INTRODUCTION

Since the introduction of acaricides a century ago, their widespread use has enhanced cattle production throughout the world by controlling tick infestations on domestic livestock. Early arsenical and organochlorine acaricides improved overall cattle health but were toxic to oxpeckers (Buphagus spp.), birds endemic to sub-Saharan Africa which eat ticks on domestic and wild ungulates (Stutterheim, 1982; Stutterheim & Brooke, 1981). Following the introduction of these acaricides, oxpecker populations declined significantly, though this trend was reversed as target-specific acaricides increased in use (Grobler, 1979; Stutterheim, 1982; Stutterheim & Brooke, 1981). The current generation of widely-used acaricide formulations (e.g. amitraz) is non-toxic to vertebrates, but concerns remain about their environmental and non-target effects (De Castro, 1997; De Meneghi, Stachurski, & Adakal, 2016). These concerns are especially pressing in regions such as sub-Saharan Africa, where the control of tick-borne disease in cattle continues to rely heavily on frequent application of acaricides and where oxpecker populations are still recovering (De Meneghi et al., 2016).

Recent studies suggest that acaricide-treated cattle can reduce the overall abundance of ticks in the environment (Allan et al., 2017; Keesing, Allan, Young, & Ostfeld, 2013; Keesing, Ostfeld, Young, & Allan, 2017). As acaricide treatment of cattle and other livestock has become widespread, tick populations may be reduced compared to historical levels. Whether depression of tick populations via acaricide use on cattle has indirect negative consequences for oxpecker populations through reduced availability of an important food source remains unknown. The link between oxpeckers and ticks was first established through behavioural observations and gut content analyses (Moreau, 1933). The extent to which oxpeckers rely on ticks for food has been challenged by observational and experimental studies reporting a preference in oxpeckers for wound- and blood-feeding (Plantan, Howitt, Kotzé, & Gaines, 2013; Weeks, 1999). Understanding the influence of tick abundance on oxpecker abundance is essential to determine whether oxpeckers can persist in areas with active tick control.

Here, we examine the relationship between oxpecker and tick abundance by combining an observational study of two oxpecker species (Buphagus africanus and Buphagus erythrorhynchus) on a common wildlife host, reticulated giraffe (Giraffa camelopardalis reticulata), with surveys of tick abundance in the environment and measures of wildlife and livestock abundance.

METHODS

2.1 Study sites

Oxpecker and tick surveys were conducted 2–18 December 2015, on six privately-owned wildlife conservancies and cattle ranches in Laikipia County, Kenya (0.397°N, 37.1588°E, 1,700–2,550 m elevation), and one property in neighbouring Meru County, ranging in size from 10,000 to 37,000 ha (Figure 1). This region supports an abundance of wildlife and is characterized by Acacia-dominated bushland and savannah with a semiarid climate (mean annual precipitation: 400–750 mm). These seven sites were selected because wildlife is abundant at all sites, but abundance of acaricide-treated cattle,
and therefore abundance of ticks in the environment, varies greatly (Keesing et al., in press). Across all sites, cattle are treated approximately weekly with acaricides, and cattle densities vary by a factor of three, ranging from 0.0576 to 0.1768/ha (mean = 0.1178/ha).

2.2 | Field observations & surveys

2.2.1 | Giraffe observations

We chose reticulated giraffes (Giraffa camelopardalis reticulata) as the focal host species as they are easily detected from a distance, occurred on all properties, were consistently observed to attract oxpeckers, and gathered in herds that were manageably observed (Grobler, 1980; Stutterheim, 1981). At each site, we discovered three giraffe herds (minimum herd size: two individuals) and observed them for oxpecker abundance and activity. Once we detected a giraffe herd, we approached within 30–50 m to observe using binoculars. We observed for a minimum of five minutes, and until no new individual oxpeckers were detected, during which time we recorded herd size, number of giraffe adults and juveniles, oxpecker abundance and oxpecker activity. Herd size included all giraffes within sight. While two oxpecker species co-occurred in this study (B. africanaus and B. erythrorhynchus), we could not consistently distinguish the two species.

2.2.2 | Tick surveys

Following the giraffe observational period, we performed drag sampling within 30–50 m of the giraffe herd to estimate abundance of host-seeking ticks. Drag sampling involves dragging a 1 m² white sheet across the ground for two 100 m transects, stopping every 20 m to count and remove attached ticks. This method helps to account for tick aggregation in the environment (Sonenshine, Atwood, & Lamb, 1966). We preserved all collected ticks in 70% ethanol for later identification according to Walker, Keirans, and Horak (2000). We identified adult ticks to species and nymphs and larvae to genus. In total, we observed 21 giraffe herds and sampled 4,200 m² for tick density.

