Interacting effects of wildlife loss and climate on ticks and tick-borne disease

Georgia Titcomb[1,2], Brian F. Allan[2,3], Tyler Ainsworth[1], Lauren Henson[7], Tyler Hedlund[3], Robert M. Pringle[2,5], Todd M. Palmer[2,6], Laban Njoroge[4], Michael G. Campana[7], Robert Fleischer[7], John Naisikie Mantas[2], Hillary S. Young[1,2]

[1] Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara

[2] Mpala Research Centre, Box 555, Nanyuki, Kenya

[3] Department of Entomology, University of Illinois at Urbana-Champaign, Urbana, IL 61801

[4] Invertebrate Zoology Section, National Museums of Kenya, Nairobi, Kenya

[5] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

[6] Department of Biology, University of Florida, Gainesville, FL 32611

[7] Center for Conservation Genomics, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20008

Corresponding author: georgiatitcomb@gmail.com

Running Head: Defaunation and climate effects on ticks

Keywords: ticks, tick-borne disease, defaunation, climate, exclosure, *Coxiella burnetii, Rickettsia*

Abstract:

Both large-wildlife loss and climatic changes can independently influence the prevalence and distribution of zoonotic disease. Given growing evidence that wildlife loss often has stronger community-level effects in low-productivity areas, we hypothesized that these perturbations would have interactive effects on disease risk. We experimentally tested this hypothesis by measuring tick abundance and prevalence of tick-borne pathogens (*Coxiella burnetii* and *Rickettsia* spp.*)* within long-term, size-selective large-herbivore exclosures replicated across a precipitation gradient in East Africa. Total wildlife exclusion increased total tick abundance by 130% (mesic sites) to 225% (dry, low-productivity sites), demonstrating a significant interaction of defaunation and aridity on tick abundance. When differing degrees of exclusion were tested for a subset of months, total tick abundance increased from 170% (only mega-herbivores excluded) to 360% (all large wildlife excluded). Wildlife exclusion differentially affected abundance of the three dominant tick species, and this effect varied strongly over time, likely due to differences among species in their host associations, seasonality, and other ecological characteristics. Pathogen prevalence did not differ across wildlife-exclusion treatments, rainfall levels, or tick species, suggesting that exposure risk will respond to defaunation and climate change in proportion to total tick abundance. These findings demonstrate interacting effects of defaunation and aridity that increase disease risk, and they highlight the need to incorporate ecological context when predicting effects of wildlife loss on zoonotic disease dynamics.

Introduction:

Zoonotic diseases are a rising concern worldwide [1–3]. Yet, amid rapidly declining wildlife populations and global climate change, there is no consensus on how these perturbations will independently and interactively affect zoonotic disease risk. Anthropogenic land-use change is likely to play a substantial role in facilitating outbreaks through a variety of mechanisms [2,4], including changes to wildlife host populations and communities [3–6]. Meanwhile, climate changes can have substantial and variable effects on zoonotic diseases [7,8], even when considered in isolation of changes to host populations. Thus, the combined effects of wildlife loss and climate change are likely to be complex [7,9], but data are lacking, especially for regions where medical resources and research efforts are low and zoonotic disease risk is highest [2]. Although there has been a widespread call for more research on the net effects of anthropogenic changes on disease and disease vectors globally [3–5], large-scale experimental tests remain scarce.

Ticks and tick-borne pathogens provide a salient system for examining the effects of wildlife loss and climate changes on disease risk. Globally, ticks are considered to be the most important disease vectors for wildlife and domestic animals [10], and are second only to mosquitoes among vectors affecting humans [11]. Estimated economic costs of ticks and tick-borne disease are variable [12] and although no recent estimate has been made, one study attributed annual losses of US$ 13.9 billion worldwide to tick-borne disease in cattle alone [13].

Globally, the pervasive decline in large-wildlife populations [14] is affecting a wide range of ecological functions and services, including disease control [15,16]. Ticks are also likely to be affected, considering their inextricable links to host population dynamics. While a substantial body of work demonstrates complex relationships among hosts, predators, and ticks (e.g., for the Lyme disease system in North America [17]), few studies have experimentally investigated how size-selective defaunation, which simulates the disproportionate vulnerability of larger animals to human disturbance [14], affects tick abundance and risk of tick-borne disease (but see [18]). Size-selective defaunation can directly affect tick abundance through the loss of hosts [19], and can also indirectly affect tick survival by altering vegetation structure [20–23] and the abundance and composition of small-vertebrate hosts [22,24]. Large-mammal loss often accompanies small-mammal abundance increases [22,24,25], leading to changes in host availability for different tick species. The relative importance of these sometimes opposing factors is poorly understood for most systems, and likely depends on vector life cycles and host associations.

Climate can also affect the prevalence and distribution of zoonotic pathogens, particularly those limited by climate-sensitive vectors [7,26–28]. This topic has become increasingly relevant in the context of global climate changes [7,9,29]. As tick survival can depend on factors such as rainfall and temperature [21,30,31], several models have predicted shifting tick ranges that result in net range expansions under climate change scenarios, although this varies among tick species [32]. This experiment is one of few field studies that consider climatic effects on multiple tick species

simultaneously, and is situated in a region where climate changes are already pervasive and will be challenging to mitigate [33].

While the independent effects of climate change and biodiversity loss on zoonotic disease have received considerable recent attention, their potential interaction has not been well explored. For tick-borne diseases, prior studies have been largely correlative, yielding mixed results on the relative importance of various climate metrics, host abundance, and their interaction in determining tick abundance [34–37], emphasizing the need for more data describing a range of interacting forces on tick biology. The indirect effects of large herbivores on other small consumers, from insects to birds and small mammals, are highly sensitive to variation in climate and productivity [22,38,39], but it is not known whether these results can be generalized to disease risk in particular.

East African savannas are hotspots of tick and tick-borne pathogen diversity [40], and tick-borne pathogens such as *Rickettsia, Coxiella,* and *Anaplasma* are major regional economic and human health concerns [41–43]. For example, a recent study in Tanzania found that bacterial zoonoses caused 26% of acute fever cases; of these, 20% were Q Fever, caused by *Coxiella burnetii*, and 30% were Rickettsiosis, caused by spotted fever group *Rickettsia* [44]. Accordingly, African savannas offer an ideal system for testing the effects of varying degrees of defaunation on tick abundance, as hosts are diverse and abundant, ranging over six orders-of-magnitude in size and occupying diverse functional roles [22,45]. However, large wildlife are experiencing widespread and precipitous declines in many parts of this region [46,47], underscoring the importance of predicting effects across ecological communities. Furthermore, climate change is also likely to affect tick-borne disease in East Africa, due in part to shifting rainfall patterns [31]. While large-scale predictions for future rainfall regimes are mixed [33], much of the region has been affected by persistent reductions in the critical 'long rains' since 1970 [48], and localized rainfall prediction models indicate that this trend is likely to continue [49].

