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Comment on Titcomb *et al.* 2017 'Interacting effects of wildlife loss and climate on ticks and tick-borne disease'

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Understanding the impact of anthropogenic disturbances such as defaunation and climate change on vector-borne disease risk is critically important. Titcomb *et al.* [1] experimentally tested the interactive effects of these perturbations on tick-borne disease risk within long-term, size-selective, large-herbivore exclosures, replicated across a precipitation gradient in East Africa. They found that the abundance of adult ticks increased with increasing degrees of wildlife exclusion (from exclusion of only mega-herbivores to exclusion of all herbivores ≥ 5 kg) and that this effect was stronger in more arid sites. Tick-borne pathogen prevalence remained unchanged. Based on these results, the authors conclude that loss of large wildlife species and climate change increase tick-borne disease risk by increasing the densities of adult ticks. However, given that adult ticks of the collected species all depend on large wildlife as final host, this conclusion is both counter-intuitive and in contrast to earlier studies that conclude that ticks disappear when their specific, final host species are lost [2-4]. Here, we would like to offer an alternative interpretation of their data.

We argue that the apparent increase in tick abundance in these exclosures may actually reflect prolonged questing activity of adult ticks that fail to find a host. Given the absence of a final host, reproduction and hence local recruitment of ticks should be minimal at best. When large wildlife are progressively excluded, the continued presence of ticks inside the exclosures will therefore increasingly depend on rodents and other small mammals that move across fences and import immature ticks from the surrounding area [5]. Once inside, these immature ticks molt into adults, which require larger wildlife as final hosts. When the latter are absent, the adult ticks will continue questing until they perish or until they are picked-up by a drag cloth (Figure 1). In contrast, in plots where (some) large wildlife are allowed, adult ticks will be picked-up by their final host, leaving fewer ticks to be captured by drag sampling [6]. Thus, the increase in collected adult ticks may be simply a result of the lack of 'removal' of these ticks by their final hosts, rather than an indication of an actual increase in the tick population.

The system described above, in which a tick population is sustained by import of immature ticks from outside the exclosure rather than by local recruitment, is typical for small-sized exclosures. In larger exclosures, immature ticks would reach the edge but not the central area of the exclosure, where the tick population is bound to crash (Figure 2). This is exactly in line with previous studies on the effect of exclosure-size on tick population dynamics: tick abundance tends to increase in small exclosures as they are no longer picked up by their wildlife hosts, but decreases in larger exclosures [7-9]. The apparent increase in adult tick abundance reported by Titcomb *et al.* [1] is therefore likely to be an effect of the small size (1ha) of their exclosures.

Titcomb *et al.* nicely illustrate the effect of local defaunation; fencing off a small area from large wildlife, e.g., a backyard, can lead to a local increase in questing activity of ticks and thereby increase tick-borne disease risk. However, their results cannot be extrapolated to effects of defaunation on a large spatial scale, nor can they be generalized to other tick species. Widespread loss of large wildlife is unlikely to be generally beneficial for ticks and their associated pathogens, since most tick species tend to feed on larger-bodied host species when in the adult stage [10,11]. As small mammal densities tend to increase following large-wildlife loss, only parasites that are host-generalists or host-specific to small mammals throughout their life cycle are expected to increase in abundance following large-scale defaunation, such as fleas [12] and macroparasitic helminths [13] in rodents. We therefore remain sceptical of the suggestion by Titcomb *et al.* that “large-wildlife loss can contribute to an increased tick-borne disease risk that may be mitigated by conservation”.

Distinguishing actual increases in tick abundance from merely prolonged questing activity requires a combination of sampling techniques to capture ticks of all life stages from both the vegetation as well as from small mammal hosts. Actual increases in the number of adult ticks should be reflected by higher immature tick burdens on small mammals inside exclosures, but it remains unclear if this is the case in the study of Titcomb *et al*. Nevertheless, even if small mammals fed more immature ticks inside than outside exclosures, the resulting adults would fail to reproduce, so that persistence of the tick population inside exclosures is dependent on the import of immature ticks. In the absence of local recruitment, densities of questing larvae should be lower inside exclosures than in control plots. Yet not a single larva was detected, even in control plots. Nymphs made up <3% of drag-sampled ticks. Given that questing larvae, nymphs, and adults typically occur in decreasing order of abundance [14], this suggests that drag sampling may not have been the most appropriate sampling method for their study area, which is characterized by dense vegetation. Indeed, tick densities followed a more typical pattern using the walking technique in another large-wildlife exclusion experiment in the same region [5, 15]. Thus, careful consideration of different sampling techniques is required to capture the complexity of tick population dynamics in response to defaunation.

Titcomb et al. also argued that climate change is likely to increase tick-borne disease risk via interactions with large-wildlife loss. The authors found that total tick abundance increased with aridity, and that the effect of wildlife exclosure treatment on tick abundance was stronger in more arid sites. However, as the authors already acknowledge, these patterns were largely driven by a single tick species: *Rhipicephalus pravus*. Given this species' strong preference for drier climates and the large differences that exist in climate preferences among other tick species [16], these findings cannot be extrapolated to tick-borne disease risk in general. Although there will likely be both winners and losers in the face of climate change, a recent study found no evidence that parasites with zoonotic potential will benefit from climate change [17]. In fact, that study found that ticks may actually be more negatively affected by climate change than other parasitic groups [17].

