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Invited reply

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What explains tick proliferation following large-herbivore exclusion?

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Our study [1] explored the effects of large-herbivore exclusion on tick abundance and tick-borne pathogens across a rainfall gradient, using a replicated long-term (5–6 years at the time of our study) size-selective exclosure experiment in Kenya. During our 13-month study, we found that tick abundance varied across time and among tick species, but that the total number of questing adult ticks was significantly greater within exclosures than in unfenced control plots (and increased with each successive level of large-herbivore removal). This effect was the strongest in the driest locations (cf. [2]), indicating that climatic context and wildlife removal can interact to affect tick abundance; we interpreted our results as being driven by increases in smaller mammalian hosts in the absence of megafauna and concluded by suggesting that the prevention of wildlife loss might help to prevent an escalation in the number of questing ticks infected with zoonotic pathogens.

Esser *et al*. [3] and Buck & Perkins [4] suggest a different interpretation for our results, namely that they might be an artefact of our experimental plot sizes (each 1 ha), and that in the absence of final hosts, ticks might have dispersed into the exclosure plots via rodent hosts. Specifically, these authors propose that immature ticks were imported into the plots, leading to a proliferation of questing adult ticks that were not subsequently 'removed' by final hosts and were therefore present to be picked up in our drag samples. If this is the case, then the observed pattern is scale-dependent, and ticks might not proliferate following large-scale large-mammal extirpation scenarios because final hosts are entirely lost. Such scale dependence has been observed in North American deer exclosures [5].

Available data are not sufficient to establish the relative support for these two interpretations, which are not mutually exclusive. These commentaries make an important contribution by outlining a hypothesis that must be explicitly tested in future research. Until a more conclusive verdict can be rendered, however, we welcome the opportunity to clarify several points and explain why we still consider our original interpretation to be a more probable explanation for our results.

Both comments point out that in the absence of final hosts, entire tick life cycles cannot be sustained [6]. Importantly, however, the total elimination of all final hosts is unlikely in our study system, and did not actually occur for any of the tick species within our 1 ha study plots. Adults of the three tick species in our study, *R. praetextatus*, *R. pravus* and *R. pulchellus*, have been documented on 25, 19 and 29 host species, respectively, that occur in our experimental plots [7], which range in size from ground squirrels (less than 1 kg) to elephants (greater than 2000 kg) [8]. It is therefore possible that tick populations in the exclosure plots are sustained by small-to-medium-sized mammalian final hosts that occur within most if not all of the large-herbivore-exclusion treatments in our study; these potential final-host species include dik-diks (*Madoqua guentheri*), hares (*Lepus* spp.), genets (*Genetta genetta*), mongooses (Herpestidae, several species) and squirrels (*Paraxerus ochraceus*, *Xerus erythropus*) [7]. Of these, dik-diks are present in all but the most-exclusive treatment, and the remainder are present in all exclosure treatments [7];

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indeed, mid-sized mammals frequently increase in density when large herbivores are excluded [2,9].

One meta-analysis has linked exclosure size to tick abundance in North American systems by combining all tick life stages [5], but more research is needed to evaluate the generality of this result across ecosystem types, host communities and tick life stages. Empirical studies of more-gradual host reduction are scarce, but at least one observed a substantial increase in questing adult ticks at sites across 176 ha and 326 ha properties, several years following initialization of deer reductions [10]. Continued deer loss led to eventual reduction of all life stages, indicating that questing adult ticks initially become abundant when final hosts are reduced, and only eventually decline once final-host abundance dips below a critical threshold for a sufficient length of time. Our study may contain evidence of similar dynamics: we found that *R. pulchellus*, the only one of our three focal species that does not use rodents during immature stages, increased in exclosures permeable to mammals up to 5 kg, but declined (to levels indistinguishable from unfenced controls) in the treatment that removed all mammals greater than 5 kg. In this respect, our results are similar to those of another exclosure experiment at the same Kenyan site in which the plots are four-times larger than ours (and above the scale-dependent threshold identified in the North American meta-analysis [5]). In that experiment, *R. pulchellus* abundance declined in total exclosures, whereas *R. praetextatus* abundance trended up to twofold higher in total exclosures (although this effect was not statistically significant after correcting for multiple comparisons across six treatments) [11].

