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G. GILIOLI, J. BAUMGÄRTNER

Parameter estimation for an eco-epidemiological model of Brown Ear tick (*Rhipicephalus appendiculatus*, Acari: Ixodidae) transmitted East Coast Fever in African livestock

Abstract - An eco-epidemiological model of the dynamics of East Coast Fever (ECF) in East Africa caused by the protozoan parasite *Theileria parva* and vectored by the Brown Ear Tick *Rhipicephalus appendiculatus* Neumann (Acarina: Ixodidae) has been developed. In the compartment model, ticks are present either on-host or off-host and, in both cases, differ in their capacity to receive and transmit the disease agent. As a result, the ticks are assigned to four compartments, while cattle are assigned to compartments of a) susceptible, b) infected and infectious as well as c) recovered animals with immunity to the disease but the capacity to infect to ticks. This paper deals with parameter estimation of the eco-epidemiological model.

For ticks, we estimated fecundity and mortality rates for populations with time invariant age structure, attachment and detachment rates. For cattle of primarily European breeds, we estimated fecundity and mortality rates in absence of disease agent. The attack rate of ticks on cattle density was represented by Monod's functional response that requires the estimation of the semi-saturation term. The transmission rate of *T. parva* from cattle to ticks, the rate of transmission of the disease from ticks to cattle, the recovery rate of infected cattle, and the additional cattle mortality were also estimated on the basis of published literature information.

A numerical simulation is carried out to illustrate the dynamics resulting from the estimated parameters. The model satisfactorily represents the ECF epidemiology, adequately takes into account important components of more realistic and complex models, despite of model development on very restrictive assumptions, and serves as an entry point for model extensions. This can efficiently be done in an adaptive management framework.

Riassunto - *Stima dei parametri di un modello eco-epidemiologico della teileriosi bovina africana trasmessa dalla zecca* Rhipicephalus appendiculatus (*Acari: Ixodidae*)

Nel lavoro si presenta un modello eco-epidemiologico per la dinamica della teileriosi bovina o East Cost Fever (ECF) nell'Africa Orientale dovuta al protozoo *Theileria parva* trasmesso dalla zecca ixodide *Rhipicephalus appendiculatus* Neumann. Il modello, di tipo compartimentale, considera la popolazione di zecche come suddivisa in 4 componenti a seconda del fatto che le zecche siano o no attaccate all'ospite e che

sia in grado di ricevere o trasmettere l'agente eziologico della malattia. Il bestiame, a sua volta, è assegnato a 3 compartimenti: suscettibili, infetti e infettivi, infetti e asintomatici per immunità nei confronti della malattia ma comunque in grado di trasmettere alle zecche l'agente infettivo. Obiettivo di questo lavoro è la stima dei parametri del modello eco-epidemiologico.
Per le zecche e il bestiame sono stati innanzitutto stimati parametri biodemografici sulla base di opportune ipotesi sulla struttura di popolazione. Per le zecche si sono stimati i tassi di fecondità e di mortalità, per il bestiame, considerato come costituito da razze europee, si sono stimati il tasso di fecondità, di mortalità naturale, incluso il prelievo. I tassi di attacco e distacco dall'ospite delle zecche sono stati modellati tramite la risposta funzionale di Monod che richiede la stima del parametro di semi-saturazione. Sono inoltre stati stimati i tassi di trasmissione di *T. parva* dal bestiame alle zecche e della malattia dalle zecche al bestiame, il tasso di guarigione e di mortalità addizionale del bestiame dovuta alla malattia. Tutti i tassi sono stati stimati a partire da informazione disponibile in letteratura.
Simulazioni numeriche sono state condotte per illustrare la dinamica del sistema epidemiologico che risulta dai parametri stimati. Il modello è in grado di rappresentare in modo soddisfacente aspetti della epidemiologia dell'ECF e di considerare aspetti della dinamica del sistema di solito rappresentata con strumenti computazionali più complessi. Questo risultato è stato raggiunto nonostante le assunzioni restrittive su cui si basa la stima dei parametri. Il modello rappresenta un punto di avvio per lo sviluppo di versioni più complesse e può essere considerato come un utile strumento a supporto delle strategie di gestione adattativa delle zecche e della parassitosi.

Key words. *Theileria parva*, *Rhipicephalus appendiculatus*, eco-epidemiology, disease transmission model, parameter estimation, numerical simulation.

