Simulating detection of cattle-fever tick (Boophilus spp.) infestations in rotational grazing systems

M.S. Corson a,*, P.D. Teel b, W.E. Grant c

a USDA Agricultural Research Service, Pasture Systems and Watershed Management Research Unit, Building 3702, Curtin Road, University Park, PA 16802-3702, USA
b Department of Entomology, Texas A&M University, College Station, TX 77843-2475, USA
c Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA

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Abstract
To evaluate the relative influence of ecological and management factors on the probability of detecting cattle-fever tick (Boophilus microplus and Boophilus annulatus) infestations in rotational grazing systems, we adapted a simulation model of Teel et al. [J. Range Manage. 51 (1998) 501] that examines interactions among Boophilus ticks, cattle, and habitat type under rotational grazing systems developed for semi-arid shrublands of south Texas. We added a submodel that estimates probability of inspectors detecting Boophilus-tick infestations when examining 1, 20, 40, or 80 cows in a tick-infested herd of 80 cattle. Results indicate that probability of detecting infestations depends most on season of initial infestation; less heavily on rotational grazing strategy, habitat type, and number of cows inspected; and only moderately on initial number of infesting tick larvae. Results showed high detection probabilities (≥0.95) usually exist as temporal windows of opportunity during brief but definite periods; outside these windows, detection of existing infestations becomes poor. Each halving of the number of cows inspected tended to shorten duration of these windows by approximately 40%. Probability of detecting tick infestations, however, also depends strongly on inspector training, cow behavior, and weather, factors that we set as implicit constants. Models such as this one can indicate gaps in knowledge about the influence of biophysical and human factors on detection efforts in tick eradication or control programs, estimate magnitude and duration of Boophilus-tick infestations, and indicate potentially favorable inspection periods.

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1. Introduction
European colonists introduced the cattle-fever ticks Boophilus microplus and Boophilus annulatus, tropical and temperate species, respectively, to the Western Hemisphere (Nuñez et al., 1985). Subsequently, B. microplus spread through much of Latin and South America, Mexico, and the southernmost United States, while B. annulatus spread through northern Mexico and the southern USA (Graham and Hourrigan, 1977; Nuñez et al., 1985; Teel, 1985). These species overlap along the USA-Mexico border in the Tamaulipan ecological biome (Graham and Hourrigan, 1977). Boophilus ticks can transmit hemoparasites (Babesia spp.) that cause bovine babesiosis, a potentially fatal disease of cattle (Nuñez et al., 1985). In 1943, state
and federal programs eradicated these tick species in the USA; however, they currently maintain a permanent quarantine zone along an 800-km section of the Texas–Mexico border (Graham and Hourrigan, 1977). The US Department of Agriculture’s Animal and Plant Health Inspection Service (APHIS) manages this quarantine zone and the Texas Animal Health Commission monitors the interior, extirpating Boophilus-tick infestations discovered within and occasionally beyond the buffer zone (Graham and Hourrigan, 1977; APHIS, 2003). Development of acaricide resistance in Mexican Boophilus ticks, however, challenges the integrity of the US eradication program (George et al., 2001).

Using simulation modelling, researchers have examined the influence of ecological and management factors such as climate, grazing strategy, and acaricide use on Boophilus-tick populations in Texas and Mexico (Weidhaas et al., 1983; Mount et al., 1991; Teel et al., 1996; Corson et al., 2001). Until recently (Teel et al., 2003), however, none had simulated the influence of these factors on the probability of detecting the presence of Boophilus ticks. Detecting the appearance of Boophilus-tick populations in areas previously free of them represents a crucial concern for countries with a Boophilus-tick eradication program (e.g. USA, Argentina) or for countries that maintain tick-free regions (e.g. Australia, Uruguay) as a component of Boophilus-tick control programs.

