

Effects of wildlife and cattle on tick abundance in central Kenya

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Abstract. In African savannas, large mammals, both wild and domestic, support an abundant and diverse population of tick ectoparasites. Because of the density of ticks and the many pathogens that they vector, cattle in East Africa are often treated with acaricides. While acaricides are known to be effective at reducing tick burdens on cattle, their effects on the overall abundance and community composition of ticks in savanna ecosystems are less well understood. It is also not known how well tick populations can be maintained in the absence of large mammals. We evaluated the effects of wildlife and of acaricide-treated cattle on host-seeking tick populations in a long-term, exclusion experiment in central Kenya. Over seven years, we sampled larval, nymphal, and adult ticks monthly on replicated treatment plots that controlled for the presence of cattle and for the presence of two guilds of large wild mammals: megaherbivores (giraffes and elephants) and all other large wild herbivores (>15 kg). Two species of ticks were found in this habitat; across all surveys, 93% were *Rhipicephalus pulchellus* and 7% were *R. praetextatus*. The presence of acaricide-treated cattle dramatically reduced the abundance of host-seeking nymphal and adult ticks but did not affect the abundance of host-seeking larval ticks. The abundance of larval ticks was determined by the presence of large wild mammals, which appear to import gravid female ticks into the experimental plots. On plots with no large mammals, either wild or domestic, larval and nymphal ticks were rare. Adult *R. pulchellus* were most abundant in plots that allowed wildlife but excluded cattle. Adult *R. praetextatus* were relatively abundant in plots without any large mammals. These differences suggest that these ticks utilize different members of the host community. The reduction in ticks that results from the presence of acaricide-treated cattle has potential health benefits for humans and wildlife, but these benefits must be weighed against potential costs, including reduced availability of food for birds such as oxpeckers that feed on ticks.

Key words: amitraz; cattle; Kenya; Kenya Long-Term Exclusion Experiment, KLEE; parasite; parasitism; *Rhipicephalus praetextatus*; *Rhipicephalus pulchellus*; tick; ungulate; vector; wildlife.

INTRODUCTION

Savannas cover over 50% of Africa and harbor a diversity and abundance of wildlife (Scholes and Archer 1997). However, savannas are also important habitats supporting humans and their livestock, and conflicts between humans and wildlife are common (Thirgood et al. 2005). One principle source of conflict is competition for food between livestock, particularly cattle, and large mammalian herbivores (Prins 2000, Young et al. 2005, Odadi et al. 2007, 2011b, Riginos et al. 2012). Large grazing mammals and cattle also share predators, parasites, and pathogens (Woodroffe et al. 2005a, Odadi et al. 2011a). For example, lions (*Panthera leo*) can inflict heavy mortality on cattle when cattle are not well protected (Frank et al. 2005). In addition, cattle can be exposed to pathogens when they are bitten by disease

vectors that have acquired infections from wildlife (Thirgood et al. 2005, Tonetti et al. 2009).

The most common method for reducing conflicts like these is to reduce contact between cattle and wildlife (Woodroffe et al. 2005b). However, the potential exists for positive interactions in shared habitats, at least under some circumstances. For example, wild predators might focus less on cattle when they have abundant wild prey. Grazing by wildlife can actually improve forage quality for cattle (Odadi et al. 2011b). And despite the fact that wildlife and cattle share parasites (Odadi et al. 2011a), host species can serve as ecological traps for parasites (Keesing et al. 2009), thereby reducing total parasite abundance in the community.

In central Kenya, wildlife and cattle share habitat with an abundant community of tick ectoparasites (Young et al. 1988, Wesonga et al. 2006). These ticks can inflict heavy costs directly through parasitism (Norval 1990), and also indirectly, by serving as the vectors of numerous pathogens (Bock et al. 2004, Parola et al. 2005, Fyumagwa et al. 2011). For decades, the management of ticks and tick-borne diseases has been

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identified as a priority for the economic development of East Africa (Young et al. 1988, Perry and Young 1995), where rangelands with high livestock production potential also provide crucial habitat for threatened wildlife populations (Sundaresan and Riginos 2010).

We conducted a long-term, experimental investigation of the effects of cattle and wildlife on tick abundance and community composition in central Kenya. To accomplish this, we utilized the Kenya Long-Term Exclusion Experiment (KLEE), which employs a combination of electrified fences and controlled herding to create different combinations of wildlife and cattle inside large, replicated savanna plots. Cattle in this habitat are treated with an acaricide, amitraz, which kills ticks as they begin feeding. Over seven years, we conducted monthly monitoring to determine how cattle and wildlife interact to influence the abundance and species composition of questing ticks. We hypothesized that ticks would be less abundant on two categories of plots: those to which cattle had access, and those to which large wild mammals did not.

