affect the inferences made at the community level [16]. If we had placed more cameras away from paths,

it is very likely that this would have resulted in fewer detections, which would have compromised our ability to conduct statistical analyses.

Criticism 3: Kuijper *et al.* [7] suggest top-down and bottom-up processes were not examined at appropriate spatial resolutions. They question the appropriateness of data collected at the scale of entire hunting grids, noting 'landscape-level data assume a homogeneous distribution of predator activity across a large scale'. Oddly, Kuijper *et al.* [7] make this same assumption when correlating data on hunting-ground scale data with data from camera traps in their criticism of our camera trapping (in *Criticism 2*). However, this criticism appears tenuous. We allowed the hunting-ground-scale data in our models to be outperformed by the camera-scale (i.e. local-scale) if the latter better explained encounter rates (as described in Dorresteijn *et al.* [6]). This allowed the strength of the response of species to predator densities at each scale to be the deciding factor, rather than assuming that predator-prey dynamics occur at a particular scale.

Criticism 4: Concern was also expressed regarding the wolf densities we reported, and which Kuijper *et al.* [7] suggest to be very high. As stated in Dorresteijn *et al.* [6], our data provide a useful relative indicator of regional-scale differences in predator density. We accept that, for track count results, there is a risk of double counting some wide-ranging animals, and if this occurred it could inflate estimated population sizes. However, as we detailed in the supplementary information of Dorresteijn *et al.* [6], the rank ordering of estimates were consistent through time (from 2006 to 2010). Thus, while the estimates of wolf abundance are likely to be inflated overall [17], they are a useful indicator of the relative differences in wolf abundance and activity, which is consistent over time.

Criticism 5: Finally, Kuijper *et al.* [7] ask why humans were not included as drivers of wolf distributions. As we state in Dorresteijn *et al.* [6], we 'did not attempt to explain wolf or bear densities obtained for hunting grounds, because these were at a much larger scale than species encounter rates obtained from cameras or human population size in nearby villages.' We therefore do not disregard that humans may have important effects on wolves, and in the discussion we state 'Indirectly, human suppression of bears, and possibly wolves ... could lift top-down control and lead to increased herbivore populations, and possibly further mesopredator release.' However, we were unable to examine this linkage effectively in Dorresteijn *et al.* [6] because of the different spatial scales that wolves and humans were measured on (importantly, humans were measured at a finer spatial scale). Examining this possibility as part of future work should be prioritized.

In summary, Kuijper *et al.* [7] highlight some important limitations of our study, some of which are already openly acknowledged in the main text and supplementary information of Dorresteijn *et al.* [6], but in some cases they overstate their ramifications. While it is important to keep the highlighted limitations in mind while interpreting the results of Dorresteijn *et al.* [6], the broader, more salient messages that emerged from our study's findings—namely, that humans play a critical role in mediating and altering trophic cascades, and that in general, more consideration should be given to the potential role of humans in shaping ecosystems—remain.

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