Rotational grazing systems, developed to promote vegetation succession or to optimize cattle production, mediate distribution and intensity of tick infestations as well (Wharton et al., 1969; Schmidtmann, 1994). Approximately 30% of south Texas ranchers use short-duration rotational grazing (SDG) systems (Hanselka et al., 1991). A simulation model built by Teel et al. (1997) indicated that SDG systems with rest periods lasting more than 98 days on uncannopied grass pastures (or more than 147 days on mixed brush-canopied or mesquite (Prosopis glandulosa)-canopied pastures) significantly reduced reinfestations of cattle by Boophilus ticks. A later model (Teel et al., 1998), however, estimated that a Boophilus-tick population, if undetected, could survive up to 21 months in mesquite-canopied habitat subject to an SDG system with relatively long rest periods of 182–238 days. Similarly, simulation of rotational grazing in Boophilus-tick-infested pastures in Venezuela suggested that rotation of cattle among four to six pastures could suppress greatly, but not eradicate, Boophilus-tick populations (Hernández-Arrieta et al., 2000).

To examine the influence of human and biophysical factors on detection of tick infestations, Teel et al. (2003) developed a submodel to estimate daily probability of detecting existing Boophilus-tick infestations and applied it to a model of continuous (i.e. non-rotational) grazing. They found that season of initiation had the largest influence on detection probabilities, followed by habitat type and level of initial tick infestation. Sensitivity analysis of the human factor, a sigmoidal curve used to estimate ability of inspectors to detect ticks on individual cows, indicated that human detection abilities usually had a relatively minor influence on detection probabilities (Teel et al., 2003). Human detection ability, however, became more important when on-host tick populations reached low levels or when the model inspected few cattle. At these times, increased detection abilities yielded windows of detection that otherwise would not have existed. Having evaluated the detection submodel’s utility in a simpler system, we present in this paper inclusion of the detection submodel in a model of Boophilus-tick dynamics under short-duration rotational grazing. We wished to evaluate the relative influence of biophysical factors on tick-detection probabilities in a more spatially and temporally complex system.

2. Model description

We adapted the model of Teel et al. (1998), which includes submodels representing (1) Boophilus-tick survival and development on one cow (Bos taurus), (2) tick reproduction and development in pasture, and (3) movement of cattle among eight pastures with homogeneous vegetation in an SDG system, by adding a submodel that calculates probability of tick detection (PTD) (Fig. 1). Using a daily time-step, the model calculates tick development on one cow and female drop-rate from a herd of 80 cattle occupying an 800-ha area divided into eight 100-ha fenced pastures. Engorged female ticks lay eggs in the pasture in which they drop. Season of drop drives preoviposition duration (3–30 days), oviposition duration (19–45 days), and egg development (28–120 days), while
Fig. 1. Conceptual diagram of the simulation model. The lower right panel represent infested (shaded) and uninfested (unshaded) pastures resulting from rotation of infested cattle through an eight-pasture, intensive or extensive, short-duration grazing schedule. The upper left panel represent cattle-tick-landscape dynamics. Within each pasture, *Boophilus* larvae attach to cattle, complete development to adults, and ultimately drop as engorged female ticks in the same or a sequential pasture. Each day, the model calculates the probabilities of detecting ticks on each cow (as a function of the number of ticks per cow (graph)) and uses them to calculate the probability of detecting at least one tick in the cattle herd. During a run, all pastures contain the same vegetation type: uncanopied grass, mixed brush-canopied grass, or mesquite-canopied grass.

larval mortality rates change monthly (Teel et al., 1996). We used data from both *Boophilus* species to set daily egg production (66–153 eggs per ovipositing female) (Hitchcock, 1955; Davey et al., 1980; Davey, 1986). The model calculates number of larvae picked up each day as a constant encounter rate (i.e. proportion of questing larvae encountered per day) of 0.0003 multiplied by a constant attachment rate (i.e. proportion of encountered larvae that attach) of 0.5. The herd moves from pasture to pasture according to either of two contrasting SDG strategies designed specifically for rangelands of south Texas: (1) an extensive strategy, in which each pasture receives 26–34 days of grazing and 182–238 days of rest per cycle, and (2) an intensive strategy, in which each pasture receives 5–10 days of grazing and 35–70 days of rest per cycle (Teel et al., 1998).