METHODS

Study site

We conducted fieldwork from 1999 to 2006 at the Mpala Research Centre (MRC) in the Laikipia District of central Kenya (0°17' N, 36°53' E). The study site is characterized by *Acacia* savanna woodland on “black cotton” vertisol soils. The greatest rainfall at the site falls in April–May, with secondary peaks in June–July and October–November. Mean annual precipitation at the study site is 550–600 mm.

Acacia drepanolobium is the dominant tree species at the study site, accounting for 98% of the overstory vegetation (Young et al. 1998). The woody species *A. mellifera*, *Balanites aegyptiaca*, *Cadaba farinosa*, *Lycium europaeum*, and *Rhus natalensis* are also present. The dominant grasses are *Brachiaria lachmantha*, *Lintonia nutans*, *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra*. Common forbs include *Aerva lanata*, *Commelina* spp., *Dyschoriste radicans*, and *Rhinacanthus ndorensis* (Young et al. 1998). Common large mammalian herbivores at the site include African elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Grevy's zebras (*Equus grevyi*), Burchell's zebras (*E. burchelli*), Grant's gazelles (*Gazella granti*), steinbucks (*Raphicerus campestris*), and domestic cattle (*Bos taurus*; Young et al. 1998). Small-mammal populations were monitored continuously at the study site during the time of the study (Keesing 1998, McCauley et al. 2006); common species include *Saccostomus mearnsi*, *Mus* spp., *Mastomys natalensis*, *Dendromus melanotis*, and *Crocidura* spp. (Keesing 1998).

This research was conducted within the Kenya Long-term Exclusion Experiment (KLEE). KLEE was established in 1995 to examine interactions between native ungulates and livestock (Young et al. 1998). The experimental design takes into account the separate

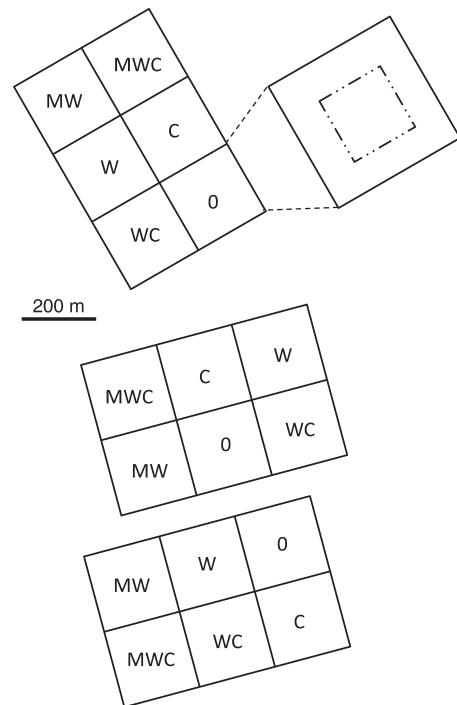


FIG. 1. The Kenya Long-Term Exclusion Experiment (KLEE) layout. Letters represent the guild of herbivore allowed: C, cattle; W, wildlife >15 kg but smaller than megaherbivores; M, megaherbivores (elephants and giraffes); and 0, no large herbivores allowed. The exploded inset shows the 400-m transect around the inner hectares surveyed for ticks (dashed-dotted line) in each plot.

and combined effects of megaherbivores (giraffes and elephants), other large wildlife (e.g., buffaloes, zebras, and antelopes), and cattle because these groups have been thought to compete for forage in African savannas (details of the design and rationale for KLEE are described in Young et al. 1998).

KLEE is composed of three 400 × 600 m (24 ha) blocks, each consisting of six 200 × 200 m (4 ha) treatments. Each treatment allows a particular combination of large mammals (Fig. 1). These six treatment types comprise three levels of large wildlife (>15 kg; hereafter “wildlife”) presence (no wildlife, all wildlife except megaherbivores, all wildlife including megaherbivores) crossed with two levels of cattle (presence vs. absence). Wildlife was excluded via 2.4 m high game fencing with 11 strands of wire electrified at 5000 volts. Megaherbivores were excluded with a live wire 2 m off the ground and two ground wires; along the live wire, there are single wires 50 cm long hanging down every 50 cm. This fencing prevents access by these largest mammals, while still allowing access to smaller mammals like buffaloes and zebras. Cattle in this habitat are continually accompanied by herders. They are allowed in experimental plots designated for cattle grazing only during designated periods, and they are not allowed to graze in plots designated only for wildlife.