INTRODUCTION

Hard ticks (Ixodidae) affect the health of livestock by feeding and by transmitting parasitic diseases. Tick-borne diseases of cattle have great economic impact especially in Sub-Saharan Africa countries, where East Coast fever (ECF) or theileriosis, caused by the protozoan *Theileria parva* and mainly transmitted by the ixodid tick *Rhipicephalus appendiculatus* is among the most important ones (Kettle, 1995). In general, tick-borne infections of cattle in Africa show great complexity because of the many different tick species interacting with many different host species and a variety of infectious agents being transmitted variously among them (Young *et al.*, 1988). *T. parva* is a parasite of Cape buffalo (*Syncerus caffer*) and infective to cattle, water buffalo (*Bubalus bubalis*) and waterbuck (*Kobus ellipsiprymnus*) (Norval *et al.*, 1992; Kettle, 1995). *T. parva* is lethal to European (*Bos taurus*) and Indian (*Bos indicus*) cattle as well as to water buffalo (Kettle, 1995). The vector *R. appendiculatus* is discontinuously distributed in fifteen East and South African countries, and the occurrence is influenced by several factors, the most important of which are climate, vegetation and host availability (Norval *et al.*, 1992). Knowledge on climatic requirements enabled Sutherst and Maywald (1985) to assess, via the CLIMEX model, the suitability of any particular area. *T. parva* has a wide distribution in eastern, central and southern Africa (Norval *et al.*, 1992).

According to Medley *et al.* (1993), the economic implications of ECF are 3-fold. Firstly, the ticks themselves reduce the growth rate and productivity of improved cattle primarily due to blood uptake, but responses of indigenous animals due to ticks are normally minimal (Mukhebi *et al.,* 1989, 1992). Secondly, the presence of ticks and tick-borne diseases, particularly ECF and heartwater, make upgrading of cattle from resistant but relatively unproductive zebus to more productive zebu/taurine crosses and exotic species currently impossible without intensive acaricide application (Young *et al.*, 1988). Thirdly, infections by some pathogens such as *T. parva*, although not causing appreciable mortality and morbidity, reduce the growth rate and productivity of infected animals (Moll *et al.*, 1986). Current estimates show that East Coast fever for example, kills 20 cows every 10 minutes and causes $200 million in annual losses in some of the poorest countries in Africa (International Livestock Research Institute ILRI, Nairobi, see www.ILRI.com for further information).

The life cycle of Ixodidae ticks is divided into egg, larval, nymphal and adult life stages. Specific life cycles differ by the number of stages in which individuals attach to a host (Kettle, 1995). *R. appendiculatus* is a three host tick, i.e. larvae, nymphs and adults each attach to a host, and within a wide host range, adults parasitize medium to large size ungulates, while the immature stages feed on most ungulate species and a variety of other mammals, including carnivores and lagomorphs (Norval *et al.*, 1992). There are several modes of disease transmission for tick-borne diseases. However, all of the *Theileria* species associated with *R. appendiculatus* are exclusively transmitted transstadially (Medley *et al.*, 1993) and hence, only the nymph and adult are able to transmit the pathogen. In order to become infected and infectious, the tick must feed on an infected and infectious *B. taurus* or *B. indicus* hosts and moult.

The development and use of models are considered as indispensable for study and management of eco-epidemiological systems (Smith *et al.*, 2005). The transmission of tick-borne diseases has been the subject of several epidemiological studies (e.g. Mwambi, 2002; Rosà *et al.*, 2003). Gilioli *et al.* (2009) reviewed these studies and developed an eco-epidemiological model of the dynamics of East Coast Fever (ECF) caused by the protozoan parasite *T. parva* and vectored by the Brown Ear Tick *R. appendiculatus* in East Africa. Eco-epidemiological models are developed for dealing with the biological and social complexities in disease transmission (Smith *et al.* 2005; March and Susser, 2006). In their paper, Gilioli *et al.* (2009) describe the ecological assumptions, the modeling strategy, the model devevelopment and use. Briefly, ticks are present in either on-host or off-host categories both of which differ in their capacity to receive and transmit the disease. Consequently, the ticks are assigned to four compartments. Cattle abundance are assigned to three compartments of susceptible, infected and infectious as well as recovered animals with immunity to the disease but the capacity to infect ticks. Moreover, the paper by Gilioli *et al.* (2009) dealt with stability analyses to identify critical aspects of the dynamics for the purpose of developing control strategies: (*i*) tick control in areas where the disease is absent, (*ii*) threshold-based tick and disease control, and (*iii*) search for conditions permitting the establishment enzootic stability of the ECF/tick/cattle system. Enzootic stability refers to an epidemiological state wherein the clinical disease is scarce despite high infection rates (Norval *et al.*, 1992; Torr *et al.*, 2002).