We used a replicated series of experimental large-herbivore exclosures to quantify the effects of size-selective defaunation, climatic context, and their interaction on tick abundance and prevalence of tick-borne pathogens. In light of evidence that other consumer groups respond both numerically and behaviorally to an interaction between defaunation and primary productivity [38,39,50,51], we hypothesized that: (1) large-herbivore removal has strong effects on ticks and their associated pathogens; (2) tick species that utilize small mammal hosts will increase in abundance when large mammals are excluded (and small-mammal densities increase); and (3) the strength of these effects are contingent on climatic context and are strongest in more arid, low-productivity areas.

Methods

Survey Site and Exclosures

Research was conducted in the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experimental plots [22,52,53], established in 2008 at Mpala Research Centre (MRC) in Laikipia County, Kenya (0º17' N, 37º52' E, 1600m elevation). MRC supports robust populations of wildlife including elephants (*Loxodonta africana*), giraffe (*Giraffa camelopardalis)*, zebra (*Equus grevyi* and *Equus quagga*), impala (*Aepyceros melampus*), and dik-dik (*Madoqua kirkii)*, among others. The UHURU plots consist of four 1-ha exclosure treatments replicated three times at each of three 'levels' of a rainfall and productivity gradient created by the rain shadow of Mt. Kenya (i.e., 9 total replicates of each treatment, 36 total plots; Table S1). The four treatments simulate different scenarios of size-selective species losses using different combinations of fencing. The treatments are as follows: (1) total exclusion of all ungulate herbivores ('Total exclosure'); (2) exclusion of all herbivores >15kg ('Meso exclosure'); (3) exclusion of only mega-herbivores (i.e., giraffe and elephant; 'Mega exclosure'), and 4) unfenced open plots ('Control') [22]. Mean annual precipitation increases ~45% from the arid northern sites (440mm $year^{-1}$), to the mesic southern sites (640mm $year^{-1}$), with central sites intermediate (580mm $year^{-1}$). Seasonal rains typically fall from March – May ('long rains') and October – December ('short rains') [54]. As in other semi-arid savannas, primary productivity is tightly linked to precipitation across this gradient [22]. Although the Normalized Difference Vegetation Index (NDVI) has been used previously in studies of tick abundance [21], we used mean annual rainfall as the primary climatic variable in our analyses, both because NDVI increases in exclosure treatments due to decreased herbivory and trampling by large mammals [22] (and thus would not isolate climatic factors), and because climatic factors tend to outperform NDVI in predicting African tick distributions [31]. We also present a complementary analysis using a categorical 'climatic level' variable in lieu of the continuous precipitation variable; results are qualitatively similar (Tables S2, S3).

Ticks

The density of infected vectors is a common metric of vector-borne zoonotic disease risk [15,55,56] and is directly related to both vector density and pathogen infection rate. Thus, changes in tick density, infection rate, or a combination of the two can affect disease risk. To measure disease risk, we used tick drags and pathogen screening to quantify the density and infection rate of ticks.

Tick Drags

Ticks were collected in Total exclosure and Control plots each month for 13 months between October 2013 and November 2014. For each survey, a standard white canvas cloth was dragged throughout all passable portions of each plot, but areas of dense thicket areas were not sampled. Because exclosure plots often featured thick, thorny vegetation that precluded drags over fixed linear distances, we conducted drags for a 1-hour period, with ticks collected every 5 minutes. We also surveyed the Mega and Meso exclosure plots for five months in 2014 (Jan, July, Aug,

Sept, Nov). To ensure that drags accurately estimated the tick species composition of each plot, the drags were complemented with CO_2 traps [57] for two months.

Ticks were subsequently identified to species using microscopy and descriptions from [58]. We focused all analyses on three congeneric tick species—*Rhipicephalus pravus*, *R. praetextatus*, and *R. pulchellus*—that dominated the tick community. These tick species vary considerably in typical host preferences for each of their three distinct life stages (Figure S1). In general, immature stages of *R. pravus* and *R. praetextatus* feed upon small mammals (particularly rodents), which roughly double in abundance within total exclosures [22,53], whereas all stages of *R. pulchellus* feed on larger mammals [58,59]. Thus, the UHURU exclosure design alters the dominant host availability for each of these tick species (Figure S1; [22,53,58,59]).

Pathogen Screening

We extracted DNA and prepared double-indexed libraries for 136 ticks following [60]. Tick sample size was calculated to detect a 10% variation in pathogen prevalence across treatments while sampling across multiple species, treatments, and levels. Ticks with insufficient read data were excluded. Libraries were captured in pools of eight individuals (12.5ng each library per capture; 100ng total library per pool) using the Ectobaits protocol [60]. Double-indexed libraries were then amplified post capture with Illumina adapters by 18 cycles of PCR. Adapter multimers were removed prior to sequencing using QIAEX II Gel Extraction Kits (Qiagen). Captured products were sequenced on a MiSeq (Illumina, USA) using paired-end 150 bp reads. MiSeq library sequences underwent quality control as described in [60], except that minimum average base quality score was 25. We differentiated between *Coxiella burnetii* and *Coxiella*-like endosymbionts, as these groups are genetically similar, but endosymbionts are non-pathogenic and often have high infection rates [61]. We reanalyzed five libraries (KenT11b-KenT15b) included in [60]. For a subset of ticks (n=20), we confirmed *Rickettsia, Coxiella, Ehrlichia*, and *Anaplasma* infection and tick species using PCR assays following [60]. Positive PCR products were sequenced with an ABI 3130xl (Thermo Fisher Scientific, USA).

Statistical Analyses

We analyzed the tick drag data with generalized linear mixed models (GLMM), using counts of adult ticks per plot as our response variable [62]. Fixed effects included treatment (Total exclosure and Control for all months; all treatments for a subset of months), mean annual precipitation, and the treatment × rainfall interaction; random effects included replicate plot identity (3 plots within each of 3 rainfall levels; n=9) and time period (month; n = 12 for Total exclosure vs. Control, n=5 for all treatments). We ran two separate sets of GLMMs, one for Total exclosure and Control plots across all months, and another for all plots for the subset of five months. Candidate-model sets included all possible combinations of the two main effects and their interaction (the "full model"), along with a null model; all models included the random effects (Table 1, Table S4). We analyzed the combined total of all tick species and each species separately. As data were overdispersed and zero-inflated for individual tick species, we used

zero-inflated negative-binomial distributions with log link functions in our GLMMs. For the two datasets that combined the three tick species, we used negative-binomial distributions with log link functions. All models were constructed using the glmmADMB package in R [63,64].

All model combinations for each tick species and the combined total of ticks were ranked using the second-order Akaike's information criterion (AICc) [62] using the MuMIn package [65]. We investigated all models (reported in S5 and S6), and present the 95% confidence interval set with individual parameter estimates and Akaike weights (w_i) in Tables 1 and 2.

Coxiella burnetii and *Rickettsia* spp. were the only pathogens sufficiently prevalent to permit robust statistical analysis. We analyzed the likelihood of infection using binomial GLMMs with logit link functions, with infection status of each tick (infected/uninfected) as the response. Experimental treatment, tick species, rainfall, and treatment × rainfall were fixed effects and plot replicate was a random effect.

All analyses were performed in R version 3.3.0 [66]. Descriptive statistics are reported as mean number of ticks per ha ± 1 standard error.