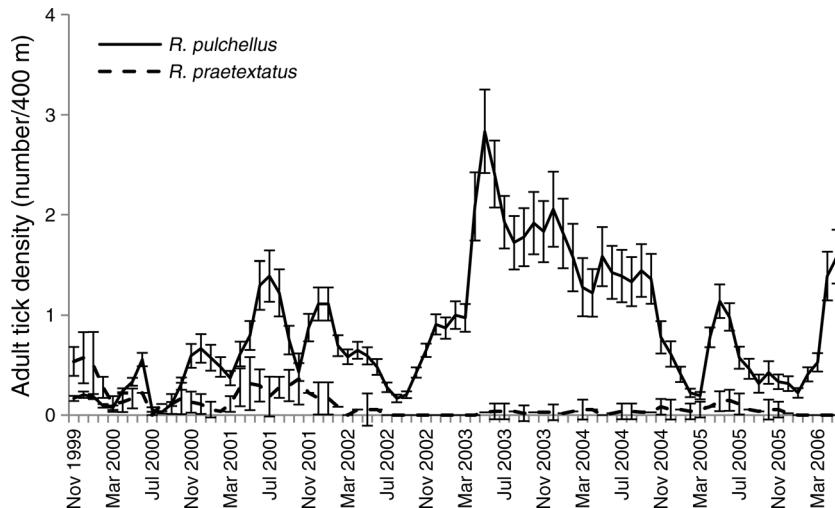


FIG. 2. Three-month moving average density (mean \pm SE) of two species of adult ticks, *Rhipicephalus pulchellus* and *R. praetextatus*, per 400 m, averaged over all six herbivore treatments: with and without cattle, and with and without three levels of large wild mammals.

In plots where cattle are allowed, *Bos taurus* cattle are herded into each plot on a regular basis. From 1995 to 1998, \sim 120 cattle were herded into each cattle treatment area for two hours 4–8 times per year, which approximates a moderate cattle stocking intensity (Young et al. 2005). Before 1999, mixed herds of cows, calves, and heifers were used, but since 1999, the herds have been heifers only.

The management of cattle in this region often involves regular treatment with acaricide, and the most commonly used acaricide is the formamidine “amitraz.” Through a combination of mechanisms of action, amitraz causes death in all life stages of ticks (Peter et al. 2006). Cattle were treated approximately weekly with amitraz at the Mpala Ranch, a frequency comparable to that of surrounding ranches (B. F. Allan, *unpublished data*).

While the KLEE design controls cattle presence and grazing intensity, wildlife and megaherbivores are allowed to move freely on plots to which they have access. One possible result is that wildlife and megaherbivores avoid plots on which cattle graze. Young et al. (2005) found that zebras spent significantly more time on plots from which cattle were excluded, but that no other large-mammal species showed a significant response to cattle presence.

Surveys of herbaceous cover in the study plots are carried out every six months. At its most dense following the rains, grass cover can range from 55% in the plots with wildlife and cattle to 85% in plots without any large mammals (Young et al. 2005). Forb cover ranges from 8% to 15% (Young et al. 2005). In cattle-only treatments, cattle reduced grass cover by 33% (Young et al. 2005). In wildlife-only treatments, native grazers reduced grass cover by 21% (Young et al. 2005). But cattle and wildlife interact through their consumption of

forage. In plots that allow both wildlife and cattle, grass cover was reduced by only 20%, suggesting that wildlife graze less in plots to which cattle have access. Cattle do not significantly reduce forb cover, but megaherbivores reduce forb cover by 33% (Young et al. 2005).

Tick sampling

We determined the abundance and species identity of questing ticks every month from October 1999 to June 2006. In nine of these 81 months, heavy rainfall left roads impassable so that tick surveys could not be conducted. During collection periods, two observers walked in single file for the 400 m perimeter of the inner hectare of each of the three replicates of the six treatments (see Fig. 1). Every 50 m along this square 400 m long transect, both observers stopped and removed any ticks attached to their clothing. Because of dense herbaceous vegetation at the study site, this method resulted in a greater number of ticks compared to standard drag-sampling techniques and thus was considered a more accurate sampling approach for estimating abundance (F. Keesing, *unpublished data*). The life stage (i.e., larva, nymph, or adult) and, in the case of adults, species identity of ticks were recorded and representative ticks were preserved in 70% ethanol.