The model was also used to identify critical epidemiological issues for further studies and to set the basis for developing more realistic models for field implementation in an Adaptive Management (AM) context. AM is a systematic approach to improving the management process and accommodating change by learning from the outcomes of a set of management tactics, strategies and policies as well as governance (Holling, 1978; Comiskey *et al.*, 1999; Jiggins and Röling, 2000; Baumgärtner *et al.*, 2003; Gilioli and Baumgärtner, 2007). The adaptive management framework is appropriate for complementary studies and the development of more realistic eco-epidemiological models. Peterson *et al.* (1997) consider models as useful if they are used within some sort of 'AM' framework that focuses on using a modelling process, rather than a specific model, to learn how a system works. In our work, models are particularly useful to continuously assess the state of subsystems including disease transmission by vectors and biophysical fluxes in ecosystems and evaluate the dynamics in relation to previous and planned management operations (Gilioli and Baumgärtner, 2007).

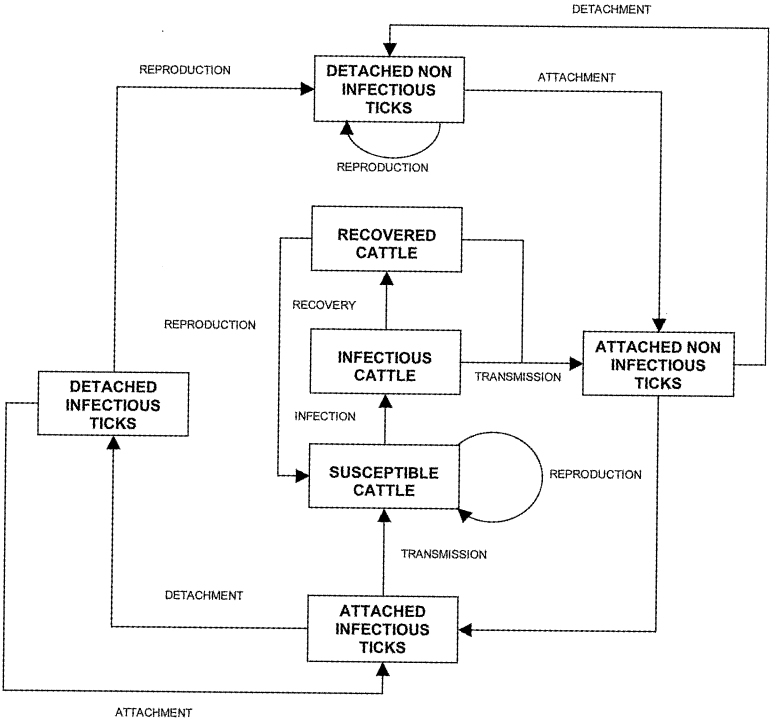

Figure 1 - Graphical representation of the compartments and processes considered in the eco-epidemiological model of East Coast Fever in African livestock (eqn. 1).

The purpose of this paper is to develop procedures for estimating the parameters and test their consistency for use in the eco-epidemiological model of Gilioli *et al.* (2009).

MATERIAL AND METHODS

Model formulation

Assumptions. The model assumes ecological conditions permitting continuous tick development and disease transmission (Dolan, 1999; Cumming, 2002) such as those found in East Africa. A stable tick age-distribution is assumed and has been confirmed by field observations in Kenya during the second half of the year (Punyua *et al.*, 1986). This assumption allows disregarding short-term changes in tick age structure and the combination of tick eggs, larvae, nymphs and adults in one compartment. Similarly, a time-invariant age distribution is assumed for cattle given good herd management practices and the absence of disturbances such as droughts or severe disease outbreaks. These assumptions allow the use of a lumped-parameter model to describe the dynamics of ticks and cattle. Other assumptions are discussed in Gilioli *et al.* (2009) and detailed in parameter estimation sections of this paper. Figure 1 depicts the relevant ecological and epidemiological processes.