Results

In total, we captured 5677 ticks across all plots, including 4180 via tick drags and 1497 via traps. Of these, >95% were adults of just three species: *R. pravus* (43%), *R. praetextatus* (36%), and *R. pulchellus* (17%). Adults were substantially more abundant than other life stages in both drag and trap collections, despite efforts to avoid under-sampling juvenile ticks. Fewer than 3% of the ticks captured were nymphs, and no larvae were collected. Tick traps did not capture additional tick species; therefore, we used only drag data for all subsequent analyses (S1, Table S4, and Figures S2 and S3) and focused all analyses on adults of the three dominant species.

Total abundance of the three dominant tick species

Total tick abundance varied seasonally over the 13-month sampling period and the scale and timing of fluctuations differed among tick species (Figure 1A). However, on average, total tick abundance doubled in Total exclosures (18.3±1.9) relative to Control plots (9.9±1.0) (Figure 1A, B, Table 1). Low-rainfall plots had 225% more ticks on average (17.8±2.3) than did mesic plots (7.9±1.0). Total tick abundance was best explained by the GLMM that included exclosure treatment, precipitation, and their interaction (Tables 1, S5) (w_i = 0.75). The interaction (z = -2.3, P=0.02; Table 1) reflected the increasing effect of wildlife exclusion on tick abundance as aridity increased (Figure 1C; Tables 1, S5). We found some support (w_i = 0.16) for a model with no interaction and a marginally-negative relationship between rainfall and tick abundance (z = -1.96, P=0.05). Net results were similar in the analysis that considered all four wildlife-exclusion treatments for a subset of months: total tick abundance increased from 170% (only megaherbivores excluded) to 360% (all large wildlife excluded) (Figure 1D). The full model was again the best fit (w_i = 0.99), with significant interactions between rainfall and the Total and Meso exclosure treatments (z = -3.61, P=0.001, Total; z = -3.38, P=0.001, Meso; Tables 2, S6).

Species-specific responses

Although *R. pravus* and *R. praetextatus,* two tick species that often parasitize smaller mammals, increased with large mammal loss, only *R. pravus* abundance showed clear evidence of an interaction between exclosure and aridity. For the full 13 months of data, the best model for *R. pravus* included treatment, rainfall, and their interaction (w_i = 0.99), whereas the best model for *R. praetextatus* included only treatment (w_i = 0.47) and a second model (w_i = 0.37) included the non-significant effect of rainfall (Table 1). Both tick species increased in Total exclosures relative to Controls (z = 8.40, P<0.001, *R. pravus*; z = 3.74, P<0.001, *R. praetextatus*), and this effect was stronger in drier sites for *R. pravus* only (z = -3.37, P<0.001). By contrast, rainfall had no detectable effect on tick abundance in Control plots (z = -1.02, P=0.31). For the subset of data collected in all four wildlife exclusion treatments, the full model was the best fit for both tick species (w_i = 0.93, w_i = 0.78, *R. pravus* and *R. praetextatus* respectively). Both tick species increased in all exclosure treatments relative to Controls, and both increased significantly in Total exclosures (z = 7.22, P<0.001; z = 4.07, P<0.001) (Table 2). This effect was more pronounced in drier sites for both species, although this was only significant for *R. praetextatus* in Meso exclosures (z = -2.26, P=0.02) and *R. pravus* in Total exclosures (z = -3.26, P<0.001) (Table 2,). A second model for *R. praetextatus* that included only treatment (w_i = 0.13) received considerably less support.

For *R. pulchellus*, which often parasitize larger-bodied mammals, the best model for all months included only exclosure treatment (w_i = 0.48), and a second model (w_i = 0.39) included the non-significant effect of rainfall; but here Total wildlife exclusion caused a 43% *decrease* in abundance relative to Controls (z = -1.95, P=0.05; Table 1, Figure 1B). For the subset of data including all four treatments, the best model (w_i = 0.46) again included only exclosure treatment, while a second model (w_i = 0.37) included the non-significant effect of rainfall. However, this secondary analysis revealed that partial wildlife exclusion caused increases in tick abundance relative to controls (z = 4.72, P<0.001, Meso; z = 2.44, P=0.02, Mega; Tables 2, S6, Figure 1D), but total exclusion had no significant effect (z = -0.57, P=0.57).

Pathogens

Prevalence of *C. burnetii* isolates was 43% (n=58 of 136 ticks screened), and prevalence of *Rickettsia spp.* was 5% (n=7 of 136 ticks; 4 of these were from the spotted fever group). We detected *Ehrlichia* in 1 adult tick and *Anaplasma* in 1 nymph (nymphs were not analyzed due to small sample size). We found a high prevalence of non-pathogenic *Coxiella*-like endosymbionts (57%; 46% of these were also present in ticks with confirmed *C. burnetii* isolates). Therefore, our analyses excluded ticks for which only a *Coxiella*-like endosymbiont was detected, but included ticks with both *C. burnetii* and *Coxiella*-like endosymbionts.

For the GLMM for *C. burnetii*, no combination of our predictors outperformed the null model (Table 3). For *Rickettsia* spp., the best model included tick species and rainfall; however, neither estimate was significant (although rainfall marginally increased infection probability; Table 3).

In sum, there were no pronounced effects of treatment, tick species, or rainfall on pathogen prevalence (Figure 2, Tables 3, S7, Figure S4).

Discussion

Our results support our hypothesis that defaunation and climate can interact to markedly affect the abundance of ticks and thus the risk of tick-borne disease exposure (although not necessarily the prevalence of these pathogens). Total exclusion of all large wildlife increased total tick abundance by 130% (mesic sites)-225% (arid sites), showing a significant interaction with aridity. Tick abundance increased from 170% (only mega-herbivores excluded) to 360% (all large wildlife excluded) during the five-month period in which all exclosure plots were surveyed. We found no significant variation in pathogen prevalence across plots or tick species, suggesting that the risk of tick-borne pathogen exposure reflects observed tick abundance patterns.

However, this overall pattern masks strong differences in the magnitude and direction of effects of wildlife exclusion across tick species and over time. Tick species-specific responses show some overlap with expectations based on tick host associations. Patterns in total tick abundance were driven by two dominant tick species, *R. pravus* and *R. praetextatus,* whose immature stages frequently feed upon small hosts, which also increase strongly following wildlife exclusion [22,50,51]. Although we do not expect changes in adult tick abundance to directly correlate with fluctuations in rodent abundance in these plots over time, a comparison of long-term rodent abundance and tick abundance within each plot produces positive correlations for *R. pravus* and *R. praetextatus* ($z = 6.59$, $P<0.001$ and $z = 3.17$, $P<0.01$, respectively; Table S8). In contrast, the third common tick species, *R. pulchellus*, whose adult stages primarily parasitize vertebrates larger than 15kg [58], and whose immature stages are not found on rodents [59], decreased with the total absence of large wildlife for the 13-month dataset. However, for the five months for which all four exclosure treatments were surveyed, abundance of this tick species in total exclosures was no different from that in controls, but we observed marked increases in abundance within partial wildlife exclosures (see Figure S1 for tick/host associations in exclosure plots).This discrepancy highlights temporal variation in exclosure effects: strong changes occur during months of peak tick abundance, which were not captured by the five-month dataset.

