

Conditions for stable parapatric coexistence between *Boophilus decoloratus* and *B. microplus* ticks: a simulation study using the competitive Lotka-Volterra model

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Abstract The autochthonous tick *Boophilus decoloratus*, and the invasive species *Bo. microplus*, the tick most threatening the livestock industry in Africa, show complex interactions in their interspecific rivalry. This study was conducted to specify the conditions under which the two competitors can co-exist in equilibrium, and to provide insight into their climate-dependant parapatric distribution in Tanzania. A model of the Lotka-Volterra type was used, taking into account population dispersal and interactions of various kinds. If the model allowed for immunity-mediated competition on cattle, reproductive interference, and an external mortality factor, it explained fairly well the field observation that the borderline between these ticks loosely follows the 22–23°C isotherm and the 58 mm isohyet (i.e. ~700 mm of annual rainfall total). Simulations fully compatible with the pattern of real co-existing populations of *Bo. decoloratus* and *Bo. microplus*, characterized by a pronounced population density trough and mutual exclusion of the two ticks on cattle in an intermediary zone between their distributional ranges, were, however, achieved only if the model also implemented a hypothetical factor responsible for some mortality upon encounter of one tick with the other, interpretable as an interaction through a shared pathogen(s). This study also demonstrated the importance of non-cattle hosts, enabling the autochthon to avoid competition with *Bo. microplus*, for the behaviour of the modelled system. The simulations indicate that a substantial reduction of wildlife habitats and consequently of *Bo. decoloratus* refugia, may accelerate the replacement of *Bo. decoloratus* with *Bo. microplus* much faster than climatic changes might do.

Keywords *Rhipicephalus (Boophilus) decoloratus* · *Rh. (Bo.) microplus* · Interspecific competition · Parapatry · Lotka-Volterra model

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Introduction

The *Boophilus* spp. (alias *Rhipicephalus* (*Boophilus*) spp.) ticks represent important livestock pests throughout the warm belt of the Earth; they transmit serious disease agents, cause skin injuries prone to secondary infection, and induce blood losses responsible for impaired animal fitness and a consequential economical cost. Since the turn of the nineteenth and twentieth century, Africa has been challenged with an invasion by *Bo. microplus*, an Asian relative of the indigenous *Bo. decoloratus* species which is now being ousted by the more aggressive and pestilent intruder. *Bo. microplus* has already advanced far into the south-east of Africa's interior (Katsande et al. 1996; Berkvens et al. 1998; Tønnesen et al. 2004; Lynen et al. 2008) and has recently become established in West Africa (Madder et al. 2007). There is great concern about future developments, particularly in connection with the foreseen climate changes. Computer modelling has therefore been utilised to assess potential shifts in the geographical ranges of these ticks in response to assumed climatic conditions (Sutherst and Maywald 1985; Estrada-Peña 2003; Cumming and Van Vuuren 2006). These extrapolative studies were biased, however, due to the lack of true equilibrium calibration data, as well as omitting inter-specific interactions, a significant determinant of species' distribution (Araújo and Luoto 2007; Sutherst et al. 2007) (the predictions based on Australian *Bo. microplus* biometric data have been further challenged by the recent finding that the African and Australian populations of this tick may not be conspecific; Labruna et al. 2009).

To date, only a few population dynamics models were devoted to interactions between tick species (Ribeiro and Spielman 1986; Bull and Possingham 1995; Tyre et al. 2004), and only one study has addressed the *Bo. microplus*–*Bo. decoloratus* competition problem (Sutherst 1987). The latter model implemented solely the slowing-down effect of abortive crossbreeding on the population growth of these ticks; nevertheless, conditional on sufficient differences between their fecundity and/or survival rates, the model satisfactorily reproduced the field observations of the gradual displacement of *Bo. decoloratus* by *Bo. microplus*.

In natural conditions, these species interact in more complex ways. Apart from reproductive interference, they compete chiefly for their principal blood-meal source in common (i.e. cattle) by mutually boosting animals' cross-protective immunity against feeding by both tick species (Norval and Short 1984; Amin-Babjee and Riek 1986; Rechav et al. 1991). While *Bo. microplus* better withstands cattle immunity, *Bo. decoloratus* has the advantage of being a more catholic feeder, thus escaping from the competition by parasitizing alternative hosts, particularly wildlife, wherever available (Mason and Norval 1980; Horak et al. 1983, 1992, 2003). Slight differences in environmental requirements make *Bo. decoloratus* more tolerant to cold and drought, whereas *Bo. microplus* thrives better in warm and humid conditions, and, simultaneously, somewhat outstrips *Bo. decoloratus* in reproductive rate (Arthur and Londt 1973; Londt and Arthur 1975). Other potential forms of between-species interactions include differential resistance to acaricides (Baker et al. 1981) and various common pathogens (Friedhoff 1988).

In congruence with experiments, field data on *Bo. decoloratus* and *Bo. microplus* indicate a nexus of interferences that govern their co-existing populations in nature. It was observed that the zone where the two species overlap exhibits a marked decrease in the population density of both *Bo. decoloratus* and *Bo. microplus* (Baker et al. 1989; Lynen et al. 2008). At the same time, cattle grazed within that zone showed a tendency towards mutual exclusion of infestation with the two ticks (Lynen et al. 2008). External factors apparently set up a balance between *Bo. decoloratus* and *Bo. microplus* in nature: advances

and retreats of their populations were observed in response to climatic fluctuations (Norval et al. 1992), as well as movements of host herds (Lynen et al. 2008). In Tanzania, where the populations of *Bo. decoloratus* and *Bo. microplus* seemingly approach an equilibrium, a border line between their eco-climatic domains loosely follows the 22–23°C isotherm and the 58 mm isohyet (i.e. annual rainfall of ~700 mm) (Lynen et al. 2008). Understanding of these observations is a prerequisite for better comprehension of the principles driving population dynamics of these important pests, and, consequently, a more realistic prediction of their distribution in the future. In this study, we employed a simulation model to explain the co-distributional pattern of *Bo. decoloratus* and *Bo. microplus* that has developed under the conditions in Tanzania.

