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**Study scale determines whether wildlife loss protects
against or promotes tick-borne disease**

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1 **Title:** Study scale determines whether wildlife loss protects against or promotes tick-borne
2 disease

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17 How does wildlife loss affect tick-borne disease risk? To test this question, Titcomb et al.
18 [1] excluded large mammals that typically support large numbers of adult ticks from 1 hectare
19 plots, and then quantified the density of questing adult ticks within enclosure versus control
20 plots. *A priori*, one might expect reduced tick density within total enclosure plots, because adult
21 ticks must take their final blood meal from an ungulate, hare, or carnivore (hereafter “large
22 mammal”) (Table 1), which were scarce to absent in enclosure plots (Titcomb et al. Figure S1).
23 However, contrary to expectations, Titcomb et al. report higher density of questing adult ticks of
24 two species (*Rhipicephalus pravus* and *R. praetextatus*) in enclosure plots compared to control
25 plots, whereas the density of a third tick species (*R. pulchellus*) declined in enclosure plots. Here,
26 we examine three possible explanations for this counterintuitive result, expanding on the
27 interpretation offered by Titcomb et al. We submit that high densities of questing adult ticks in
28 enclosure plots indicate that the tick population there is failing, not flourishing. This pattern is
29 maintained through time because small mammals import ticks from outside the plot. Therefore,
30 this pattern would be expected to reverse in a larger plot.

31 Given that all three tick species require large mammals to complete their life cycles [2,3,
32 Titcomb et al. Figure S1, Table 1], Titcomb et al.’s results beg the question: why did the density
33 of two tick species more than double in enclosure plots? Where did all those ticks come from?
34 One explanation is that these ticks hatched before experimental treatments were implemented.
35 Rand et al. [4] demonstrate that loss of large mammals that serve as final hosts for ticks can lead
36 to an initial increase in questing tick density, followed by a crash in the tick population. This
37 occurs because questing ticks that do not find a host continue to quest until they deplete their
38 energy reserves and die [5]. However, the experimental plots used by Titcomb et al. were set up
39 in 2008 [6]. Because experimental treatments had been maintained for >5 years before data were

40 collected (and the reported pattern of increased tick density in exclosure plots remains to this
41 day, Titcomb et al. pers. comm.), we consider it unlikely that adult ticks found in total exclosure
42 plots hatched before experimental setup.

43 A second possible explanation is that questing adult ticks found in total exclosure plots
44 hatched from eggs laid by gravid females that dropped off large mammals not excluded by the
45 exclosure treatment. Although the total exclosure plots excluded or reduced the density of most
46 large mammals on which ticks feed as adults, it is possible that a few carnivores (e.g., genets,
47 mongooses) might have entered exclosure plots (Titcomb et al. Figure S1) and dropped gravid
48 ticks. However, in a similar experiment (Kenya Long-term Exclosure Experiment; KLEE) in the
49 same system, questing larval ticks were completely absent in plots that allowed carnivores and
50 excluded large herbivores, but were common (~50 per 400m transect) in control plots that
51 allowed all large mammals [7]. This pattern suggests that carnivores contributed only negligibly,
52 if at all, to the tick population in exclosure plots.

53 Finally, a third explanation is that the ticks found in exclosure plots recruited there as
54 larvae or as nymphs on rodents and shrews (hereafter “small mammals”), which are abundant [8]
55 and small enough to freely cross plot fences. Previous studies have demonstrated fence-crossing
56 behavior by small mammals [9], and suggested that this could explain increased tick densities
57 inside large mammal exclosures [5,10,11]. G. Titcomb kindly provided data showing that density
58 of questing adult *R. pravus/praetextatus* in the inner 25% of exclosure plots was more than
59 double that in the outer 75% of exclosure plots (Figure 1A), but this pattern did not hold for *R.*
60 *pulchellus*, nor did it hold in control plots (Titcomb, unpublished data). We consider this
61 concentric increase in tick density from the edge of the exclosure to the center as convincing
62 evidence that small mammals are crossing plot fences and moving larval and nymphal ticks with

63 them. Although one might expect the opposite pattern (i.e., higher density of questing ticks near
64 plot edges), the observed pattern likely resulted from the combination of tick import, tick export,
65 and movement of ticks within plots (both independently and on small mammals). Perkins et al.
66 [10] observed a similar pattern in small deer exclosures, and suggested that it resulted from tick
67 “sharing”; small mammals whose home ranges overlap with the edge of exclosure plots dropped
68 some of their ticks outside the plots, where they were picked up by large mammals. In contrast,
69 small mammals whose home ranges are in the center of exclosure plots dropped all of their ticks
70 in the plot center, where they continued to quest and could be detected in tick surveys. Hence, we
71 consider the import of larval and nymphal ticks by small mammals to be the most plausible
72 explanation for increased density of questing adult ticks in exclosure plots.