Statistical analysis

For each life stage and for each plot, we determined the total number of ticks collected during each sampling month. Because there was considerable monthly variability but no long-term trend in abundance (Fig. 2), we took the mean of treatment totals across the 72 sampling months to obtain a study-wide mean for each treatment type in each block. When necessary, we transformed data to achieve normality. We used two-way analysis of variance (ANOVA) to assess effects of treatment with

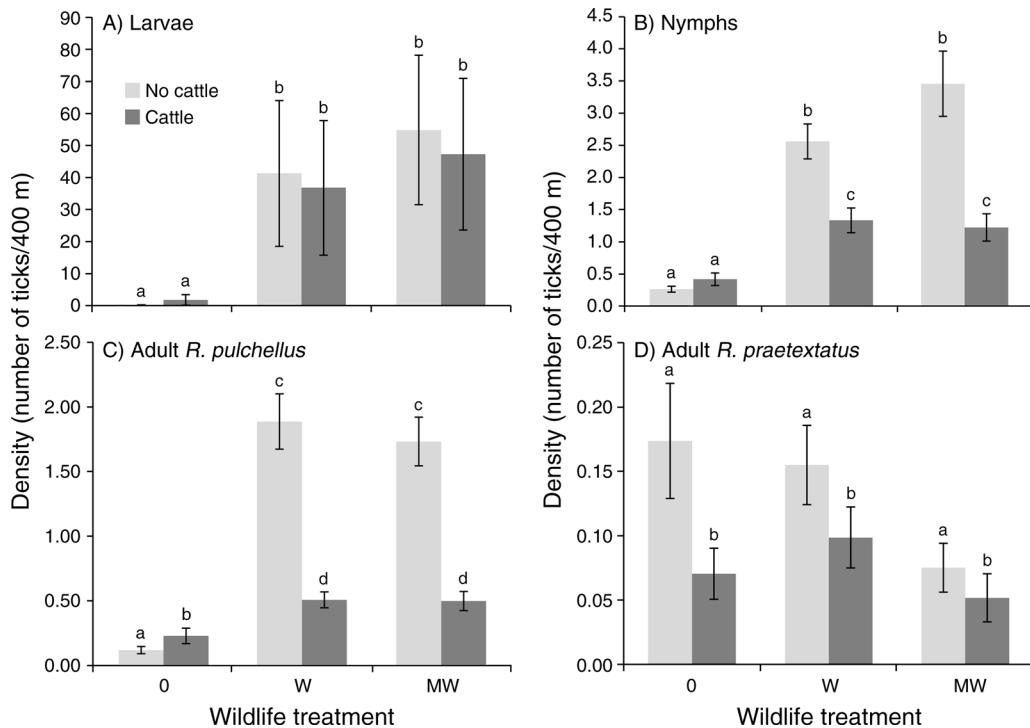


FIG. 3. Density of ticks per 400 m (mean \pm SE) over the 81-month study period (1999–2006) with three levels of wildlife, and with or without the presence of cattle: (A) larval, (B) nymphal, and (C) adult *Rhipicephalus pulchellus*; and (D) adult *R. praetextatus*. Wildlife treatments are: 0, no large wild mammals; W, wild mammals (>15 kg) other than megaherbivores (giraffes and elephants); and M, megaherbivores. Lowercase letters indicate differences that are statistically significant ($P < 0.05$).

two factors: wildlife (with three levels: 0, wildlife, or wildlife + megaherbivores) and cattle (with two levels: presence or absence). For post hoc pairwise comparisons, we used the Holm-Sidak method. All statistical analyses were conducted using SigmaStat version 11.0 (SYSTAT 2007).

RESULTS

We collected 41 952 ticks over the 81-month period, with sampling that covered 540 km of transect. Two species of ticks were abundant, *Rhipicephalus praetextatus* and *R. pulchellus*. *Rhipicephalus pulchellus* was the most common, representing 93% of adult ticks captured; *R. praetextatus* comprised the remaining 7%. Larvae and nymphs were not identified to species because of difficulties in identification; both larval and nymphal abundances were analyzed in aggregate. Given the numerical dominance of adult *R. pulchellus*, it is likely that the large majority of larval and nymphal ticks belong to this species.