The PTD submodel calculates the probability that cattle inspectors will detect at least one “detectable” tick (≥ 3mm diameter) on cows selected from the herd. First, it generates detectable ticks on each cow in the herd by randomly drawing one value per cow from a
normal distribution with a mean equal to the number of detectable ticks on the simulated “average” cow (Teel et al., 2003). We calculated a standard error for this distribution (0.396) using the number of ticks found on cows in the middle of herd hierarchies (Aguilar and Solis, 1984). A sigmoidal detection curve, set by expert opinion (P.D.T., co-author), estimates probability of detecting ticks on each cow during a visual and physical examination by two inspectors as a function of the number of detectable ticks each carries (Fig. 1) (Palmer et al., 1976; Teel et al., 2003). The PTD submodel calculates the probability of detecting ticks on the \(i\)th cow on the \(j\)th day as follows:

\[ P_i(\text{detection} | \text{number of ticks}) = P_i(n_{ij}), \]

where \(n_{ij}\) is number of ticks for the \(i\)th cow, \(j\)th day. The PTD submodel then calculates the probability of detecting at least one tick on at least one of the \(N\) cows examined on the \(j\)th day:

\[ P(\text{at least one of } N \text{ cows has ticks detected}) = 1 - \prod_{i=1}^{N} (1 - P_i(n_{ij})). \]

where \(N\) is number of cows examined. To explore the influence of number of cows inspected, we calculated daily detection probabilities when inspecting 1, 20, 40, and all 80 cows. Each grouping of inspected cows (1, 20, 40, or 80) represented an independent sample. To aggregate and compare data for each number of cows inspected, we counted the number of days on which the model calculated detection probabilities at or above the following thresholds: 0.25, 0.50, 0.75, and 0.95. We developed the model using STELLA® (High Performance Systems, Inc., Hanover, NH) and QuickBasic® (Microsoft Corp., Redmond, WA) software on a personal computer.

As an experimental design for simulations, we chose to control the following five factors that influence establishment of tick infestations in south Texas and their subsequent detection:

1. habitat type (uncanopied grass (hereafter, “grass”), mixed brush-canopied grass (hereafter, “mixed brush”), or mesquite-canopied grass (hereafter, “mesquite”),
2. season of first infestation (spring (1 March) or autumn (27 September)),
3. initial number of larval ticks on the “average” cow (5, 10, 50, 100, 250, 500, or 1000),
4. number of cows inspected (1, 20, 40, or 80), and
5. rotational grazing strategy (intensive or extensive).

The start dates we selected correspond to peak purchases of replacement cows and introduction of stocker steers in south Texas (Teel et al., 1998). We ran all combinations of these factors to estimate combined effect on probability of detection over a simulated 2-year period. To keep standard deviation of mean daily detection probabilities below 0.05, we ran the model 300, 25, 10, and 5 times in each scenario when inspecting 1, 20, 40, and 80 cows, respectively. We then compared scenarios using the number of days on which the mean detection probability equalled or exceeded 0.25, 0.50, 0.75, and 0.95.

3. Model results

In extensive rotation scenarios, detection probability in herds grazed in grass never exceeded 0.25 regardless of initiation season, and tick populations died out within 289 days. In mixed brush and mesquite, the probability did not exceed 0.25 in simulations begun in autumn, despite having tick populations in mesquite that survived more than 2 years. Simulations begun in spring in mixed brush estimated detection probabilities ≥0.50 existing on up to 87 individual days, but only when examining 80 cows. Detection probabilities ≥0.95 existed on no more than 21 individual days in this scenario, even though infestations lasted up to 632 days. In simulations beginning in spring in mesquite, populations initiated with 250 or more ticks on each cow survived more than 2 years. When examining 80 cows in mesquite, however, detection probabilities equalled or exceeded 0.50 on up to 99 individual days and 0.95 on up to 68 individual days.

In intensive rotation simulations, detection probability in simulations started in autumn only equalled or exceeded 0.25 when cows began with 1000 ticks each, grazed in mixed brush or mesquite, and inspectors examined 80 cows. This small window of weak detection lasted only 6–7 consecutive days, despite
tick populations that survived 423 days in mixed brush and more than 2 years in mesquite. Simulations started in spring revealed that tick populations in grass died out within 277 days and had a probability of detection $\geq 0.50$ on no more than 25 individual days. In mixed brush, the same total duration of detection widened to 222 individual days, with a population that survived more than 2 years. Simulations of grazing in mesquite estimated tick populations surviving more than 2 years when initialized with 100 or more ticks per cow. Tick densities reached such high levels in this scenario that detection probabilities $\geq 0.50$ and $\geq 0.95$ occurred on 411 and 268 individual days, respectively, when examining 80 cows. When examining one cow at random, the same probabilities occurred 106 and 12 individual days, respectively. For all scenarios, examination of 40, 20, and 1 cow instead of all 80 cows reduced the frequency of exceeding any given probability threshold (e.g. 0.75) by a mean of 40, 64, and 94%, respectively.