We agree with Esser *et al.* [3] and Buck & Perkins [4] that rodents almost certainly import immature ticks across plot boundaries, and that this effect is probably most pronounced at plot edges. To fully explain our results, however, this would require very large numbers of plot-crossing rodents and/or very high densities of ticks per rodent. We question the likelihood of this scenario in our system, especially in arid sites, where we observed the strongest effects and where the rodent population was a third of that at mesic sites (and at times drops to near zero in unfenced controls) [7]. A rough calculation using data from the arid plots suggests that the number of ticks imported by rodents is probably low, in contrast to high tick abundance measurements. Previous sampling found an average of approximately 11 rodents per ha across exclosure treatments [7], tightly coupled with vegetation density [12], and with individual home ranges of 100–300 m^2 [13]. Assuming 6–10 m non-overlapping home-range radii, we approximate that 20–35% of home ranges might overlap a plot boundary. Given a mean tick intensity of 1.5 ticks per rodent, with approximate prevalence of 5% across sites, hosts and tick species [14], and assuming ticks feed for 3 days, we would expect all rodents to transport approximately three ticks per plot across boundaries (without any subtraction for tick mortality, which is often substantial [15]). Thus, this effect seems unlikely to account for the magnitude of the observed treatment effects in arid plots, given that we sampled an average of 25 adult ticks per exclosure each month, up to a maximum of 81 using drags and 154 using traps. We consider it more likely that the hares, sciurids, small carnivores and dwarf antelopes present in the exclosures sustain tick populations by hosting gravid females that can produce thousands of larvae that quickly attach to abundant intermediate hosts [8]. Because larval mortality is usually very high [15,16], any improvements in environmental conditions and increased contact rate with intermediate hosts in the absence of megafauna—such as increased vegetation density [12]—may substantially elevate larval survival and in turn the abundance of questing adults. We concede, however, that the mechanistic effects of defaunation on the various stages of tick life cycles are complex, especially when coupled with variability in the environmental factors that also strongly affect tick survival. Studies designed to test for the tick-abundance gradient proposed by Buck & Perkins would be particularly informative, ideally across a range of exclosure sizes and permeability.

Esser *et al.* [3] also stress the importance of sampling all life stages, both on and off hosts, to better understand tick population dynamics. We agree that this would provide greater clarity and would enable more robust tests of our hypothesis that the most important parameter for determining adult tick abundance in this system is larval, not adult, questing success. We pilot-tested the walking method of tick sampling recommended by Esser *et al.*, which is effective in environments with tall grasses, but which gave very low yield in our plots and was not feasible in many areas owing to impenetrably dense thorny vegetation. We therefore still believe that drags are the most effective method for collecting adults in these plots. It is unfortunately true that timed drags do not reliably sample immature stages, and we recovered very low numbers in both control plots and exclosures. Larval ticks usually attach to drag cloths as a single mass, which quickly disperse or drop off a moving cloth, while adults attach more consistently. For this reason, we did not analyse immature stages in our study, but concur that future studies should incorporate efforts to sample all life stages.

Ultimately, a conclusive test of both our hypothesis and the hypotheses outlined by Esser *et al.* [3] and Buck & Perkins [4] (both of which might have contributed to our results) will require further research—ideally combining theoretical, experimental and large-scale comparative approaches to tease out the effects of spatial scale on tick populations and disease dynamics. This exchange highlights the need to define the scale(s) at which we discuss conservation, as well as the importance of scale in understanding conservation–disease relationships. It is self-evident that any perturbation that caused the total elimination of final hosts at large scales would ultimately cause tick populations to crash. However, at our study site, with several dozen mammal species spanning six orders of magnitude in body size, the size-biased removal of the largest-bodied hosts does not imply the total elimination of all final hosts. This is probably a common defaunation scenario, as megafaunal declines are generally associated with increases in mesofauna [2], many of which may be able to sustain entire tick life cycles. It is therefore critical to understand not only the scale dependence of manipulative studies (which inherently entail trade-offs between plot size, replication and experimental control) but also the full range of host breadth for ticks at all life stages—especially in understudied tropical locations where tick diversity and natural history remain incompletely characterized. We also note that conservation on small scales is increasingly important in light of increasing habitat fragmentation and fencing [17,18] in African landscapes, which may create many ‘real-world’ analogues of our experimental plots.

We agree that wildlife conservation does not always contribute directly to disease prevention (a topic of much debate [19,20]), but believe it is critical to understand when and where such synergies might occur—especially in landscapes where both defaunation and zoonotic disease are major contemporary threats.

Data accessibility. This article has no additional data.

Authors' contributions. G.T. wrote the first version of the manuscript; T.M.P. provided feedback; and R.M.P. and H.S.Y. assisted in writing the final report.

Competing interests. We declare we have no competing interests.

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