The abundance of ticks was highly variable over the study period (Fig. 2). The overall abundance of adult *R. pulchellus* ticks reached a high of 3 individuals/400 m in May 2003, while *R. praetextatus* were most abundant in December 1999. We conducted subsequent analyses on the overall mean across all sampling periods.

Averaged across all sampling sessions, larvae were significantly more abundant when large wild mammals

(“wildlife”) were present, with an average of 18 larvae/400 m (Fig. 3A). The presence of megaherbivores did not have a significant effect on larval abundance, nor did the presence of cattle (Table 1). There were no larvae in plots that had no large mammals, either wild or domestic (Fig. 3A).

Nymphal ticks were less abundant than larvae due to attrition between life stages (Ostfeld 2011). Nymphs had a long-term average of 1.6 nymphs/400 m across all treatments. Nymphs were only abundant in plots that allowed large wild mammals, but that did not allow cattle (Fig. 3B). There were significantly more nymphs on plots with large wild mammals than on those without. There was no significant difference in the abundance of nymphs whether or not megaherbivores were present (Table 1, Fig. 3B). Overall, plots with cattle had significantly fewer nymphs than plots without cattle (Table 1, Fig. 3B). Because this effect of cattle was only evident on plots with large mammals, there was a statistically significant interaction between wildlife and cattle (Table 1).

Adult *R. pulchellus*, the most common tick species, were only abundant in plots that allowed large wild mammals, but that prevented access by cattle (Fig. 3C). Across all sampling sessions, there were 1.8 adult ticks/400 m on plots that allowed large wild mammals, while there were, on average, 10 \times fewer (0.16 adults/100 m) on plots that excluded them. On plots with large wild

TABLE 1. Analysis of variance for the effects of the presence of wildlife and cattle on the abundance of questing larval, nymphal, and adult ticks (genus *Rhipicephalus*) in the Kenya Long-Term Exclusion Experiment.

Tick stage/species and source of variation	df	SS	MS	F	P
Larvae					
Wildlife	2	8314.580	4157.29	13.06	<0.001
Cattle	1	51.318	51.318	0.16	0.70
Wildlife × cattle	2	63.972	31.986	0.10	0.905
Residual	12	3820.898	318.408		
Total	17	12 250.768	720.633		
Nymphs					
Wildlife	2	2.948	1.474	31.86	<0.001
Cattle	1	0.566	0.566	12.23	0.004
Wildlife × cattle	2	0.561	0.281	6.07	0.015
Residual	12	0.555	0.0463		
Total	17	4.630	0.272		
<i>R. pulchellus</i> adults					
Wildlife	2	12.832	6.416	68.05	<0.001
Cattle	1	1.705	1.705	18.08	0.001
Wildlife × cattle	2	3.797	1.898	20.13	<0.001
Residual	12	1.131	0.0943		
Total	17	19.465	1.145		
<i>R. praetextatus</i> adults					
Wildlife	2	0.0160	0.00799	2.77	0.102
Cattle	1	0.0177	0.0177	6.13	0.029
Wildlife × cattle	2	0.00431	0.00215	0.75	0.494
Residual	12	0.0346	0.00288		
Total	17	0.0725	0.00427		

mammals, cattle presence reduced tick abundance threefold compared to corresponding plots without cattle, a difference that was highly significant (Table 1, Fig. 3C). The presence of megaherbivores did not significantly increase tick abundance compared to wildlife treatments from which megaherbivores were absent (Table 1, Fig. 3C). On plots with no large wild mammals, tick abundance was low overall. However, the presence of cattle doubled the abundance of *R. pulchellus* adults on these wildlife exclusion plots (Table 1, Fig. 3C). Because cattle increased tick abundance on plots without large wild mammals but decreased tick abundance on plots with large mammals, there was a significant interaction between wildlife and cattle.

For adult *R. praetextatus*, the presence of cattle reduced tick abundance by approximately half overall (Table 1, Fig. 3D). However, the presence of large wild mammals did not have a significant effect on tick abundance. Indeed, the highest average tick abundance

for adult *R. praetextatus* was on plots with neither cattle nor large wild mammals (Fig. 3D).