Methods

Modelling species environmental requirements

The classical logistic growth model assumes that population dynamics of a species is regulated by two parameters, the intrinsic rate of natural increase, r , and the carrying capacity of the environment, K (MacArthur 1972). The former parameter reflects species' fecundity, development time, and mortality in particular environmental conditions, and can thus be viewed as a function of environmental variables θ , $r = f(\theta)$, ranging between some finite negative and positive values: $r > 0$, natality exceeds mortality; and $r < 0$, mortality exceeds natality. Assuming that a species' responses to environmental variables follow a normal distribution as well as being independent, then $f(\cdot)$ would be multivariate gaussian. Since species' responses are usually skewed on natural scales of environmental variables, we optionally allow $f(\cdot)$ to be log-gaussian. For example, if temperature, T , and rainfall, R , are the only driving variables being considered, then $\theta \equiv (T, R)$, and $f(\theta) \sim a A(\Delta_T, \mu_T, \sigma_T) A(\Delta_R, \mu_R, \sigma_R) + b$, where $A(\cdot)$ denotes the log-normal pdf, Δ , μ , and σ are the shifting, mean, and shape parameters, respectively, and a and b are scaling coefficients (Limpert et al. 2001). The model's second parameter, K , is the asymptote of population size, and reflects limited resource supply available to the species (in this case, the limited tolerance of cattle to tick feeding). Considering two species, indexed with d and m , in isolation, their population growths would be given by:

$$\frac{dN_d}{dt} = \alpha_d f_d(\theta) N_d \left[\frac{K_d - N_d}{K_d} \right] \quad (1a)$$

$$\frac{dN_m}{dt} = \alpha_m f_m(\theta) N_m \left[\frac{K_m - N_m}{K_m} \right], \quad (1b)$$

where N and t denote the population size and time, respectively, and α_d and α_m are coefficients adjusting overall species' performances. The environmental requirements of *Bo. decoloratus* and *Bo. microplus* were assessed from the available literature (e.g. Gothe 1967; Mason and Norval 1980; Short et al. 1989; Solomon and Kaaya 1998; Lynen et al. 2008), and $f(\cdot)$'s were parameterized as shown in Fig. 1.

Modelling species interactions

The species were allowed to compete for their common resource (cattle) according to Lotka-Volterra conditions:

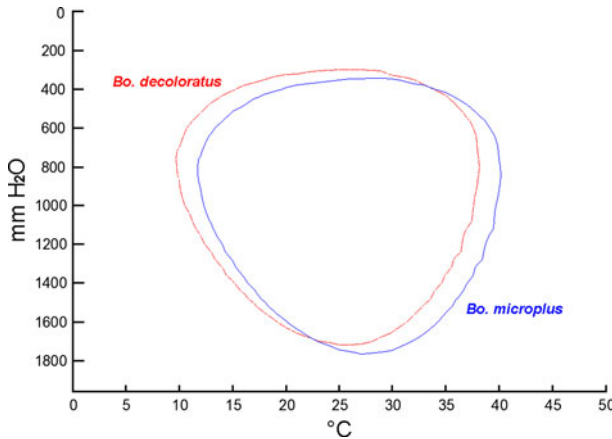


Fig. 1 Disposition of *Boophilus decoloratus* and *B. microplus* fundamental niches in an environmental space defined by the two most significant variables—the mean annual temperature and rainfall—based on literature data as well as field observations in Tanzania; the assumed distribution is bivariate log-gaussian ($\Delta_T = 7.225, \mu_T = 2.0, \sigma_T = 0.15, \Delta_R = 2.220, \mu_R = 1.0, \sigma_R = 0.45, a = 7.610, b = -0.2$), and shown are envelopes encompassing 99% of the populations. Note that the two niches are considered equivalent with the exception that *Bo. decoloratus* is set a bit more drought and cold-tolerant (to adjust the niches in this way, the climatic variables were re-scaled: for *Bo. decoloratus* $T = (^{\circ}\text{C} - 25.5)/6.0, R = (780 - \text{mm H}_2\text{O})/310$; for *Bo. microplus* $T = (^{\circ}\text{C} - 27.5)/6.0, R = (825 - \text{mm H}_2\text{O})/310$)

$$\frac{dN_d}{dt} = \alpha_d f_d(\theta) N_d \left[\frac{K_d - N_d - \beta_{dm} N_m}{K_d} \right] \tag{2a}$$

$$\frac{dN_m}{dt} = \alpha_m f_m(\theta) N_m \left[\frac{K_m - N_m - \beta_{md} N_d}{K_m} \right], \tag{2b}$$

where β_{dm} and β_{md} quantify the oppressing effect the species have on one another. This mechanism assumes that the two species reciprocally control their population growths in a density-dependent manner, while each species maintains its own growth rate and carrying capacity.

The ‘satyrization’ effect was included in the model to simulate the reproductive interference between the two species (Ribeiro and Spielman 1986):

$$\frac{dN_d}{dt} = [\text{Equation 2a}] \frac{N_d}{N_d + \gamma_{dm} N_m} \tag{3a}$$

$$\frac{dN_m}{dt} = [\text{Equation 2b}] \frac{N_m}{N_m + \gamma_{md} N_d}, \tag{3b}$$

where γ_{dm} and γ_{md} represent the degree of sterilization resulting from interspecific mating between males of one species and females of the other. Assuming a unitary sex ratio in both species, the ‘satyrization’ term specifies the proportion of viable eggs as a function of the relative abundance of males of each species and their ability to induce sterility in females of the other species.

One way in which species can potentially interact is through shared pathogens. For example, when two species, each carrying its own co-evolutionally adapted variant of a pathogen, join ranges, then the fitness of each species is reduced by cross-infections with the alternate, more destructive, variant of the pathogen, which constrains the species

co-existence (Cornell 1974). The interaction potentially arising from cross-species infection can be very complex (Holt and Pickering 1985). In our model, it was substantially simplified by assuming an existence of only a single shared pathogen, and in each species: complete susceptibility, no vertical transmission to offspring, no recovery from infection, and the pathogen-induced death rate being additive to the intrinsic death rate. The equation then reduces to:

$$\frac{dN_d}{dt} = [\text{Equation 3a}] - \delta_{dm} N_d N_m \quad (4a)$$

$$\frac{dN_m}{dt} = [\text{Equation 3b}] - \delta_{md} N_m N_d, \quad (4b)$$

where δ_{dm} and δ_{md} quantify the death rate per encounter with the other species.

Finally, an external mortality term was added to the model to make allowance for miscellaneous factors which cause death independently of the above factors (e.g. chemical control, meteorological disasters, etc.):

$$\frac{dN_d}{dt} = [\text{Equation 4a}] - \varphi_d N_d \quad (5a)$$

$$\frac{dN_m}{dt} = [\text{Equation 4b}] - \varphi_m N_m, \quad (5b)$$

where φ_d and φ_m represent the extrinsic death rates.

Modelling spatial relations

In principle, the spatial pattern of co-existence of species can be influenced by multitudinous environmental factors and their phenology. In a previous study of *Bo. decoloratus* and *Bo. microplus* co-existence in Tanzania, however, we discovered that it is the mean yearly temperature and rainfall that dominantly control the distribution of the two species (Lynen et al. 2008). Therefore in most of our simulations, an environmental space restricted to these two most significant climatic variables was considered. This space was modelled with an array of cells organized in 50 rows and 50 columns which represent the temperature and rainfall gradients encompassing the species' niches (Fig. 1). To allow for some environmental heterogeneity, each cell was subdivided into 100 subunits in which the conditions were allowed to vary slightly according to the normal distribution function and zero mean, so that overall environmental space was smooth.