73 Regardless of whether ticks hatched in exclosure plots or were imported, the success rate
74 of questing larval and nymphal *R. pravius/pratextatus* in exclosure plots might be especially
75 high, because, in such plots, rodent density roughly doubles [8]. However, the success rate of
76 questing adult ticks in exclosure plots should be quite low, as the large mammals from which
77 ticks take their final blood meal are scarce to absent. As a result, adult ticks accumulate in total
78 exclosure plots, where they continue to quest until they deplete their energy reserves and die,
79 which might take months to years [4,12]. Compounding this, survival rates of questing ticks
80 might be particularly high in exclosure plots compared to control plots, due to an abundance of
81 vegetation [13]. Thus, for the two tick species that feed on small mammals as larvae and
82 nymphs, exclosure plots are a sink. In contrast, the third tick species, *R. pulchellus*, does not feed
83 on small mammals at any stage of its life cycle [2,3, Titcomb et al. Figure S1, Table 1]. This
84 species declined in total exclosure plots relative to control plots, indicating that either it cannot

85 mature in enclosure plots due to absence of large mammal hosts, or it cannot recruit into
86 enclosure plots because it is not imported by small mammals.

87 Critically, if tick importation by small mammals explains the high density of questing
88 adult ticks in enclosure plots, then this pattern is scale-dependent. Many ticks might recruit into a
89 1 hectare plot because the ratio of edge:interior habitat is high. In contrast, the center of a larger
90 plot (e.g., 10 hectares) should be free of ticks (Figure 1B), because ticks cannot recruit there
91 from outside the plot. Though such a large-scale study would be logistically challenging, it could
92 reveal the effect of wildlife loss on ticks at a large scale; since large mammals are a required
93 component of the tick life cycle (Table 1), reducing their density should negatively affect tick
94 populations. In support of our assertion that Titcomb et al.'s results would reverse at a larger
95 scale, in a similar experiment, the density of questing adult *R. praetextatus* did not differ between
96 4 hectare plots that allowed vs. excluded large wildlife [7]. Presumably, even fewer adult ticks
97 would be found in an even larger enclosure plot. Indeed, Perkins et al. [10] found that compared
98 to control areas, tick density increased in deer enclosures less than 2.5 hectares, but decreased in
99 deer enclosures greater than 2.5 hectares. Although the studies included in this meta-analysis
100 occurred in a different system (deer and their ticks in North America), the results should be
101 expected to apply to any system in which larval and/or nymphal ticks take blood meals from
102 small mammals and adult ticks rely on large mammals as hosts. However, the inflection point of
103 2.5 hectares would be expected to vary with study system, tick species, small mammal home
104 range, environmental conditions, etc. [5].

105 We stress that Titcomb et al.'s results are valid at the scale at which they were measured;
106 in a small plot, large mammals pick up ticks, thereby decreasing questing tick density (Figure
107 2A). Therefore, wildlife extirpation on local scales (such as might occur near human dwellings)

108 should increase questing tick density [10] and potentially tick-borne disease risk for humans.
109 However, at larger scales, Titcomb et al.'s results should reverse; large mammals produce ticks,
110 thereby increasing questing tick density (Figure 2B). Therefore, wildlife extirpation on global
111 scales should decrease questing tick density and tick-borne disease risk for humans. Although
112 Titcomb et al. suggest that "wildlife loss can contribute to an increased tick-borne disease risk
113 that may be mitigated by conservation," wildlife loss at larger scales is likely to have the
114 opposite effect. We conclude that when examining the effects of biodiversity loss on infectious
115 disease risk, researchers should carefully consider whether their results might reverse with scale.

116 **Ethics**

117 This work did not involve human or animal subjects.

118 **Data accessibility**

119 This article has no additional data.

120 **Authors' contributions**

121 J.C.B. developed the idea for the manuscript based on prior work by S.E.P. J.C.B. drafted the
122 manuscript. J.C.B. and S.E.P. edited the manuscript and gave final approval for publication.

123 **Competing interests**

124 We declare we have no competing interests.

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164 **Table 1.** Hosts used by each tick species at each life stage. Reproduced from Titcomb et al.

165 Figure S1.

Tick species	Life stage	Hosts
<i>R. pravius</i>	Larva and nymph	Rodents Elephant shrews Hares Small carnivores
	Adult	Variety of ungulates Hares Carnivores
<i>R. praetextatus</i>	Larva and nymph	Rodents
	Adult	Carnivores Some ungulates Hares
<i>R. pulchellus</i>	Larva and nymph	Variety of ungulates Hares Carnivores
	Adult	Variety of ungulates Carnivores

166

167 **Figure 1.** Conceptual figure showing the observed gradient in tick density in exclosure plots (A),
168 which is likely due to tick “sharing,” and the gradient we hypothesize would be found in a larger
169 exclosure plot (B).

170 **Figure 2.** Conceptual figure showing that in a small-scale study (A), loss of large mammals
171 increases questing tick density, as detected by Titcomb et al. [1]. However, in a study of larger
172 spatial scale (B), loss of large mammals would be expected to reduce questing tick density, as
173 ticks require large mammals to complete their life cycles. Non-linearities result from ticks
174 distributing themselves among available large mammal hosts.