In treatments with no large wild mammals, only 40% of adult ticks collected were *R. pulchellus*, a significantly lower percentage than in other treatments (Table 2, Fig. 4). When large wild mammals were present, for example, 94% of host-seeking ticks were *R. pulchellus*. The presence of cattle did not significantly affect the relative abundance of host-seeking adult ticks (Table 2, Fig. 4). In plots with large wild mammals, the relative abundance of *R. pulchellus* was lower when cattle were present; on plots without large wild mammals, *R. pulchellus* was more common when cattle were present (Fig. 4). This switch was reflected in a statistically significant interaction between cattle and wildlife (Table 2).

These differences in sampled tick abundance were not driven by differences in grass cover. Based on the May 2001 vegetation survey (Young et al. 2005: Fig. 2), the complete enclosure plots had the highest vegetation

TABLE 2. Analysis of variance for the effects of the presence of wildlife and cattle on the species composition of questing adult ticks.

Source of variation	df	SS	MS	F	P
Wildlife	2	0.44	0.22	30.3	<0.001
Cattle	1	0.03	0.03	3.6	0.082
Wildlife × cattle	2	0.18	0.09	12.8	0.001
Residual	12	0.09	0.01		
Total	17	0.73	0.04		

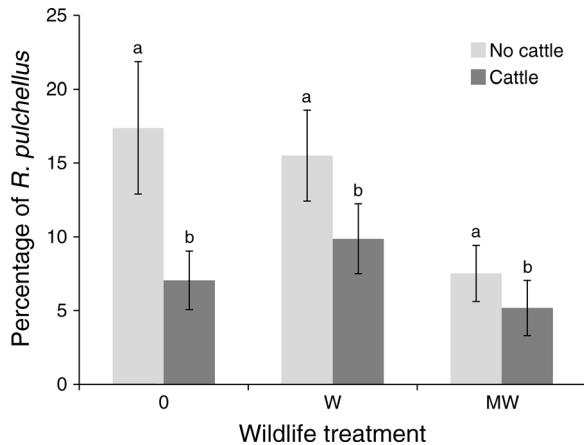


FIG. 4. Percentage (mean \pm SE) of the tick community consisting of adult *Rhipicephalus pulchellus* ticks, with three levels of wildlife, and with or without the presence of cattle. The tick community is composed of two species, *R. pulchellus* and *R. praetextatus*. Wildlife treatments are: 0, no large wild mammals; W, large wild mammals other than megaheirbivores (giraffes and elephants); and M, megaheirbivores. Lowercase letters indicate differences that are statistically significant ($P < 0.05$).

cover, but the lowest overall tick abundance. The cattle-only and cattle-with-wildlife plots had similarly low vegetation cover, but dramatically different tick abundances (Fig.3).

DISCUSSION

We sampled the abundance of questing ticks at each host-seeking stage: larva, nymph, and adult. In any area, the abundance of host-seeking ticks at each stage

consists of the sum of (1) the in situ pool of ticks from the prior stage that molted successfully, plus (2) those prior-stage ticks that were imported via host movements from surrounding areas; minus the sum of (3) the ticks that failed to find a host and died, (4) the ticks that found a host and died on the host, and (5) the ticks that found a host and survived (Fig. 5). This last category (surviving ticks) then produces the in situ pool for the next stage. Our study design crosses the exclusion of three different groups of hosts: cattle, medium-to-large wildlife, and megaheirbivores, without excluding smaller wildlife such as small ungulates and carnivores and rodents. This design allows us to interpret the abundance of host-seeking ticks at each life stage in each treatment.

In an ecosystem representative of integrated cattle and wildlife management in central Kenya, we demonstrate for the first time that cattle dramatically reduced the abundance of host-seeking nymphal and adult ticks, but did not affect the abundance of host-seeking larval ticks. The abundance of larval ticks was determined by the presence of large wild mammals, which appear to import gravid female ticks into the study plots. On plots with no large mammals, larval and nymphal ticks were rare. Adult *R. pulchellus* were most abundant in plots that allowed wildlife but excluded cattle. In contrast, adult *R. praetextatus* were relatively abundant in plots without any large mammals. These differences suggest that these species of ticks utilize different members of the host community.