Each cell was occupied by a population unit—a deme—of either species. Field data indicated that in a zone where *Bo. decoloratus* and *Bo. microplus* populations in Tanzania overlap, the number of co-infested cattle is disproportionately low compared to numbers of animals infested by either tick singly (Lynen et al. 2008). In our models, this effect of mutual avoidance of the two ticks could be quantified by the expression $n \sum_n N_d N_m / \sum_n N_d \sum_n N_m$, referred to hereafter as the avoidance index, in which N_d and N_m indicate sizes of the two tick demes in a particular cell, and n is a number of neighbouring cells over which this effect was evaluated ($n > 1$; optimal $n = 5$). Obviously, in the case of neutrality, the avoidance index equals unity, whereas values below unity indicate segregation.

Passive, density-independent migration was assumed to exist between neighbouring demes; the migration parameter, ε , quantified the proportion of a deme which moved into the territory of neighbouring demes. Each species' sub-model consisted of two symmetric compartments, one holding the subpopulation feeding on cattle, and the other that fed on

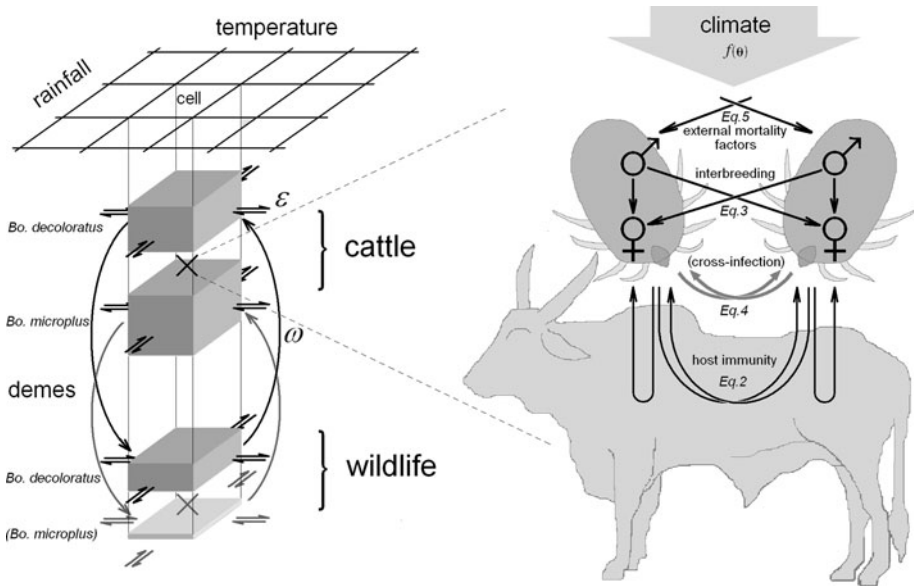


Fig. 2 A schematic representation of the population flows and interactions allowed for in the co-existence model for *Boophilus decoloratus* and *B. microplus* (optional terms are shown in brackets)

alternative hosts (e.g. wildlife). Between-compartment diffusion was regulated with the exchange rate, ω , representing the proportion of a deme in the cattle-compartment moving to a corresponding deme in the wildlife-compartment, and vice versa. All movements were considered constant throughout the environmental space. A schematic representation of the population flows and interactions within the model is shown in Fig. 2.

Calibration and simulation

Equilibrium within the above system of equations was searched for numerically, as the movement terms included in the model prevent calculation of accurate analytic Jacobians. Each cell was seeded with starting populations of both species and iterated until their growth rates dropped below an insignificant threshold; generally, 1,000 iterations were required to satisfactorily approach equilibrium in all cells. Records of *Bo. decoloratus* and *Bo. microplus* from 817 localities in Tanzania were utilized for calibrating the model; details regarding this data-set are given elsewhere (Lynen et al. 2008). This data-set patterns the prevalence of infested cattle across environmental conditions in Tanzania as illustrated in Fig. 5. The model was fitted to that pattern using the L-BFGS-B algorithm (Byrd et al. 1995) by maximizing the criterion: $w_B \tau_B + w_d \tau_d + w_m \tau_m$, where τ is regularized Kendall's tau, w is a weight reflecting data quality, and B , d , and m symbolize the *Boophilus* spp., *Bo. decoloratus*, and *Bo. microplus* data subsets; that is to say, both species abundances and their joint abundance were fitted as one in a balanced manner. The process of obtaining the model parameters through automatic calibration can be summarized as follows:

- (1) all parameters of the model were adjusted to some initial values; then
- (2) the model was iterated until equilibrium in all cells was reached,

- (3) the fit of the equilibrated model to the Tanzania field data was measured,
- (4) using the Lbfgsb.2.1 optimisation software (<http://www.eccs.northwestern.edu/~nocedal/lbfgsb.html>), the setting of the parameters was modified to improve the fit, and
- (5) proceeding with the second step, this procedure was repeated many times until it eventually converged onto the best fit model.

To have control over accuracy of our models, the calibration was performed one hundred-times, each time against another independent bootstrap sample from the field data, and the final parameters were estimated as bootstrap means. These parameters, believed to best explain the field observations, were then utilised for simulating the co-existence of *Bo. decoloratus* and *Bo. microplus*.

Validation data

Historical evidence exists for at least three geographical areas in Tanzania, namely Mbizi Mountains, highlands in southern Iringa, and Usambara Mountains, that *Bo. decoloratus* and *Bo. microplus* have co-existed there since the 1960s or earlier (Yeoman and Walker 1967). Recent survey data from these areas (Lynen et al. 2008) thus exemplifies equilibrium between these ticks under local conditions.

Surveys of free-living ticks in Döhne, the Eastern Cape, South Africa, revealed lengthy co-existence of *Bo. decoloratus* and *Bo. microplus* populations, reflecting local, at least temporary, equilibrium (Nyangiwe and Horak 2007). Environmental data on this exceptional locality (courtesy of Prof. I.G. Horak, University of Pretoria, SA) was utilized as an independent validation point.

In a field survey in the Soutpansberg region, Limpopo Province, South Africa, cattle at 35 dip tanks and commercial farms were monitored for several years for changes in infestation rates of *Bo. decoloratus* and *Bo. microplus*; these sites included those where *Bo. microplus* had replaced *Bo. decoloratus* as well as those where the two species persisted either side by side or singly (Tønnesen 2002). Data on these particular localities (courtesy of Dr. M.H.Tønnesen, Norwegian Food Safety Authority (Mattilsynet), Førde, Norway) were differentially considered in model validation.