Other factors beyond the release of intermediate hosts may have also influenced the marked differences in adult tick abundance among experimental plots. Increases in small carnivores (potential hosts for all three tick species) in response to elevated rodent density in exclosure plots may increase total tick abundance [18]. Likewise, increases in understory vegetation cover following large wildlife loss may increase tick survivorship (via lowered risk of desiccation) [22]. The relative importance of these factors may vary among tick species depending on their life histories. The complex pathways by which wildlife loss may affect the abundance of different tick species likely explains why the few previous studies on the effects of large wildlife exclosure on tick abundance have produced mixed results [18,67].

Total tick abundance was greater in drier areas, although this pattern was largely driven by the most common tick species, *R. pravus*. *Rhipicephalus praetextatus* and *R. pulchellus* only increased modestly in these areas, and annual rainfall was not a major explanatory factor in models of their abundance. This is consistent with previous observations of climate preferences for these species, as *R. pravus* may particularly favor areas with extended dry seasons [61]. Notably, tick community composition varied considerably over seasons, and the most significant responses to exclosures occurred at months of peak abundance (Figure 1A). These months of peak abundance drove overall patterns for each species, and are likely to be a result of strong differences in tick phenology and responsiveness to rainfall.

Rhipicephalus pravus also drove an interaction between wildlife-exclosure treatment and aridity on tick abundance, despite variation among tick species. This interaction and its variation are consistent with prior studies of the effects of defaunation on consumer communities, including a recent meta-analysis that found these effects are often context-dependent and mediated by site productivity [39,50,68]. In this region, rodent-borne pathogens have shown a similar response: anthropogenic disturbance tends to cause stronger increases in rodent-borne disease in drier climates with lower productivity [69]. However, consistent with our findings here, responses are variable across specific hosts and pathogens [69].

Both pathogens analyzed in this study are globally important. *C. burnetii,* the causative agent of Q Fever, is considered to be an emerging zoonotic disease [70], while rickettsial pathogens are responsible for a variety of spotted fevers—including African tick-bite fever (caused by *Rickettsia africae*) in our study location [42]. We observed no significant differences in prevalence of either *C. burnetii* or *Rickettsia* spp. due to wildlife exclosure treatment, rainfall, or tick species. Larger sample sizes and screening over many seasons might reveal finer-scale dynamics; however, on a coarse level, this result suggests that tick-borne disease risk is likely to be well-approximated by estimates of total tick abundance (Figure 2). *Coxiella burnetii* prevalence was surprisingly high. Although we excluded ticks for which only an endosymbiont was detected, 67% of the ticks infected with *C. burnetii* were also positive for the *Coxiella*-like endosymbiont. Endosymbionts may benefit some ticks [61], and recent work suggests that *C. burnetii* recently emerged from this group [71]. Thus, the genetic similarity between *C. burnetii* and *Coxiella*-like endosymbionts may have yielded some false positives given that the full *Coxiella* phylogeny is incomplete. However, we do not expect this to bias our results, given that the likelihood of false positives is consistent across all predictors.

Our study demonstrates the significant potential for size-selective defaunation to alter the risk of tick-borne disease. Substantial variation in tick abundance and species composition over time reflect the inherent complexity of a system that depends on host, environmental, and vector variables, but total effects suggest long-term patterns, especially when ticks peak in abundance. On average, when all large wildlife were excluded, the total number of ticks nearly doubled; and, when only Mega wildlife and Meso wildlife were excluded (perhaps a more realistic short-term defaunation scenario for much of the world), ticks of all three major species increased,

suggesting that large-wildlife loss can contribute to an increased tick-borne disease risk that may be mitigated by conservation in many contexts. Furthermore, the costs of wildlife loss on tick-borne disease in this region may be intensified in drier, less productive areas that are likely to worsen with a changing climate [48], demonstrating interacting effects of wildlife loss and climate change on tick-borne disease risk. On a more global scale, our study highlights the challenge of predicting the effects of either biodiversity loss or climate change in isolation of other stressors on vector ecologies and infectious disease dynamics.

Author contributions:

GCT conducted fieldwork, performed analyses, and wrote the first version of the manuscript; BFA and TH identified ticks and contributed to the final report; TA conducted fieldwork, tick identification, sample logistics, and data-entry; LH conducted all biomolecular lab work; RMP and TMP designed and provided access to experimental plots, contributed data, and assisted with data interpretation and writing the final report; LN assisted in obtaining Kenyan research permits and provided report feedback; MGC conducted bioinformatic analyses and provided report feedback; RF coordinated and supervised molecular work; JNM conducted fieldwork; HSY conceived the project and analyses, and assisted with data interpretation and writing the manuscript.

Competing interests:

We declare no competing interests.

Data availability:

Datasets and R code for all analyses are available at: https://github.com/gtitcomb/Wildlife-loss-climate-ticks.

Read data from this project are available in the BioProject Archive, accession PRJNA362357. Reanalyzed library accessions are: SRS1133052, SRS1133057, SRS1133060, SRS1133069, SRS1133099.

Funding statement:

Financial support for this project came from the National Science Foundation Graduate Research Fellowship, the National Geographic Society (Grants 8846-10, 9291-13), the National Science Foundation (DEB-1556786, DEB-1547679, DEB-1355122, DEB-09-09670, CNH-1313822), the National Sciences and Engineering Research Council of Canada, the University of Wyoming, the University of Florida, and the Princeton Environmental Institute's Grand Challenges Initiative.

Acknowledgements:

We thank the National Commission for Science, Technology, and Innovation of the Kenyan Government, Kenya Wildlife Service, National Museums Kenya, and Mpala Research Centre for their assistance.

REFERENCES

1. Smith, K. F., Goldberg, M., Rosenthal, S., Carlson, L., Chen, J., Chen, C. & Ramachandran, S. 2014 Global rise in human infectious disease outbreaks. *J. R. Soc. Interface* **11**, 20140950–20140950. (doi:10.1098/rsif.2014.0950)

2. Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L. & Daszak, P. 2008 Global trends in emerging infectious diseases. *Nature* **451**, 990–993. (doi:10.1038/nature06536)

3. Gottdenker, N. L., Streicker, D. G., Faust, C. L. & Carroll, C. R. 2014 Anthropogenic land use change and infectious diseases: a review of the evidence. *Ecohealth* **11**, 619–632.

4. Patz, J. A. et al. 2004 Unhealthy Landscapes: Policy Recommendations on Land Use Change and Infectious Disease Emergence on JSTOR. *Environ. Health Perspect.* **112**, 1092–1098.