The design of the KLEE experimental plots allows cattle presence to be carefully controlled, but wildlife are free to respond numerically and functionally on the

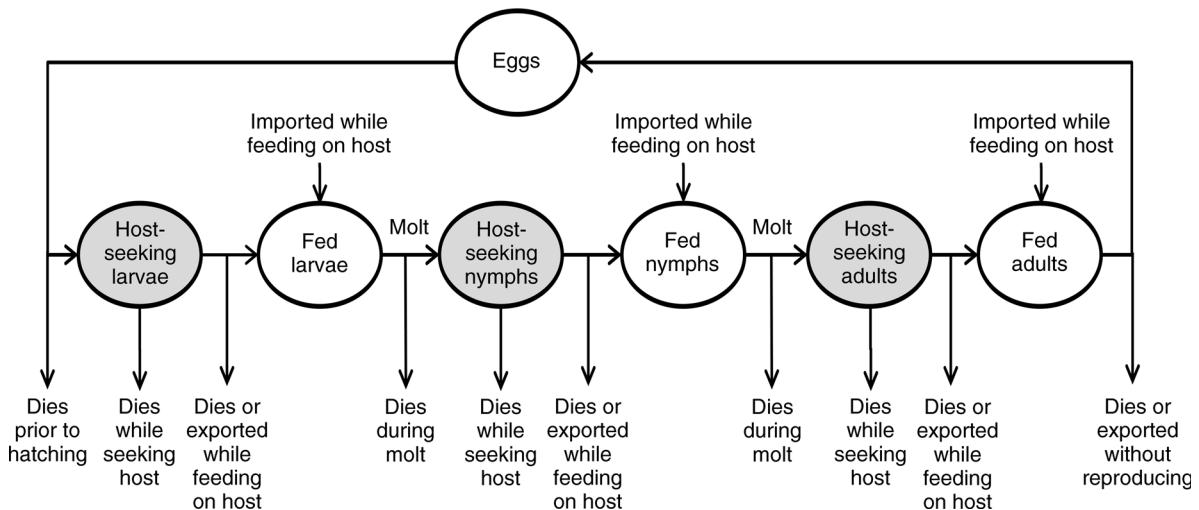


FIG. 5. Life cycle of ixodid ticks. At each host-seeking stage (larva, nymph, and adult), ticks seek a host on which to take a blood meal. If they fail to find a host, they will die. If they find a host, they might feed successfully or die during the attempted meal. If they successfully feed, they molt into the next stage in the case of larvae and nymphs, or reproduce, lay eggs, and die in the case of adults. In this study, we sampled host-seeking ticks at all three post-egg life stages (gray shading). Ticks that we captured at each stage could have been ticks that successfully found and fed on a host in situ during the prior stage meal, or ticks that were imported from surrounding areas while feeding on a host during the prior life stage.

treatments to which they have access. One possible consequence is that wildlife might avoid areas on which cattle graze. If so, the observed effects of cattle on ticks might have been due to differences in wildlife visitation to these plots, and thus, reduced tick abundance may be only indirectly due to the presence of cattle. Research on the KLEE plots has shown that zebras spend 15% less time on plots to which cattle have access compared to plots accessed by all wildlife (MWC vs. WC treatments in Fig. 1; Young et al. 2005). However, the presence of cattle does not significantly affect the abundances of any other species of wildlife (Young et al. 2005). The relatively modest behavioral response by zebras seems unlikely to account for the dramatic differences in tick abundances we observed on plots with and without cattle.

Instead, cattle appear to have reduced nymphal and adult tick abundance primarily directly as a result of the widespread use of a specialized acaricide (amitraz), which is applied to cattle that are grazed commercially in this region (Mwongela 2001, Mugambi et al. 2012), including all cattle that visited the study plots. Ticks on treated animals are killed during their attempt to feed, rather than being repelled prior to feeding. As a result, treated livestock remove ticks from the landscapes in which they graze. Treated cattle thus function as ecological traps for ticks (Robertson and Hutto 2006, Keesing et al. 2009). Reduced abundances of nymphs and adults on plots with cattle result from the combined effects of these acaricide-treated hosts on prior-stage and current-stage ticks. To reduce adult ticks, for example, cattle kill host-seeking adults plus the prior generation of nymphs. Because larvae were not significantly reduced in the presence of cattle, we interpret the reduced nymphal abundance as being caused by direct mortality of nymphs that encounter cattle. Declines in nymphal abundance could also have occurred if host-seeking larvae found cattle hosts and died due to acaricide. In contrast to cattle-produced reductions of nymphs and adults, the abundance of larval ticks was determined by the presence of large wild mammals, which appear to import gravid female ticks into the plots. On plots with no large wild mammals, with or without cattle, larval and nymphal ticks were rare.