Results

Effects of interactions

In order to understand the influences of particular inter-specific interactions on the simulated populations, we tested a variety of relationships and initial conditions that were adjusted between the two virtual species which were considered symmetrical, differing only in environmental preferences. The effects of different interactions on model behaviour are illustrated in Fig. 3 for this special case. This figure shows a profile of equilibrium population density for each species, their sum total, and a diagram of the avoidance index along an environmental gradient thought to pass through the two species' optima (i.e. positioned diagonally to the temperature and rainfall gradients in Fig. 1). An overall impression from Fig. 3 is that while constant diffusion keeps up interspersed of both populations, and each species prevails at its favoured end of the environmental gradient, the degree of their segregation is determined primarily by the character of interactions. In the case of complete

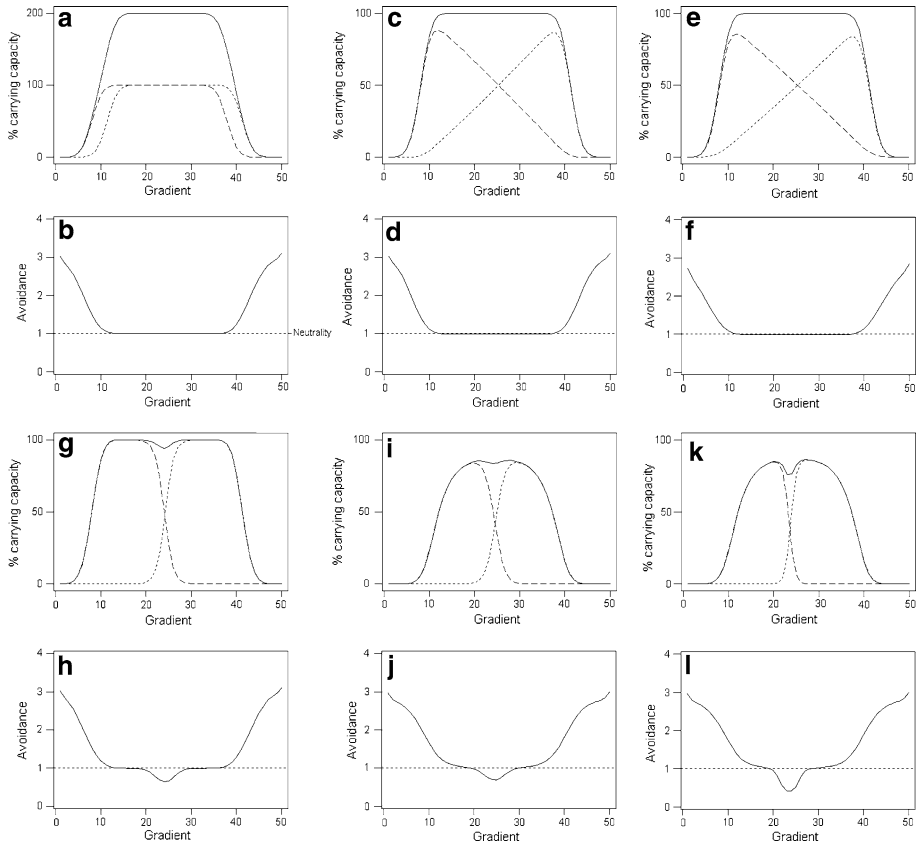


Fig. 3 Simulated effects of interspecific interactions upon two virtual species (differing in environmental preferences but otherwise equivalent); shown are abundances (in terms of % of K) for each species separately as well as their sum total (dotted, dashed, and solid line, respectively), and the avoidance index, along an environmental gradient passing through both species' optima (x -axis). Parameters were adjusted as follows: K , $\alpha = 1$, $\varepsilon = 0.2$, and alternatively: **a, b** β , γ , δ , $\varphi = 0$; **c, d** $\beta = 1$, γ , δ , $\varphi = 0$; **e, f** $\beta = 1$, $\gamma = 0.2$, δ , $\varphi = 0$; **g, h** $\beta = 1$, $\delta = 0.1$, γ , $\varphi = 0$; **i, j** $\beta = 1$, $\gamma = 0.2$, $\delta = 0$, $\varphi = 0.1$; and **k, l** $\beta = 1$, $\gamma = 0.2$, $\delta = 0.1$, $\varphi = 0.1$. Note that only the three latter conditions generate effects (e.g. overall abundance trough; avoidance index < 1), compatible with field observations

absence of any interaction, both species overlap (Fig. 3a). Sole Lotka-Volterra competition promotes dominance of either species at their ends of the gradient but does not prevent complete intermixing of the populations (Fig. 3c). Similarly, 'satyrization' neither singly nor in combination with Lotka-Volterra competition, shows a significant segregation effect even if high parameter levels are adjusted (Fig. 3e). Patterns compatible with real populations of *Bo. decoloratus* and *Bo. microplus* can be obtained only if the virtual species interact in specific ways: either through a shared pathogen and Lotka-Volterra competition, or Lotka-Volterra, 'satyrization', and (inflated) external mortality factors, or, of course, if all these factors are involved. These latter models simulate realistically the typical population density trough as well as a zone of mutual avoidance of the two species at the abut of their population domains (Fig. 3g–l).

Species' replacement

Figure 4 illustrates replacement of one virtual species by another in the process of establishing their parapatric co-existence. This simulation is an extension of the model shown in Fig. 3k: a population of one species in equilibrium was challenged with the other species introduced in a quantity equivalent to 2% of carrying capacity into its environmental optimum, and iterated until a new equilibrium was achieved. Three phases of invasion are realistically simulated: (1) the lag phase preceding the proliferation of the 'intruder', (2) the phase of replacement, and (3) the phase of stable parapatric co-existence of the two species (in prolongation). The model indicates that the population density trough develops early on at the beginning of the replacement phase, and is not symptomatic for equilibrium only.