5. Civitello, D. J. et al. 2015 Biodiversity inhibits parasites: Broad evidence for the dilution effect. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 8667–71. (doi:10.1073/pnas.1506279112)

6. Keesing, F. et al. 2010 Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**, 647–652.

7. Rohr, J. R., Dobson, A. P., Johnson, P. T. J., Kilpatrick, A. M., Paull, S. H., Raffel, T. R., Ruiz-Moreno, D. & Thomas, M. B. 2011 Frontiers in climate change-disease research. *Trends Ecol. Evol.* **26**, 270–277. (doi:10.1016/j.tree.2011.03.002)

8. Lafferty, K. D. 2009 The ecology of climate change and infectious diseases. *Ecology* **90**, 888–900.

9. Patz, J. A., Olson, S. H., Uejio, C. K. & Gibbs, H. K. 2008 Disease Emergence from Global Climate and Land Use Change. *Med. Clin. North Am.* **92**, 1473–1491. (doi:10.1016/j.mcna.2008.07.007)

10. Young, A. S., Groocock, C. M. & Kariuki, D. P. 1988 Integrated control of ticks and tick-borne diseases of cattle in Africa. *Parasitology* **96**, 403. (doi:10.1017/S0031182000058388)

11. de la Fuente, J., Estrada-Peña, A., Venzal, J. M., Kocan, K. M. & Sonenshine, D. E. 2008 Ticks as vectors of pathogens that cause disease in humans and animals. *Front. Biosci.* **13**, 6938–6946.

12. Jongejan, F. & Uilenberg, G. 2004 The global importance of ticks. *Parasitology* **129**, S3–S14. (doi:10.1017/S0031182004005967)

13. de Castro, J. J. 1997 Sustainable tick and tickborne disease control in livestock improvement in developing countries. *Vet. Parasitol.* **71**, 77–97. (doi:10.1016/S0304-4017(97)00033-2)

14. Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. & Collen, B. 2014 Defaunation in the Anthropocene. *Science (80-.).* **345**, 401–406. (doi:10.1126/science.1251817)

15. Young, H. S. et al. 2014 Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *Proc. Natl. Acad. Sci.* **111**, 7036–7041. (doi:10.1073/pnas.1404958111)

16. Estes, J. A. et al. 2011 Trophic Downgrading of Planet Earth. *Science (80-.).* **333**, 301–306. (doi:10.1126/science.1205106)

17. Levi, T., Kilpatrick, A. M., Mangel, M. & Wilmers, C. C. 2012 Deer, predators, and the emergence of Lyme disease. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 10942–7. (doi:10.1073/pnas.1204536109)

18. Keesing, F., Allan, B. F., Young, T. P. & Ostfeld, R. S. 2013 Effects of wildlife and cattle on tick abundance in central Kenya. *Ecol. Appl.* **23**, 1410–1418. (doi:10.1890/12-1607.1)

19. Wilson, M. L., Adler, G. H. & Spielman, A. 1985 Correlation between Abundance of Deer and That of the Deer Tick, Ixodes dammini (Acari: Ixodidae). *Ann. Entomol. Soc. Am.* **78**, 172–176. (doi:10.1093/aesa/78.2.172)

20. Civitello, D. J., Flory, S. L. & Clay, K. 2008 Exotic grass invasion reduces survival of *Amblyomma americanum* and *Dermacentor variabilis* ticks (Acari: Ixodidae). *J. Med. Entomol.* **45**, 867–872. (doi:10.1093/jmedent/45.5.867)

21. Randolph, S. E. 2000 Ticks and tick-borne disease systems in space and from space. *Adv. Parasitol.* **47**, 217–43.

22. Goheen, J. R., Palmer, T. M., Charles, G. K., Helgen, K. M., Kinyua, S. N., Maclean, J. E., Turner, B. L., Young, H. S. & Pringle, R. M. 2013 Piecewise Disassembly of a Large-Herbivore Community across a Rainfall Gradient: The UHURU Experiment. *PLoS One* **8**, e55192. (doi:10.1371/journal.pone.0055192)

23. Pringle, R. M., Kimuyu, D. M., Sensenig, R. L., Palmer, T. M., Riginos, C., Veblen, K. E. & Young, T. P. 2015 Synergistic effects of fire and elephants on arboreal animals in an African savanna. *J. Anim. Ecol.* **84**, 1637–45. (doi:10.1111/1365-2656.12404)

24. Dirzo, R. et al. 2015 KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Ecology* **11**, 205–215. (doi:10.1038/38271)

25. Mills, J. N. 2006 Biodiversity loss and emerging infectious disease: An example from the rodent-borne hemorrhagic fevers. *Biodiversity* **7**, 9–17. (doi:10.1080/14888386.2006.9712789)

26. Estrada-Peña, A., Ostfeld, R. S., Peterson, A. T., Poulin, R. & de la Fuente, J. 2014 Effects of environmental change on zoonotic disease risk: an ecological primer. *Trends Parasitol.* **30**, 205–214. (doi:10.1016/j.pt.2014.02.003)

27. Xu, L., Schmid, B. V., Liu, J., Si, X., Stenseth, N. C. & Zhang, Z. 2015 The trophic responses of two different rodent–vector–plague systems to climate change. *Proc. R. Soc. London B Biol. Sci.* **282**, 20141846. (doi:10.1098/rspb.2014.1846)

28. Wilcox, B. a & Gubler, D. J. 2005 Disease ecology and the global emergence of zoonotic pathogens. *Environ. Health Prev. Med.* **10**, 263–272. (doi:10.1007/BF02897701)

29. Eisen, L. 2008 Climate change and tick-borne diseases: A research field in need of long-term empirical field studies. *Int. J. Med. Microbiol.* **298**, 12–18. (doi:10.1016/j.ijmm.2007.10.004)

30. Randolph 1993 Climate, satellite imagery and the seasonal abundance of the tick Rhipicephalus appendiculatus in southern Africa: a new perspective. *Med. Vet. Entomol.* **7**, 243–258.

31. Cumming, G. S. 2002 Comparing climate and vegetation as limiting factors for species ranges of African ticks. *Ecology* **83**, 255–268. (doi:10.1890/0012-9658(2002)083[0255:CCAVAL]2.0.CO;2)

32. Olwoch, J. M., Van Jaarsveld, A. S., Scholtz, C. H. & Horak, I. . 2007 Climate change and the genus *Rhipicephalus* (Acari : Ixodidae) in Africa. *Onderstepoort J. Vet. Res.* **74**, 45–72. (doi:10.4102/ojvr.v74i1.139)

33. IPCC 2014 *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.

34. Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J. & Keesing, F. 2006 Climate, deer, rodents, and acorns as determinants of variation in Lyme-Disease risk. *PLOS Biol* **4**, e145. (doi:10.1371/journal.pbio.0040145)

35. Gilbert, L. 2009 Altitudinal patterns of tick and host abundance: a potential role for climate change in regulating tick-borne diseases? *Oecologia* **162**, 217–225. (doi:10.1007/s00442-009-1430-x)

36. Gallivan, G., Spickett, A., Heyne, H., Spickett, A. & Horak, I. 2011 The dynamics of questing ticks collected for 164 consecutive months off the vegetation of two landscape zones in the Kruger National Park (1988-2002). Part III. The less commonly collected species. *Onderstepoort J. Vet. Res.* **78**, 27–35.