In plots without large mammals, adult *R. praetextatus* achieve relatively high densities (Fig. 2D). One explanation could be that ticks are imported into these plots from surrounding areas while feeding on hosts that can penetrate the enclosure fencing. Hosts that have access to these "enclosure" plots include steinbucks (*Raphicerus campestris*), a small antelope that is twice as abundant inside these plots as it is outside them (Young et al. 2005), mesocarnivores, and small mammals such as rodents. Like steinbucks, rodents are twice as abundant when larger mammals are experimentally excluded (Keesing 1998). Neither steinbucks nor rodents have been detected traveling between exclusion plots and surrounding habitats, which would be necessary for

them to import ticks, but such movements are plausible. For these animals to import ticks into the central sampling area, they would need to travel as little as 50 m, which is within reasonable movement distances for small mammals (Keesing 1998). If these animals import nymphal ticks while the ticks are feeding to repletion, the fed nymphs could then molt into the adult stage within the exclusion plots and begin questing as adults after molting. The plausibility of this hypothesis is supported by the fact that (1) larvae and questing nymphs are rare to absent in these plots, suggesting that the adults did not mature from larvae in situ; (2) *R. praetextatus* are known to feed on small- and medium-sized mammals that occur in the study area, including steinbucks, common genets (*Genetta genetta*), Natal multimammate mice (*Mastomys natalensis*), unstriped grass rats (*Arvicanthis* spp.), and white-tailed mongooses (*Ichneumia albicauda*) (Walker et al. 2000); and (3) immature life stages of *R. praetextatus* feed primarily on small mammals, including rodents, while adults are more frequently found feeding on large mammals, including cattle (Walker et al. 2000).

In contrast, for *R. pulchellus*, adult ticks were relatively rare when all large mammals were excluded, but they were more abundant if only cattle were permitted, although still far fewer than in wildlife plots (Fig. 3C). This increase could result from the importation of *R. pulchellus* by cattle due to an incomplete success rate of the weekly treatment with amitraz (e.g., incomplete topical coverage of an animal) or the acquisition of amitraz resistance within a segment of the tick population. While amitraz is considered widely effective against ticks, there are recent reports of resistance occurring in the cattle tick (*Rhipicephalus microplus*), though this compound may offer some efficacy even in resistant populations (Foil et al. 2004). However, there is scant information concerning the extent of amitraz resistance in Africa (Jonsson and Hope 2007).

Overall, the reduction in ticks that results from the presence of cattle has several potential health benefits to wildlife, to livestock, and to humans. First, reducing tick abundance should have strong positive effects on wildlife condition. Large tick burdens and their associated pathogens can pose a substantial cost to the health of large mammals (Norval 1990, Nijhof et al. 2003, Fyomagwa et al. 2007). In addition, both *R. pulchellus* and *R. praetextatus* are vectors of infectious agents for wildlife, livestock, and humans. Pathogens transmitted by *R. praetextatus* include Nairobi sheep disease virus and *Rickettsia conorii*, while *R. pulchellus* is capable of transmitting these pathogens, as well as *Babesia equi*, Crimean-Congo hemorrhagic fever virus, and *Theileria parva* (Walker et al. 2000). Reducing tick abundance decreases transmission of tick-borne pathogens between ticks and their hosts, resulting in a potentially large benefit to human and animal health.

Because of their effects on ticks, acaricide-treated cattle may offer benefits for wildlife conservation. These benefits, however, must be weighed against potential costs. Negative effects could arise from the acaricide treatment itself, or from the effects of the cattle. A previous generation of acaricides based on arsenic compounds led to reports that exposed ticks could be lethal to birds that feed on ticks, such as oxpeckers (Bezuidenhout and Stutterheim 1980). These compounds are no longer widely used. Modern acaricides could affect tick-feeding birds negatively as well, though less directly. For example, oxpeckers consume ticks while the ticks are feeding on their mammalian hosts. If treating cattle reduces the abundance of ticks on wildlife, as the results of this study suggest, oxpeckers might decline in abundance as the number of ticks feeding on large mammals declines.

Cattle themselves could have negative effects on wildlife by competing for forage. Recent evidence suggests that wildlife and cattle compete for forage during the dry season, but that cattle are facilitated by the presence of wildlife during the wet season (Odadi et al. 2011b). Whether wildlife benefit similarly from the presence of cattle during the wet season is more difficult to determine. Certainly the abundance of both cattle and wildlife at the study site suggests that both groups can coexist at sustainable densities. Future research should address the ratio of wildlife to cattle that achieves optimal outcomes for both.

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