In conclusion, we caution against extrapolation of these small-scale experimental results to large-scale inferences about the effects of wildlife loss and climate change on ticks and tick-borne disease risk. It is crucial to keep in mind that small hosts can transport (immature) ticks across fences in large-wildlife exclosure experiments. In large exclosures, transport of ticks across fences will give rise to edge effects that should be considered in the sampling strategy. In small exclosures, the number of collected ticks can increase due to a constant influx of immature stages from outside and a local lack of removal of adult ticks by final hosts. Although these adults will fail to reproduce, their prolonged questing activity results in an apparent (or 'visible', as Dobson [6] coined it) increase in tick abundance that can easily be mistaken for an actual increase in tick population size. We therefore strongly suggest that future studies take into account the size of wildlife exclosures, movement of small hosts that can transport ticks across fences, and the problem of 'actual' versus 'apparent' increases in tick abundance [6].

Authors' contribution

HJE and NAH conceived the presented idea; HJE and NAH designed the figures; HJE, NAH, and FWB wrote the paper.

Ethics statement

This work was conducted without experiments involving animal or human subjects.

Data accessibility

This work contains no data.

Competing interests

We have no competing interests to declare.

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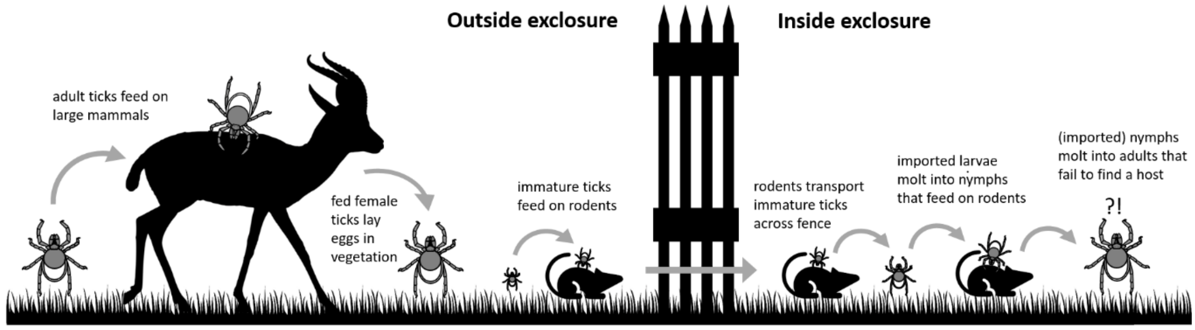

Figure 1. Outside exclosures, adult ticks are picked up by large mammals, allowing them to feed and reproduce. Inside exclosures, adult ticks fail to find their final host and will continue questing until they perish or are picked up by a drag cloth. In the absence of local recruitment, continued presence of adult ticks inside the exclosure depends on a constant influx of immature ticks via rodent hosts that are able to cross the fence.

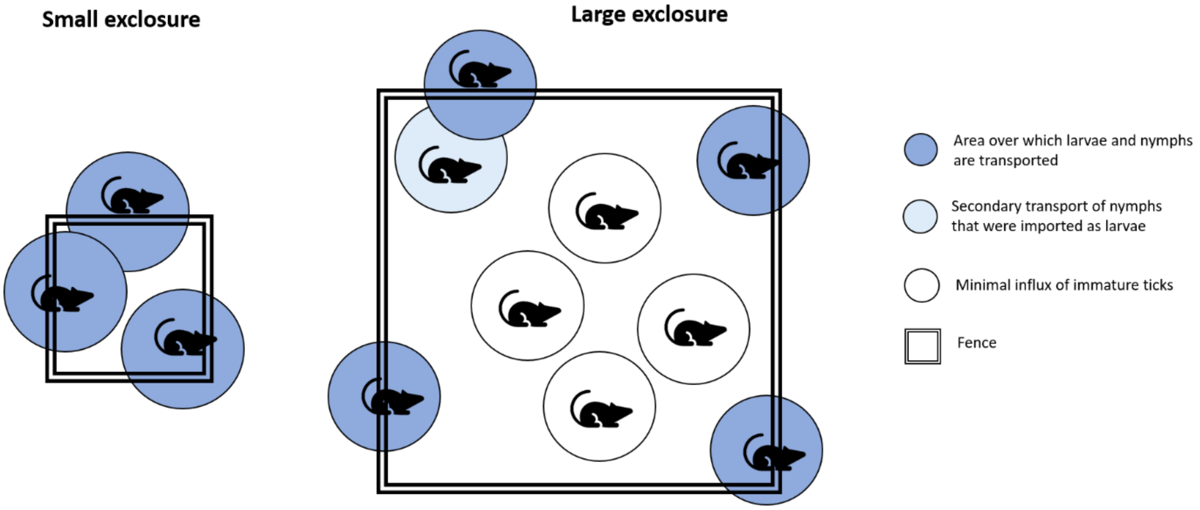

Figure 2. In small exclosures, foraging rodents that cross the fence can easily reach the centre of the exclosure, allowing for a constant influx of immature ticks to large parts of the exclosure. In large exclosures, influx of immature ticks will be limited to the edges of the exclosure.