Figs. 2–4 show temporal dynamics of mean detection probability for selected scenarios initiated with 1000 ticks per cow in a mesquite habitat. In all simulations, the herd began the rotation cycle in pasture 1. Probabilities of detection at or above given levels existed as temporal windows that increased in length both as number of cows inspected increased and detection-probability thresholds decreased. Simulations that began in spring and simulated an extensive rotation strategy predicted larval activity within pastures 1–3 (Fig. 2). The tick population survived more than 2 years and detection probabilities $\geq 0.25$ occurred only during two short periods. The first window of opportunity lasted for 1 month in autumn of the first year, as cows picked up larvae in pasture 1 produced by ticks that dropped there 7 months earlier. Here detection windows of similar length for 20, 40, and 80 inspected cows at all detection thresholds signified a sharp peak in detectable ticks on each cow. The second window occurred during summer of the second year, as cows picked up ticks in pastures 1 and 2. Simulations begun in spring with intensive rotation reveal distribution of tick larvae among all eight pastures and a tick population that survived throughout the 2-year simulation (Fig. 3). Pastures 2 and 5 show the largest peaks in larval density because cows dropped relatively more ticks in them. When examining 20, 40, or 80 cows, daily detection probabilities $\geq 0.50$ occurred most often at intervals from summer to mid-winter in both years. During the second year, examining one cow gave detection probabilities $\geq 0.50$ only for a few days in the summer and 1 month in autumn. When inspecting 80 cows, however, the same detection probabilities extended almost continuously from summer to mid-winter. Simulations begun later in the year (autumn) with the same intensive rotation strategy showed larval activity only in pastures 1–4 (Fig. 4). In this scenario, the tick population also survived more than 2 years at a very low density (note change in scale), yet detection probabilities equaled or exceeded 0.25 only for 6–7 consecutive days in spring of the first year, after cattle picked up larvae that had hatched from overwintering eggs.

4. Discussion

Results suggest that probability of detecting *Boophilus*-tick infestations depends most heavily on season of initial infestation; less heavily on rotational grazing strategy, habitat type, and number of cows inspected; and only moderately on initial number of infesting ticks. Ticks introduced in autumn generated populations that survived sometimes nearly as long or longer as populations begun in the spring, but at lower densities; probability of detecting these populations almost always remained below 0.25. Supporting this prediction, Graham and Hourrigan (1977) believed that some *Boophilus*-tick infestations beyond the quarantine zone in Texas may have existed at low densities for 1–2 years before detection.

Compared to continuous grazing, rotational grazing reduces tick–host contact because cattle graze a larger proportion of available rangeland (Coughenour, 1991), distributing ticks over a larger area, and may move to an uninfested pasture after dropping engorged females. Although empirical studies show that longer rest periods suppress tick infestations more quickly (Wilkinson, 1957; Harley and Wilkinson, 1964), data show a correlation between longer rest periods and reduced cow reproductive and calf-weaning rates (Heidtschmidt and Taylor, 1991). In this study, the longer grazing periods of the extensive SDG strategy provided longer pasture-rest intervals and reduced the number of pastures infested, tick population densities, frequency of cattle reinfestation, and number of
larvae picked up by cows. That these lower population densities often persisted for years in favorable mixed brush and mesquite habitats, yet rarely exceeded a detection probability of 0.25, suggests that extensive rotational grazing could have the unintended consequence of decreasing *Boophilus*-tick populations to sustainable but rarely detectable densities. In a previous simulation study, acaricide applications tended to reverse this influence of grazing strategy: simulated *Boophilus*-tick populations without acaricide
resistance survived longer and achieved greater densities under extensive grazing than intensive grazing because reduced tick-host contact also reduced their exposure to acaricide-treated cattle (Corson et al., 2001). Simulated tick populations survived longer and reached higher densities with increasing canopy cover of vegetation. Canopy cover provides microclimates with lower ambient temperature and higher relative humidity, both of which reduce tick mortality rates (Daniel, 1978). As noted by Fleetwood (1985), however, natural defoliation of mesquite during water stress leads to higher microclimate temperatures in that habitat compared to mixed brush habitats. In the model, more extensive canopy cover also promoted relatively larger increases in detection window duration under intensive grazing than extensive grazing, perhaps due to the greater probability in each pasture that grazing would occur during periods of high tick density. In a previous model (Corson et al., 2001), we
found the same relationship between simulated grazing strategy and changes in habitat type: as canopy cover increased, infestation longevity increased at a faster rate under intensive grazing than under extensive grazing.