Simulation of real populations

Although being biologically comparable species, *Bo. decoloratus* and *Bo. microplus* differ significantly from the assumption of symmetry in the above two virtual species. The so far published data are, however, insufficient to furnish proper parameters for a realistic simulation of the two species co-existence. Therefore, we only prearranged in our model a framework of inter-species relations and set invariant parameters to unity, and relied upon the strategy of automatic calibration against empirical observations. Except for a hypothetical cross-species infection, all the interactions between *Bo. decoloratus* and *Bo. microplus* implemented in the model have been shown to take place in nature. Close similarities in biology of these species allowed us to expect equivalence in their dispersal rates as well as in external mortality rates; and the events of cross-mating were also assumed to occur equally likely in both species. Any non-cattle population of *Bo. microplus* (i.e. wildlife compartment) was neglected. Three variants of the model were tested, differing in allowances made for the cross-species infection term: (1) no interaction through a pathogen exists (7 parameters to be estimated include α_d , β_m , γ , ε , φ , ω_d , and K_{wd} , the carrying capacity of the wildlife compartment), (2) the two species interact through one shared pathogen which is equally virulent to both species (8 missing parameters: ditto plus $\delta_d = \delta_m$), and (3) ditto but the pathogen differs in virulence to the two species (9 missing parameters: ditto but $\delta_d \neq \delta_m$). The missing parameters were estimated by fitting the respective models to the Tanzania tick data documented in Fig. 5. The results are summarized in Table 1 and the predicted population densities are shown in Fig. 6. The cross-species infection-free variant of the model, i.e. the 7-parameter version, showed the loosest fit (though insignificantly: overall Spearman's rho was estimated as 0.637 versus 0.675 and 0.657 in the 7-, 8-, and 9-parameter models, respectively), and did not account for the population density trough (Fig. 6b). In contrast, both models implementing that interaction (i.e. the 8 and 9-parameter versions) simulated the density trough adequately (Fig. 6d, f). In addition, Table 1 shows that, on average, more realistic estimates of the populations' parameters were obtained if that interaction was considered; the model omitting that interaction (i.e. the 7-parameter model) diverged mainly in an increased level of Lotka-Volterra competition and much stronger sexual interference, though the differences fit within the limits of bootstrap standard error (Table 1). All three models fairly well explain the climate-underlain division between *Bo. decoloratus* and *Bo. microplus* observed in Tanzania: the cores of the simulated populations are best separated just along the axes passing through the temperature of ca. 22°C and precipitation of ca. 700 mm, as seen on the density diagrams in Fig. 6a–f. Our modelling approach also gives us an opportunity to quantify the benefit for *Bo. decoloratus* in feeding on alternative hosts.

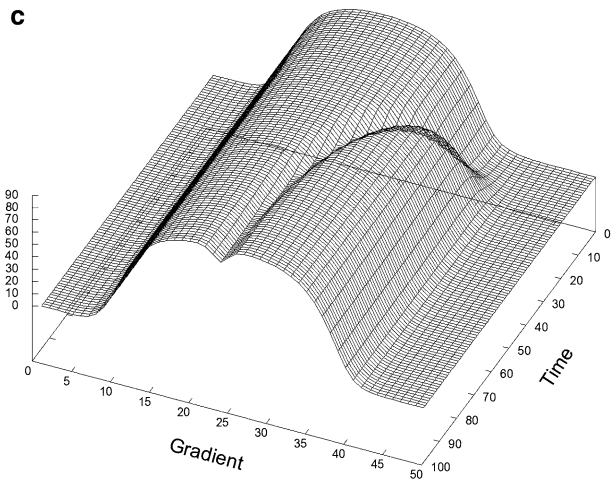
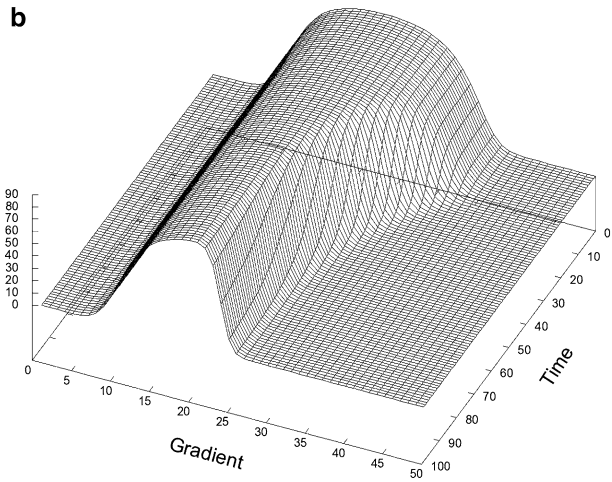
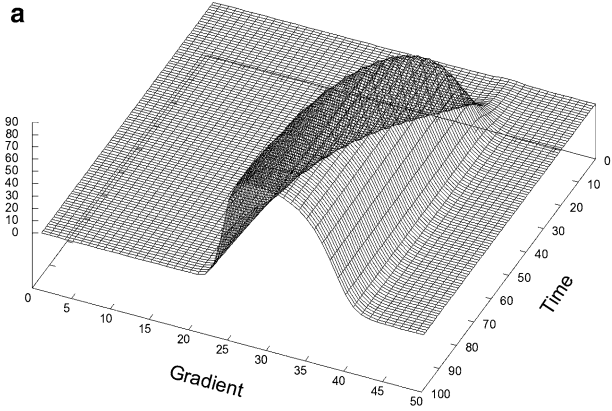


Fig. 4 An extension of the model defined in Fig. 3k, l along the time axis illustrates the process of ousting of a resident species by an intruder species. A seed of the intruder's population was introduced at time '0' into the resident's population in equilibrium, and iterated to a new equilibrium; shown are **a** the intruder's abundance, **b** the resident's abundance, and **c** a sum total of both abundances. Note three phases of the invasion: (1) a lag phase preceding the proliferation of the intruder, (2) a phase of replacement, and (3) a phase of stable parapatric co-existence (in prolongation)

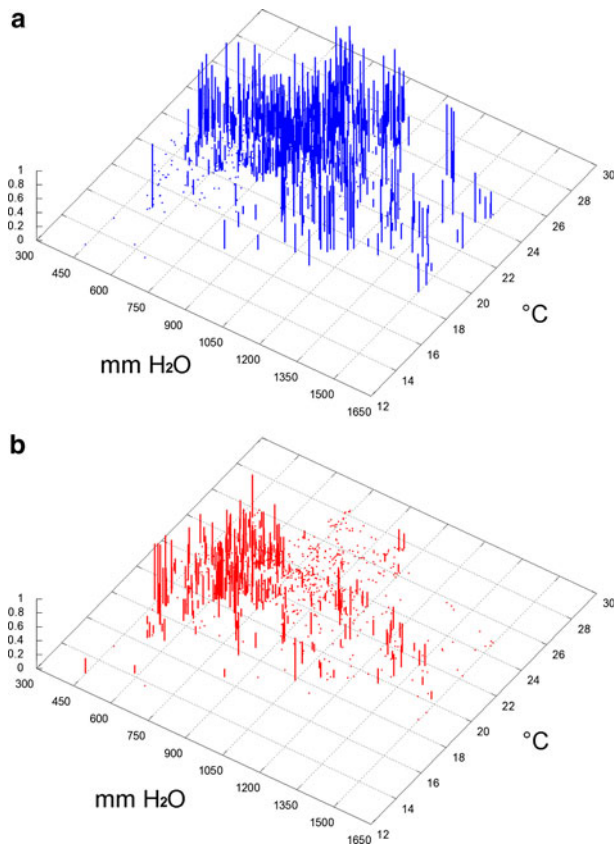


Fig. 5 Field survey data from Tanzania on **a** *Boophilus microplus*, and **b** *Bo. decoloratus*; each abscissa corresponds to the prevalence of infested cattle in any of the 817 inspected localities throughout the country

Figure 7 shows simulations performed with the same parameters estimated in Table 1, but cutting off the *Bo. decoloratus* support from the wildlife compartment by nullifying the ω parameter. Such modified models predict a significant shrinkage of the environmental space, defended by *Bo. decoloratus* against *Bo. microplus*, in reaction to a loss of alternative hosts, no matter what model variant was considered.