Model description. Equations 1a-g describe the change in tick and cattle densities [individuals per hectare^{-1}] in the different compartments as defined above.

$$\dot{v}_0 = \varphi W + \delta w_0 - a\frac{\alpha H}{\lambda + H}v_0 - \mu v_0 \qquad \text{detached non infectious ticks} \tag*{[1a]}$$

$$\dot{v}_1 = \delta w_1 - a\frac{\alpha H}{\lambda + H}v_1 - \mu v_1 \qquad \text{detached infectious ticks} \tag*{[1b]}$$

$$\dot{w}_0 = a\frac{\alpha H}{\lambda + H}v_0 - \delta w_0 - \eta w_0 - \beta(h_1 + c\varepsilon h_2)w_0 \qquad \text{attached non infectious ticks} \tag*{[1c]}$$

$$\dot{w}_1 = a\frac{\alpha H}{\lambda + H}v_1 + \beta(h_1 + c\varepsilon h_2)w_0 - \delta w_1 - \eta w_1 \qquad \text{attached infectious ticks} \tag*{[1d]}$$

$$\dot{h}_0 = \gamma(h_0 + h_2) - \sigma h_0 w_1 - \omega h_0 \qquad \text{susceptible cattle} \tag*{[1e]}$$

$$\dot{h}_1 = \sigma h_0 w_1 - b\vartheta h_1 - \omega\rho h_1 \qquad \text{infected and infectious cattle} \tag*{[1f]}$$

$$\dot{h}_2 = b\vartheta h_1 - \omega h_2 \qquad \text{recovered cattle} \tag*{[1g]}$$

with $V = v_0 + v_1$, $W = w_0 + w_1$, $H = h_0 + h_1 + h_2$. The model parameters and per capita rates are defined as follows

φ = Fecundity rate of engorged ticks [time^{-1}];
α = Tick attachment rate [time^{-1}];
δ = Tick detachment rate [time^{-1}];

μ = Mortality rate of detached ticks [time^{-1}];
η = Mortality rate of attached ticks [time^{-1}];
λ = Semi-saturation term in the functional response [individuals x land area^{-1}];
β = Transmission rate of infection from infected and infectious cattle to ticks [time^{-1}];
σ = Transmission rate of infection from infected and infectious ticks to cattle [time^{-1}];
ε = Proportion of infectious recovered cattle;
γ = Fecundity rate of cattle [time^{-1}];
ω = Natural mortality rate of cattle [time^{-1}];
ρ = Additional mortality coefficient for sick animals that depends on the level of host resistance;
ϑ = Recovery rate of infected cattle [time^{-1}].

Coefficients define the differences in resistance among cattle relative to highly susceptible European breeds
a = Coefficient for cattle resistance to ticks ($a > 0$) as measured by attachment efficiency (i.e. resistance increases as $a \rightarrow 0$);
b = Coefficient for cattle resistance to the parasite ($b > 0$) that with increasing b slows the development of clinical disease and the transition rate to the recovered host compartment;
c = Coefficient to characterize the ability to transmit disease by recovered but still infectious cattle ($0 < c \leq 1$) with the transmission rate increasing as $c \rightarrow 1$.

Functional response model component. In equations [1c-d], tick attachment is represented by the Monod functional response model (DeAngelis, 1992), which was selected because of its simplicity in comparison to other models, because it has no restrictive assumptions, and because both the tick behavioral parameter α and the semi-saturation term λ can easily be estimated. Moreover, the Monod model has been widely used in ecology including epidemiology (Anderson and May, 1978). We are aware of the critical importance of functional model selection (Wang and Gutierrez, 1980), but argue that the simplicity and generality of the Monod model and its contribution to the intelligibility of the role of the functional response in the behavior of the system are sufficient arguments for considering this function at this stage of model development. Moreover, Monod's functional response enables us to make efficient use of time series data for parameter estimation (Gilioli *et al.*, 2008) which is important in attempts of continually improving the modeling tools for obtaining better insight into the dynamics and more reliable decision-support (Gilioli and Baumgärtner, 2007).

Cattle resistance model component. Resistance of cattle has two forms that depend on livestock breed and type (de Castro, 1997): *i*) resistance that modifies the tick attachment rate modeled by the coefficient a, and *ii*) the capacity of the cattle to display an immune reaction modeled by the coefficient b that affects the rate of recovery ϑ but not the transmission coefficient σ. Another form of resistance affects pathogen transmission from recovered but infectious cattle to ticks modeled by c that affects ability of to pass the pathogen. Note that when $a = b = 1$ (the absent resistance in cattle) and $c = 0$ (recovered cattle do not transmit the parasite), the model simplifies considerably, and stability analysis of the system can easily be carried out (Gilioli *et al.*, 2009).