37. Oorebeek, M. & Kleindorfer, S. 2008 Climate or host availability: What determines the seasonal abundance of ticks? *Parasitol. Res.* **103**, 871–875. (doi:10.1007/s00436-008-1071-8)

38. Pringle, R. M., Young, T. P., Rubenstein, D. I. & McCauley, D. J. 2007 Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 193–7. (doi:10.1073/pnas.0609840104)

39. Daskin, J. H. & Pringle, R. M. 2016 Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis. *J. Anim. Ecol.* **85**, 857–68. (doi:10.1111/1365-2656.12522)

40. Cumming, G. S. 2000 Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). *J. Biogeogr.* **27**, 425–440. (doi:10.1046/j.1365-2699.2000.00419.x)

41. Minjauw, B. & McLeod, A. 2003 Tick-borne diseases and poverty: the impact of ticks and tick-borne diseases on the livelihoods of small-scale and marginal livestock owners in India and eastern and southern Africa.

42. Parola, P. et al. 2013 Update on tick-borne rickettsioses around the world: a geographic approach. *Clin. Microbiol. Rev.* **26**, 657–702. (doi:10.1128/CMR.00032-13)

43. DePuy, W. et al. 2014 Q fever risk across a dynamic, heterogeneous landscape in Laikipia County, Kenya. *Ecohealth* **11**, 429–33. (doi:10.1007/s10393-014-0924-0)

44. Crump, J. A. et al. 2013 Etiology of severe non-malaria febrile illness in Northern Tanzania: a prospective cohort study. *PLoS Negl. Trop. Dis.* **7**, e2324. (doi:10.1371/journal.pntd.0002324)

45. Young, T. P., Okello, B. D., Kinyua, D. & Palmer, T. M. 1997 KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African J. Range Forage Sci.* **14**, 94–102. (doi:10.1080/10220119.1997.9647929)

46. Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E. & Hutton, J. M. 2010 Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228. (doi:10.1016/j.biocon.2010.06.007)

47. Ogutu, J. O., Piepho, H.-P., Said, M. Y., Ojwang, G. O., Njino, L. W., Kifugo, S. C. & Wargute, P. W. 2016 Extreme Wildlife Declines and Concurrent Increase in Livestock Numbers in Kenya: What Are the Causes? *PLoS One* **11**, e0163249. (doi:10.1371/journal.pone.0163249)

48. Camberlin, P. & Philippon, N. 2002 The East African March–May Rainy Season: Associated Atmospheric Dynamics and Predictability over the 1968–97 Period. *J. Clim.* **15**, 1002–1019. (doi:10.1175/1520-0442(2002)015<1002:TEAMMR>2.0.CO;2)

49. Williams, A. P. & Funk, C. 2011 A westward extension of the warm pool leads to a westward extension of the Walker circulation, drying eastern Africa. *Clim. Dyn.* **37**, 2417–2435.

50. Young, H. S. et al. 2015 Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. *Ecol. Appl.* **25**, 348–360. (doi:10.1890/14-0995.1)

51. Long, R. A., Wambua, A., Goheen, J. R., Palmer, T. M. & Pringle, R. M. 2017 Climatic variation modulates the indirect effects of large herbivores on small-mammal habitat use. *J. Anim. Ecol.* (doi:10.1111/1365-2656.12669)

52. Pringle, R. 2012 How to be manipulative. *Am. Sci.* **100**, 30–37.

53. Kartzinel, T. R., Goheen, J. R., Charles, G. K., DeFranco, E., Maclean, J. E., Otieno, T. O., Palmer, T. M. & Pringle, R. M. 2014 Plant and small-mammal responses to large-herbivore exclusion in an African savanna: five years of the UHURU experiment. *Ecology* **95**, 787–787. (doi:10.1890/13-1023R.1)

54. Schmocker, J., Liniger, H. P., Ngeru, J. N., Brugnara, Y., Auchmann, R. & Brönnimann, S. 2016 Trends in mean and extreme precipitation in the Mount Kenya region from observations and reanalyses. *Int. J. Climatol.* **36**, 1500–1514. (doi:10.1002/joc.4438)

55. Ostfeld, R. S. & Keesing, F. 2000 Biodiversity series: The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Can. J. Zool.* **78**, 2061–2078. (doi:10.1139/z00-172)

56. LoGiudice, K., Ostfeld, R. S., Schmidt, K. A. & Keesing, F. 2003 The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. *Proc. Natl. Acad. Sci.* **100**, 567–571. (doi:10.1073/pnas.0233733100)

57. Ginsberg, H. S. & Ewing, C. P. 1989 Comparison of flagging, walking, trapping, and collecting from hosts as sampling methods for northern deer ticks,Ixodes dammini, and lone-star ticks,Amblyomma americanum (Acari: Ixodidae). *Exp. Appl. Acarol.* **7**, 313–322. (doi:10.1007/BF01197925)

58. Walker, J. B., Keirans, J. E. & Horak, I. G. 2000 *The Genus Rhipicephalus (Acari, Ixodidae): A Guide to the Brown Ticks of the World*. Cambridge, UK: Cambridge University Press.

59. Guerra, A. S. et al. 2016 Host-Parasite Associations in Small Mammal Communities in Semiarid Savanna Ecosystems of East Africa. *J. Med. Entomol.* (doi:10.1093/jme/tjw048)

60. Campana, M. G. et al. 2016 Simultaneous identification of host, ectoparasite and pathogen DNA via in-solution capture. *Mol. Ecol. Resour.* **16**, 1224–39. (doi:10.1111/1755-0998.12524)

61. Zhong, J. 2012 Coxiella-like Endosymbionts. In *Coxiella burnetii: Recent Advances and New Perspectives in Research of the Q Fever Bacterium* (eds R. Toman R. A. Heinzen J. E. Samuel & J.-L. Mege), pp. 365–379. Springer Netherlands. (doi:10.1007/978-94-007-4315-1_18)

62. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. 2009 *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer.

63. Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A. & Sibert, J. 2012 AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* **27**, 233–249. (doi:10.1080/10556788.2011.597854)

64. Skaug, H., Bolker, B., Magnusson, A. & Nielsen, A. 2016 *Generalized Linear Mixed Models using 'AD Model Builder'. R Package Version 0.8. 3.3.*

65. Barton, K. 2013 MuMIn: Multi-model inference. R package version 1.15. 6. *R Proj. Stat. Comput. Vienna, Austria*

66. R Core Team 2016 R: A language and environment for statistical computing.

67. Perkins, S. E., Cattadori, I. M., Tagliapietra, V., Rizzoli, A. P. & Hudson, P. J. 2006 Localized deer absence leads to tick amplification. *Ecology* **87**, 1981–1986. (doi:10.1890/0012-9658(2006)87[1981:LDALTT]2.0.CO;2)

68. Augustine, D. J. & McNaughton, S. J. 2007 Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* **9**, 1242–1256. (doi:10.1007/s10021-005-0020-y)

69. Young, H. S. et al. 2017 Interacting effects of land use and climate on rodent-borne pathogens in central Kenya. *Philos. Trans. R. Soc. London B Biol. Sci.* **372**.