Model validation

Altogether 30 localities in Tanzania, where long-term co-existence of *Bo. decoloratus* and *Bo. microplus* has been documented, were plotted on a climatic diagram along with a projection of inter-species boundaries, predicted by the models, as shown in Fig. 8. The

Table 1 Estimated model parameters for stable parapatric populations of *Boophilus decoloratus* and *Bo. microplus* based on the Tanzania tick data and 100 bootstrap simulations

Parameter ^a	7-parameter model		8-parameter model		9-parameter model		Explanation
	Mean	SE	Mean	SE	Mean	SE	
α_d	0.935	0.068	0.926	0.090	0.917	0.072	Population growth rate coefficient
β_{md}	0.677	0.169	0.534	0.137	0.488	0.110	Lotka-Volterra competition coefficient
γ	0.210	0.098	0.130	0.024	0.119	0.023	Ribeiro-Spielman's satyrization parameter
δ_{dm}	–	–	0.216	0.107	0.116	0.066	Per encounter mortality rate
δ_{md}	–	–	Ditto	Ditto	0.176	0.073	Ditto
ε	0.301	0.103	0.239	0.052	0.242	0.036	Dispersal rate coefficient
φ	0.036	0.041	0.034	0.041	0.054	0.041	External mortality rate
ω_d	0.099	0.103	0.124	0.046	0.099	0.030	Between-compartment population flow rate
K_{Wd}	0.163	0.113	0.172	0.052	0.155	0.043	Carrying capacity of 'wildlife' compartment

^a $K_d, K_m, \alpha_m, \beta_{dm} = 1$

diagrams in Fig. 8 clearly show that good agreement between the prediction and situations in the field is achieved if the models allow for alternative host populations favouring *Bo. decoloratus*; of these models, the 8-parameter variant (i.e. that allowing for a shared pathogen with equal virulence) was the one most close to reality. On the other hand, variants of the model which disregarded alternative hosts did not explain the Tanzanian data satisfactorily.

The data from South Africa were combined together and used to challenge the models in an analogical way; the results are illustrated in Fig. 9. In this case, the comparison created an opposite picture: the model variants excluding any *Bo. decoloratus* support from wildlife matched the field observations markedly better than those allowing for it. The former models account well for the displacement of *Bo. decoloratus* by *Bo. microplus* on the intruder's side of the predicted inter-species boundaries as well as for *Bo. decoloratus* persistence at the localities situated close to- or behind these boundaries.

Discussion

In the last a few decades, numerical simulations have become an indispensable methodology for gaining insight into the complex behaviour of tangled ecological systems such as biotically and abiotically interacting populations of organisms (Jørgensen et al. 1995). From all tick species, population models of the one-host *Boophilus* ticks have been subject to the greatest number of applications to date, and are the ones best elaborated (e.g. Sutherst 1985, 1987; Mount et al. 1991; Teel et al. 1996; Corson et al. 2004). In this study, we opted for a more approximate model of the Lotka-Volterra type (though other choices could have been made), allowing for population dispersal and various potential interferences, to simulate co-existing populations of *Bo. decoloratus* and *Bo. microplus*. An advantage of this modelling choice lies in the simplicity of the model structure facilitating automatic calibration when there is a shortage of more conveniently obtained parameters. Although it is generally admitted that the Lotka-Volterra model is not literally correct, its behaviour is believed to be sufficiently close to the behaviour of the real competing

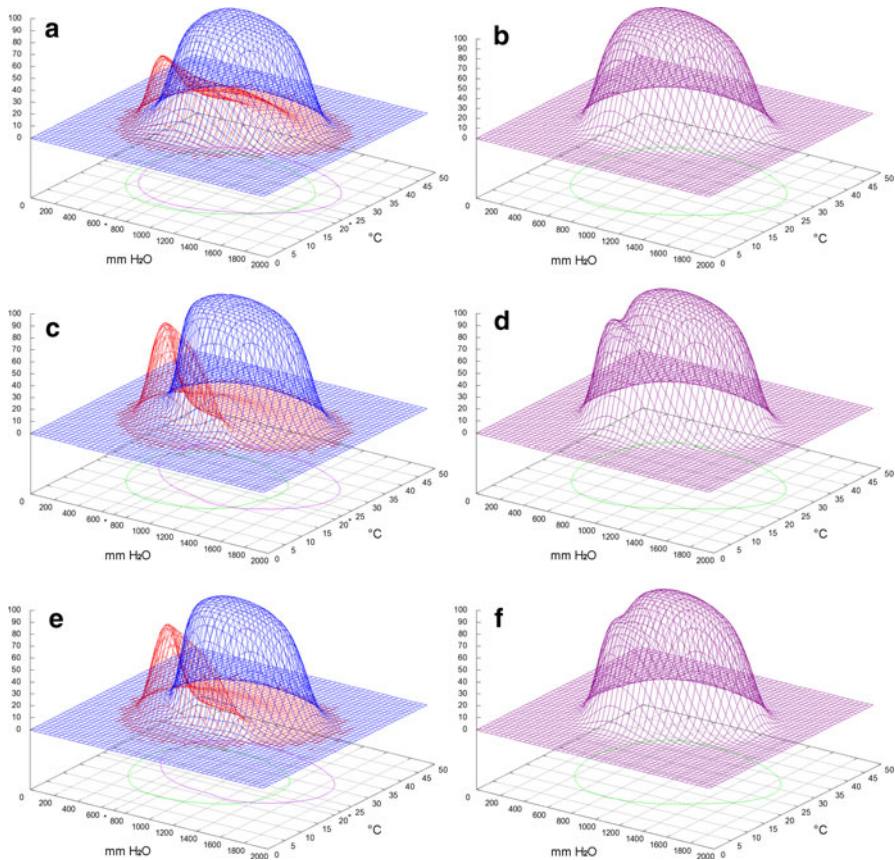


Fig. 6 Models of stable co-existing populations of *Boophilus decoloratus* and *B. microplus* on cattle in the presence of alternative *Bo. decoloratus* hosts; both populations are in equilibrium with the environmental conditions indicated, as well as with each other. The left side diagrams show *Bo. decoloratus* (red) and *Bo. microplus* (blue) abundances, the right side diagrams show the corresponding *Boophilus* spp. abundance totals; model parameters are as shown in Table 1: **a,b** 7-parameter model, **c,d** 8-parameter model, and **e,f** 9-parameter model (abundances are given in terms of percent of carrying capacity; projected ellipses encompass 99% of tick populations, and illustrate the realised niches of the species)

populations, its usefulness has been proven in multitudinous practical applications, and is endowed with a well researched theoretical background (MacArthur 1972). In view of the model's intrinsic limitations, as well as necessary simplifications and some tentative assumptions made in this study, one should look upon the obtained forecasts cautiously and consider these simulations merely as an approximate solution to the two species' parapatry problem. Nevertheless, a comparison of the results obtained with empirical observations reveals remarkably close parallels, which substantiates the chosen approach.