Frequency of detection probabilities at or above a given threshold decreased as number of cows examined decreased. Model results suggested that for a given detection probability, each halving of the number of cows examined reduced frequency of that threshold over the course of 2 years by an average of 40%. Thus, a window of opportunity lasting 30 days (consecutive or separate) when examining 80 cows would tend to shrink to ca. 18 days when examining 40 cows, ca. 11 days when examining 20 cows, and ca. 6 days if examining only one cow. Stated another way, doubling the number of cattle inspected (+100%) may increase the frequency of a given
Detection probability (over the course of 2 years) ca. 67%. Factors such as inspector training and experience, cow behavior, quality of facilities, and weather, however, may shift the sigmoidal detection curve and strongly affect ability of inspectors to detect a *Boophilus* infestation. The baseline sigmoidal curve (Fig. 1) predicts certain detection if all inspected cattle have 150 or more detectable ticks. This level of infestation can occur fairly easily in *B. taurus* cattle, which have a lower innate resistance to ticks than *Bos indicus* cattle (Sutherst et al., 1988). For example, cattle with 100, 50, 25, and 0% *B. taurus* content in central Queensland carried a daily average of 465, 79, 65, and 5 detectable ticks respectively; however, cattle that carried more than 200 detectable ticks per day for 8 months either died or required removal from the experiment (Bourru et al., 1988).

We know of no empirical studies of *Boophilus*-tick population dynamics in rotational grazing systems with which to evaluate our model results. Waters (1972), however, provides anecdotal support by reporting suppression of *Boophilus*-tick populations in a rotational grazing system of three to seven pastures. Although we cannot evaluate the validity of our results, the model can identify gaps in knowledge and generate hypotheses for empirical field or laboratory studies. For example, more accurate prediction of detection probabilities will require data on the relationship between the number of detectable ticks on a cow and the probability of detecting them.

Tick detection seems less important in regions focusing on *Boophilus*-tick control instead of eradication, such as Australia, South Africa, Brazil, and Venezuela, especially in pastures already containing *Boophilus*-tick populations. As genetic characterization of populations improves, however, a model such as this one could predict how subpopulations differing in acaricide resistance might propagate among pastures under a rotational grazing system. In addition, periods of high detection probability may represent optimal periods for assessing the effectiveness of tick vaccines or the enzootic stability of *Babesia* infection rates.

Our model results reveal systems patterns and processes comparable to those found in other models. For example, a model of mite (*Varroa destructor*) infestation on honeybees (*Apis mellifera*) showed that host-related factors had more influence on parasitoid population dynamics than parasite-related factors (Wilkinson and Smith, 2002). A second model, of gypsy moth (*Lynxiantra dispar*) population dynamics, generated the hypothesis that success of gypsy moth eradication programs depends on initial gypsy moth population density and the type of functional response of small mammal predators (Sharov and Colbert, 1996). In a third model, stochastic simulation of interactions between Townsend’s ground squirrels (*Spermophilus townsendii*) and two of its internal parasites suggested that chance events had great influence in the system, especially at low host densities (Wilber and Shapiro, 1997). Given our model’s assumptions and deterministic output, it seems better suited to evaluate the relative influence of control factors than to make quantitative predictions. Nonetheless, models such as this one may help in understanding the complex systems within which cattle, habitat types, and production practices interact to influence tick population dynamics and the probabilities of tick detection.

**References**

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