569 70. Njeru, J., Henning, K., Pletz, M. W., Heller, R. & Neubauer, H. 2016 Q fever is an old and
570 neglected zoonotic disease in Kenya: a systematic review. *BMC Public Health* **16**, 297.
571 (doi:10.1186/s12889-016-2929-9)

572 71. Duron, O. et al. 2015 The Recent Evolution of a Maternally-Inherited Endosymbiont of
573 Ticks Led to the Emergence of the Q Fever Pathogen, Coxiella burnetii. *PLOS Pathog.* **11**,
574 e1004892. (doi:10.1371/journal.ppat.1004892)

575

Figure 1: (A) Tick abundance varied over time, across rainfall levels, among species, and between treatments for the full 13-month dataset. (B) While total tick abundance increased in Total exclosures, the magnitude and direction of this effect varied by tick species for the 13-month dataset. (C) For all tick species summed together, exclusion interacted with annual rainfall, with stronger effects of exclusion in drier environments. (D) When all exclosures were surveyed for the 5-month subset of data, tick species responded differently to varied wildlife loss levels. Asterisks indicate significant ($P<0.05$) differences from Control plots (green); dots indicate non-significant trends ($P<0.1$).

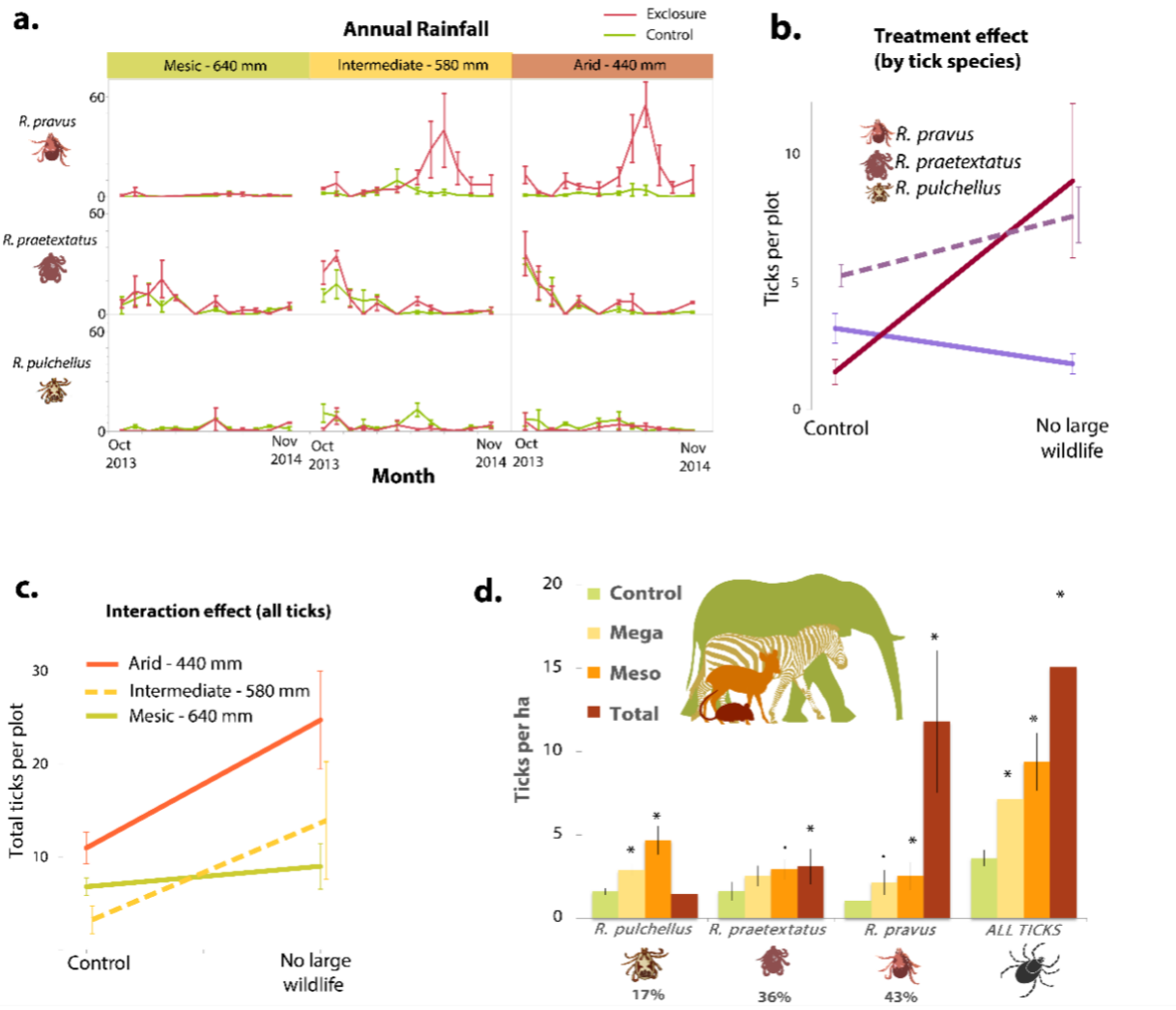
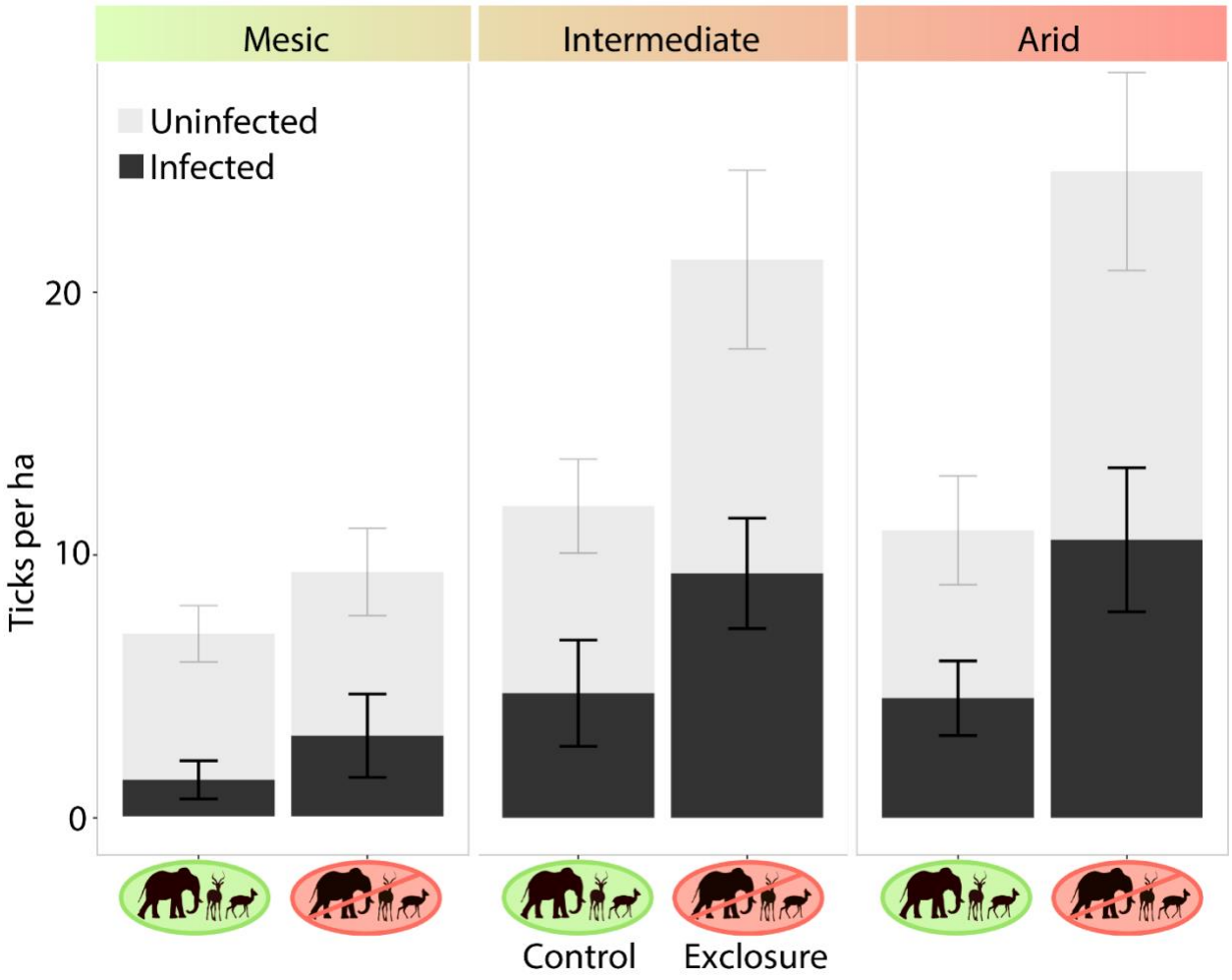