For example, the puzzle as to why the *Bo. decoloratus* and *Bo. microplus* populations segregate just along the ca. 22°C isotherm and 58 mm isohyet, as observed in Tanzania (Lynen et al. 2008), has been well explained by all versions of this model, regardless of whether the pathogen interaction was considered or not. It indicates that at least some characteristics of the model are robust enough. In nature, the borderline between *Bo. decoloratus* and *Bo. microplus* apparently follows an isoline of equal fitness of the two

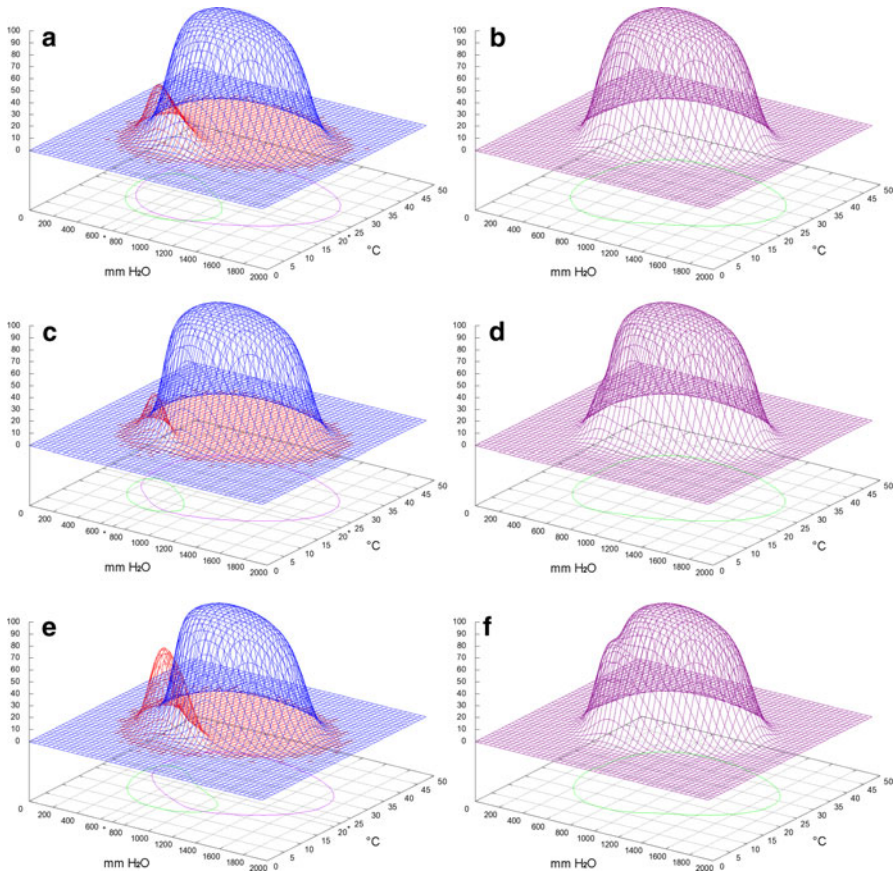
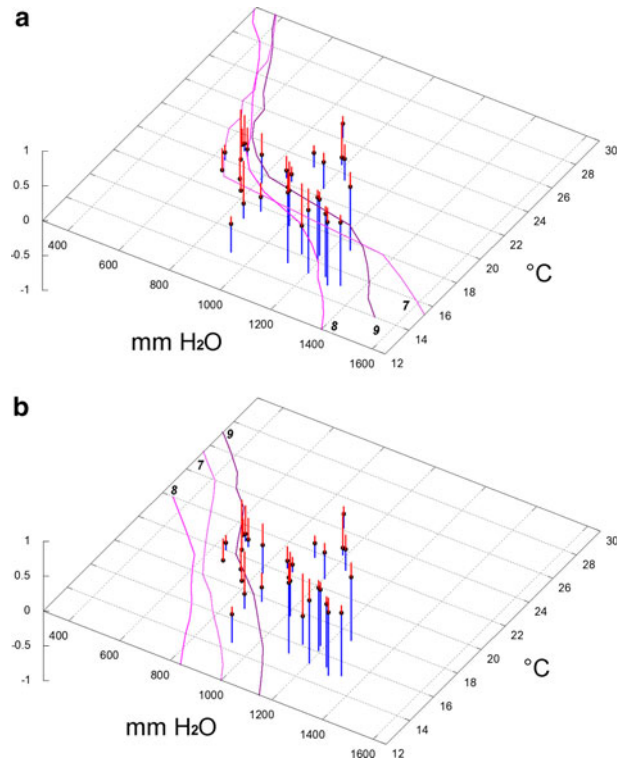


Fig. 7 Models of stable co-existing populations of *Boophilus decoloratus* and *B. microplus* on cattle in the absence of alternative *Bo. decoloratus* hosts; model characteristics are the same as those shown in Fig. 5 with the exception that non-cattle hosts of *Bo. decoloratus* were excluded; note that a lack of alternative hosts causes a substantial shrinkage of the *Bo. decoloratus*-occupied space (compared to the models shown in Fig. 5)

species across existing environmental conditions; in terms of the model, it is predetermined by the disposition of the species' fundamental niches in an environmental space, as well as the species' relative performances.