2.2.3 | Wildlife & livestock surveys

To estimate herbivorous mammal abundance for each property as part of a previous study (Keesing et al., in press), we established 100 m transects in a spatially-stratified random design in which we selected transect locations randomly in a 5 × 5 km grid overlaid on each property. As property size was variable, the number of transects ranged from three to six per property. In July-August 2015, we counted dung piles within 1 m along each transect and recorded with species identifications where possible and as unknown when not. Dung of domestic cattle and Cape buffalo (Syncerus caffer) were not distinguishable and were indicated as “bovid dung.” “Livestock” in this study included cattle, camels, donkeys, sheep and goats. We estimated wildlife or livestock populations by summing all dung counts for each species or group per transect then averaging these sums for each property. We calculated the ratio of wildlife to livestock per property by dividing the mean wildlife dung per property by the mean livestock dung per property.

2.3 | Statistical analysis

We performed univariate analyses to illustrate overall patterns in oxpecker abundance, giraffe herd size and tick density. We used one-way ANOVAs to test for the presence of among-site differences in oxpecker abundance, giraffe herd size and tick density. To estimate the relationship between oxpecker abundance and tick density, we used generalized linear models with density of oxpeckers per giraffe herd as the response variable and tick density (nymphs and adults only), mean livestock dung, mean wildlife dung and the ratio of wildlife to livestock as predictor variables. We performed model selection using backward selection and Akaike information criterion (AIC). We assessed collinearity using a variance inflation factor cut-off value of 5. Counts of oxpeckers and ticks were aggregated at the site level, as we expected no direct relationship between the number of oxpeckers on a herd and the number of ticks found questing in vegetation at the drag-sampling transect associated with each herd. Tick counts included only nymphs and adults, as these stages have been suggested as the life stages preferred by oxpeckers (Mooring & Mundy, 1996). All statistical analyses were performed in R 3.2.3.

3 | RESULTS

An average of 2.76 ± 2.70 (mean ± SD) oxpeckers was observed associated with each giraffe herd, with a range of 0–9 individual birds per
herd. Giraffe herd size ranged from 2 to 24 individuals, with a mean of 9.48 ± 6.84. Across all sites, there was a mean of 0.513 ± 0.862 oxpeckers/giraffe for both oxpecker species combined. Overall tick abundance per drag sampling event for all life stages varied across the sampling locations, from 0 to 352 per 200 m². Tick abundance varied by approximately an order of magnitude between each life stage, with larval ticks most abundant and adult ticks least abundant (Table 1).

One-way ANOVAs revealed no statistically significant among-site differences in oxpecker abundance ($p = 0.315$), giraffe herd size ($p = 0.0685$), overall tick density ($p = 0.318$), or adult ($p = 0.334$), nymphal ($p = 0.828$) or larval ($p = 0.297$) tick densities. Furthermore, oxpecker abundance was not significantly correlated with giraffe herd size ($p = 0.091$).

The best-fitting model to describe the density of oxpeckers on giraffes included mean livestock dung and the ratio of wildlife to livestock dung as significant predictors and tick abundance as a marginally non-significant predictor (Table 2). Livestock dung and the ratio of wildlife to livestock were both positively associated with oxpecker density, while tick abundance was negatively associated with oxpecker density. Livestock dung, the ratio of wildlife to livestock, and tick density were all within the variance inflation factor cut-off value of 5.

**4 | DISCUSSION**

We conducted a short-term study to assess the relationship between tick density, livestock abundance, wildlife abundance and oxpecker density on a common wildlife host. Results suggest that oxpecker abundance in this region may be driven more by availability of hosts than by tick abundance. Oxpecker density on giraffes across all sites was significantly positively correlated with mean livestock dung and the ratio of wildlife to livestock but was not significantly correlated with tick abundance.