Figure 2: The estimated number of infected and uninfected ticks increased in plots where large wildlife had been removed (Exclosure), and this was further increased in arid sites, regardless of tick-borne pathogen infection.



Model	Intercept		Exclosure		Rainfall		Exclosure × Rainfall	
All Ticks $w_i = 0.75$	2.117 ± 0.200	10.61 <0.001	**0.587 ± 0.130**	4.53 <0.001	-0.092 ± 0.142	-0.65 0.52	**-0.295 ± 0.128**	-2.30 0.02
R. pravus $w_i = 0.99$	-0.173 ± 0.388	-0.44 0.66	**1.452 ± 0.173**	8.40 <0.001	-0.304 ± 0.297	-1.02 0.31	**-0.596 ± 0.177**	-3.37 <0.001
R. praetextatus $w_i = 0.47$	1.157 ± 0.441	2.63 0.009	**0.431 ± 0.115**	3.74 <0.001				
R. pulchellus $w_i = 0.47$	0.896 ± 0.312	2.87 0.004	**-0.441 ± 0.227**	-1.95 0.05				

Legend:

Estimate ± SE	z-score
	P-value

Table 1: Effects of exclosure treatment, rainfall, and their interaction for all months (Control and Total exclosure plots only) from four GLMMs. Control plots are designated as the reference, and rainfall (mm) is scaled by standard error (84 mm) and centered at the mean (533 mm) for ease of interpretation. Significant relationships (P<0.05) are bolded. Positive relationships are shaded in blue; negative relationships are shaded yellow. All estimates are shown with standard errors, *z*-score (upper right), and P-value (lower right). Full model sets and parameters are shown in Table S5.

Model	Intercept		Exclosure		Rainfall		Exclosure × Rainfall	
All Ticks w_i = 0.99	1.424 ± 0.232	6.14 <0.001	TOTAL **1.161 ± 0.168**	6.92 <0.001	0.219 ± 0.162	1.35 0.176	TOTAL **-0.62 ± 0.2**	-3.61 <0.001
			MESO **0.698 ± 0.170**	4.11 <0.001			MESO **-0.585 ± 0.173**	-3.38 <0.001
			MEGA **0.511 ± 0.170**	3.01 0.003			MEGA -0.150 ± 0.173	-0.87 0.39
R. pravus w_i = 0.93	-0.511 ± 0.520	-0.98 0.33	TOTAL **1.904 ± 0.264**	7.22 <0.001	-0.228 ± 0.365	-0.62 0.53	TOTAL **-0.874 ± 0.268**	-3.26 0.001
			MESO **0.627 ± 0.282**	2.23 0.03			MESO -0.428 ± 0.288	-1.49 0.14
			MEGA 0.537 ± 0.283	1.89 0.06			MEGA -0.267 ± 0.295	-0.91 0.37
R. praetextatus w_i = 0.78	0.159 ± 0.516	0.31 0.76	TOTAL **1.050 ± 0.258**	4.07 <0.001	0.499 ± 0.268	1.86 0.062	TOTAL -0.350 ± 0.278	-1.26 0.208
			MESO 0.448 ± 0.263	1.70 0.09			MESO **-0.628 ± 0.278**	-2.26 0.024
			MEGA 0.292 ± 0.266	1.10 0.27			MEGA -0.030 ± 0.286	-0.10 0.92
R. pulchellus w_i = 0.46	0.463 ± 0.200	2.32 0.021	TOTAL -0.155 ± 0.273	-0.57 0.57				
			MESO **1.184 ± 0.251**	4.72 <0.001				
			MEGA **0.630 ± 0.258**	2.44 0.015				

Legend:

Estimate ± SE	z-score
	P-value

Table 2: Effects of all exclosure treatments on tick abundance (for a subset of months) from four GLMMs. Exclosure compares Control plots (all wildlife allowed), the reference, to plots that selectively exclude mega herbivores (MEGA), mega and meso herbivores (MESO), and all herbivores greater than 5kg (TOTAL). Rainfall (mm) is scaled by standard error (84 mm) and centered at the mean (533 mm) for ease of interpretation. Significant relationships (P<0.05) are bolded, marginally significant relationships (P<0.1) are bordered by a broken line, positive relationships are shaded blue, and negative relationships are yellow. All estimates are shown with standard errors, z-score (upper right), and P-value (lower right). Full model sets and parameters are shown in Table S6.

	Intercept		Species		Exclosure	Rain		Exclosure x Rain
C. burnetii								
Model 1								
w_i = 0.26	-0.42 ± 0.2	-2.38 0.02						
Rickettsia sp.								
Model 1			RHPU	-0.02				
w_i = 0.35	-2.44 ± 0.7	-3.48 <0.001	-14.8 ± 799	0.99		1.16 ± 0.6	1.87 0.06	
			RHPV	-1.53				
			-1.25 ± 0.8	0.13				
Model 2								
w_i = 0.18	-3.37 ± 0.6	-5.74 <0.001				1.09 ± 0.6	1.87 0.06	
Δ AIC$_c$ = 1.36								

Table 3: Results of GLMMs for *Coxiella burnetii* and *Rickettsia* sp. 'Species' compares the probability of tick infection with each pathogen for each tick species (*R. pravus* – RHPV, and *R. pulchellus* – RHPU, as compared to *R. praetextatus* – RHPR). Marginally significant relationships (P<0.1) are bordered by a broken line. All estimates are shown with standard errors, *z*-score (upper right), and P-value (lower right).