Occurrence of the population density trough in-between areas where either species dominate (Baker et al. 1989; Lynen et al. 2008) is contingent on the character of interactions operating between these species (Fig. 3). Various mechanisms explaining this phenomenon have been proposed and are thoroughly discussed in the literature (for a review see Bull 1991; Lynen et al. 2008). Contrary to what is commonly believed, sexual interference between *Bo. decoloratus* and *Bo. microplus* was not capable of giving rise to the population density trough in our simulations, and thus cannot, on its own, explain the two species' parapatry. Even if the effect of external mortality was taken into account, it was still insufficient to explain the Tanzanian field data satisfactorily (Fig. 6a, b). All simulations indicate, that in isolation interference-induced restraint on population growth is insufficient, and that a factor responsible for some mortality upon encounter of one tick

Fig. 8 Juxtaposition of the model predictions with the validation data from Tanzania; shown are predicted inter-species boundaries (defined as isolines of equal species' abundances, and numbered according to model versions), and tick survey data from regions with long co-existence of *Boophilus decoloratus* (+ abscissas) and *B. microplus* (– abscissas). Note that **a** models allowing for non-cattle hosts of *Bo. decoloratus* correspond well with the field observations, while **b** models disregarding non-cattle hosts do not correspond with the data

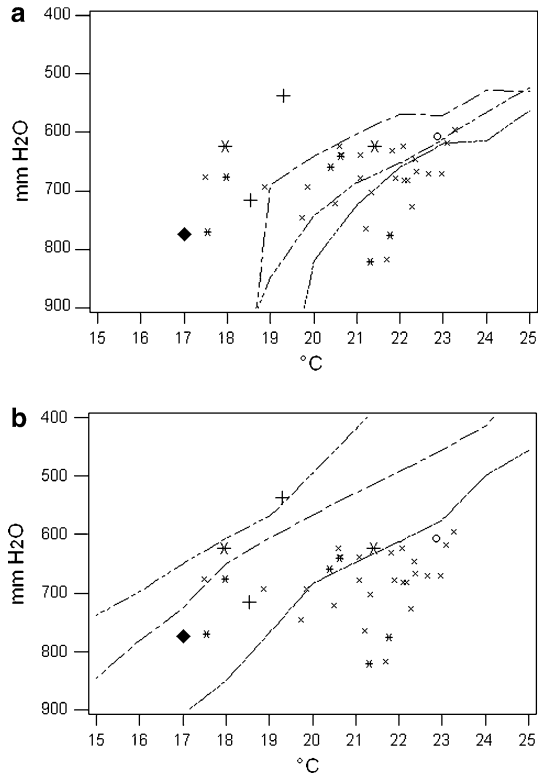


with the other is also required in the model for results to adequately approach the field data. In this study, that component is interpreted as being the interaction through a shared pathogen, however, some other factor(s) might produce the same effect. Although experimental data are lacking, several studies have shown that, for example, babesial infection may have a harmful effect on survival of *Boophilus* ticks, and that the effect depends on tick-strain adaptation (Friedhoff 1988), which might potentially be compatible with the model.

The curious situation that the cattle grazed in the transitional zone between the ticks' areas show a tendency towards mutual exclusion of infestation with the two ticks (Lynen et al. 2008) has also been satisfactorily explained by the model (Fig. 3). The simulations showed that probability forces can generate an exclusion effect by themselves, and that, most likely, no physiological mechanism is involved. Furthermore, the data from Tanzania suggested that the coincidence of the two ticks on cattle in that zone is reduced by 42% relative to that which could be expected in the case of completely independent occurrence, which corresponds to an avoidance index of ca. 0.58 (Fig. 3I). Such a reduction rate (or even greater) was achieved if the model allowed jointly for the respective factors of Lotka-Volterra competition, sexual interference, external mortality, as well as a shared pathogen; the other combinations/subsets of factors produced either zero or a less profound reduction (Fig. 3b–f), which further underscores the importance of the latter factor in the model.

The model predicts that a net rate of population growth in *Bo. decoloratus* is ca 92–94% of that in *Bo. microplus* (Table 1). Indeed, experimental studies have suggested that the reproductive potential of the latter species is higher: its development is somewhat faster, fully ingested females of *Bo. microplus* are heavier on average, and lay more eggs than do

Fig. 9 Juxtaposition of the model predictions with the validation data from South Africa; shown are predicted interspecies boundaries (see Fig. 7), the one locality in Eastern Cape (diamond) where *Boophilus decoloratus* and *B. microplus* co-exist, and the localities in Limpopo Province where either *Bo. microplus* (crosses) or *Bo. decoloratus* (pluses) occurred singly, or where both species co-existed (asterisks) or were absent (circle), while large symbols indicate that *Bo. decoloratus* managed to withstand the competition, and small symbols mean that the tick had been replaced by *Bo. microplus* during the course of the study. Note that, in contrast with Fig. 7, **a** models allowing for non-cattle hosts of *Bo. decoloratus* fail to explain the data satisfactorily, while **b** models excluding them correspond quite well with the observations



Bo. decoloratus females (Arthur and Londt 1973; Londt and Arthur 1975). Similarly, the model correctly predicts an asymmetry in the interspecific competition between the two ticks. While a *Bo. microplus* individual is rated equivalent to a *Bo. decoloratus* individual in its effect on the latter species (i.e. while β_{dm} equals unity), in the opposite direction, a *Bo. decoloratus* individual represents only ca 50 or 70% of a *Bo. microplus* individual (i.e. β_{md} estimates at ca 0.5 or 0.7), depending on whether the common pathogen interaction is allowed for or not, respectively (Table 1). Notably, experimental evidence showed that *Bo. microplus* enhances the cattle's resistance to *Bo. decoloratus* more intensely than *Bo. decoloratus* does in the other direction (Norval and Short 1984).

The frequency of abortive interspecific mating predicted by the model, is remarkably close to experimental observations, showing that ca 10% of females of either species lay sterile eggs when the species co-infest cattle (Norval and Sutherst 1986). Our simulations predict the sterility rates of 11.9 ± 2.3 , 13 ± 2.4 , and $21 \pm 9.8\%$ for the 9, 8, and 7-parameter versions of the model, respectively (Table 1); thus, the cross-species infection-allowing model versions are once more closer to reality.

Eventually, the simulations indicate that even a minor subpopulation of *Bo. decoloratus*, protected from competition with *Bo. microplus*, e.g. by being perpetuated in the wild on alternative hosts, may substantially influence the behaviour of the modelled system. The carrying capacity of the 'wildlife' compartment was estimated to vary about 16% of that for cattle, and the exchange rate to range around 10%, consistently in all model versions (Table 1). Such estimates seems realistic for at least some localities—considering the infestation rates of wild ungulates, their abundance, resistance to tick feeding and limited

contact with browsing cattle herds etc. (Mason and Norval 1980; Horak et al. 1983, 1992, 2003). These conditions obviously may vary from locality to locality and could thus significantly influence the distribution of the two ticks in nature (Figs. 8, 9). Overall, these simulations indicate that a substantial reduction of wildlife habitats and consequently of *Bo. decoloratus* refugia, may accelerate the replacement of *Bo. decoloratus* with *Bo. microplus* much faster than climatic changes might do. Further studies will be needed to more clearly understand the co-existence of these important pests in nature.

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