Oxpeckers have historically been considered mutualists of wild ungulates due to their removal of ectoparasites (Nunn, Ezenwa, Arnold, & Koenig, 2011). However, recent research suggests that oxpeckers may act opportunistically as parasites on their hosts, re-opening wounds and directly feeding on host blood, particularly in the absence of attached ticks (Plantan et al., 2013; Weeks, 1999, 2000). Resistance behaviour of wild ungulates towards oxpeckers (Bishop & Bishop, 2014) suggests that oxpeckers may also be acting as parasites on their wildlife hosts. Thus, the mutualistic/parasitic dynamic of the oxpecker–host relationship may be context-dependent and driven by the availability of ticks. Removal of ticks from the environment could inhibit oxpecker populations in a region, or it could shift the oxpecker–ungulate relationship away from mutualism and towards parasitism (Bishop & Bishop, 2014; Weeks, 1999). Our results are consistent with the hypothesis that oxpeckers may act as opportunistic parasites on ungulates in the absence of ectoparasites (Plantan et al., 2013; Weeks, 1999, 2000). This study is the first to directly measure environmental tick density with oxpecker abundance.

We sampled oxpeckers and ticks in December 2015 following a period of high precipitation when overall tick abundance was low compared to previous surveys (Keesing et al., in press). Thus, these findings may reflect one end of the tick-oxpecker relationship, and the lack of a relationship here between tick abundance and oxpecker presence may be an underestimate. Future studies should sample across seasons to capture fluctuations in tick populations (see Plantan, 2009) and to compare with oxpecker surveys. We detected multiple adult tick species and immature tick genera (Table 1). Studies in southern Africa found that oxpeckers prefer certain tick species (Rhipicephalus decoloratus, Rhipicephalus appendiculatus, Hyalomma truncatum and Amblyomma hebraeum) (Bezuidenhout & Stutterheim, TABLE 1  Tick counts for each sampling location, separated by life stage and genus/species

<table>
<thead>
<tr>
<th>Site</th>
<th>Amblyomma spp.</th>
<th>Rhipicephalus spp.</th>
<th>Rhipicephalus praetextatus</th>
<th>Rhipicephalus pulchellus</th>
<th>Rhipicephalus sanguineus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nymphs</td>
<td>Larvae</td>
<td>Nymphs</td>
<td>Larvae</td>
<td>Adults</td>
</tr>
<tr>
<td>A</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>61</td>
<td>6</td>
</tr>
<tr>
<td>B</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>C</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
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<td>10</td>
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<tr>
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<td>18</td>
<td>382</td>
<td>5</td>
</tr>
<tr>
<td>F</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>44</td>
<td>0</td>
</tr>
<tr>
<td>G</td>
<td>1</td>
<td>0</td>
<td>7</td>
<td>13</td>
<td>0</td>
</tr>
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</table>

TABLE 2  Summary of best-fitting GLM

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Estimate</th>
<th>SE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>−2.323</td>
<td>0.757</td>
<td>0.0545</td>
</tr>
<tr>
<td>Ticks</td>
<td>−0.098</td>
<td>0.040</td>
<td>0.0897</td>
</tr>
<tr>
<td>Mean livestock dung</td>
<td>0.183</td>
<td>0.057</td>
<td>0.0491*</td>
</tr>
<tr>
<td>Wildlife: livestock</td>
<td>1.663</td>
<td>0.355</td>
<td>0.0184*</td>
</tr>
<tr>
<td>Adjusted $R^2$: 0.807</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F-statistic: 9.367 on 3 and 3 df, p-value: 0.049</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*p < 0.05.
This study suggests that acaricide use does not affect oxpecker populations consequences for ectoparasite-eating birds and their ungulate hosts. (2013).

Erin C. Welsh

ORCID assistance with map construction. This research was supported by Hedlund for assistance with tick identification, and Ginger Kowal for Kiai and Sharon Okanga for assistance with oxpecker surveys, Tyler properties on which this research was conducted. We thank Henry We are grateful for the support of the owners and managers of the ACKNOWLEDGEMENTS

While acaricide use benefits agricultural practices and prevents tick-borne disease outbreaks, it is important to consider potential consequences for ectoparasite-eating birds and their ungulate hosts. This study suggests that acaricide use does not affect oxpecker populations via a reduction in tick abundance. Rather, our findings suggest that oxpeckers can persist in regions with low tick abundance, and a higher ratio of wildlife to livestock abundance may lead to an increase in oxpecker population size. However, in regions with low tick density, oxpeckers may be opportunistically parasitizing their hosts directly, which could have negative implications for overall animal health. Future studies focusing on feeding behaviours of oxpeckers across a range of tick densities could illuminate complex relationships among oxpeckers, ectoparasites and ungulate hosts.

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ORCID

Erin C. Welsh http://orcid.org/0000-0002-9073-5849
Felicia Keesing http://orcid.org/0000-0002-8561-695X

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