2.2. *Parameter estimation*

Origin of the data. The procedure of parameter estimation relies on information reported in the literature. As detailed below, the tick parameters have mainly been derived from the work of Branagan (1973), Randolph and Rogers (1997), Randolph (1997, 2004). The lumped parameters for the disease transmission and evolution have been obtained from Medley *et al.* (1993) and O'Callaghan *et al.* (1998), while Reynolds *et al.* (1996) and Getachew *et al.* (2006) provide the important demographic parameters for cattle in Kenya and Ethiopia, respectively.

Demographic requirements. The approach requires lumped parameter estimates on a per capita basis, hence the definition of biodemographic and behavioural traits of an *average individual* is necessary. This implies the simplification of a system in which populations are structured according to biological stage and functional state. Parameter estimation procedures require the following conditions to be satisfied: *i*) sufficiently large number of individuals in a population, *ii*) asynchronous development (overlapping generations), *iii*) stable stage and state-structures. Most of the parameter are expressed in per day units, the probability per time unit for demographic, behavioral or epidemiological events to occur in a given stage or state are calculated. Considering the complete population, the probability for an average individual also depends on the stage/state structure (i.e. the proportion of individuals in each stage or state). Under the assumption of a stable stage/state structure, the per capita mean rate at which an event occurs is a weighted average of stage/state-specific rates weighted by the proportion of individuals in the different stages/states.

RESULTS

Table 1 lists the structure of *R. appendiculatus* populations, while Table 2 reports the estimates for all parameters used in system [1a-g] with the exception of the resistance parameters *a, b, c.* At this stage in model development, the information in the published literature was sufficient to parameterize the model.

Functional state durations. Let *E, L, N, A* denote both the biological stage and the corresponding density (individuals per unit area) of tick eggs, larvae, nymphs, and adults respectively. The tick life stages are subdivided into 11 functional states according to the epidemiological status (infected and infectious, not infected) and the occupied habitat (off-host, on host). The definitions of these states are reported in Table 1. The duration of each state depends on both environmental conditions and the interactions between the ticks and the hosts which influence the questing phase of ticks. We disregard diapause,

Table 1 - The structure of *Rhipicephalus appendiculatus* populations with state variables (State), symbols used in text (Symbol) and the definition of biodemographic and behavioural traits for an average individual (duration [days] and the probability $p(i)$ for a generic individual to be in the *i-th* state ($i = 1, 2, 3, \ldots, 11$).

State	**Symbol**	**State**		**Duration [days]**		**$p(i)$x100**
		from $i =$	**to** $i =$	**state** $D(i)$	**sum**	
1 = Eggs	E	0	1	30.3	30,3	65,56
2 = Questing larvae	L_q	1	2	30.0	60,3	22,58
3 = Feeding larvae	L_f	2	3	4.0	64,3	1,59
4 = Moulting larvae	L_m	3	4	11.9	76,2	3,60
5 = Questing nymphs	N_q	4	5	20.0	96,2	3,51
6 = Feeding nymphs	N_f	5	6	5.5	101,7	0,61
7 = Moulting nymphs	N_m	6	7	17.3	119,0	1,30
8 = Questing adults	A_q	7	8	10.0	129,0	0,46
9 = Feeding adults	A_f	8	9	7.5	136,5	0,25
10 = Post-feeding adults	A_p	9	10	6.2	142,7	0,16
11 = Ovipositing adults	A_o	10	11	24	166,7	0,39

Table 2 - Parameters, their definition, the values estimated and the source of the information for the model on disease transmission in the *Rhipicephalus appendiculatus* tick - East Cost Fever - cattle system.

	Definition	**Estimate**	**Source of Information**
φ	Tick fecundity rate	3.9691 day^{-1}	Randolph and Rogers, 1997
α	Tick attachment rate	0.014033 day^{-1}	Branagan (1973), Randolph and Rogers, 1997
δ	Tick detachment rate	0.06487 day^{-1}	Assumption (Randolph and Rogers, 1997)
μ	Mortality rate of detached ticks	0.035 day^{-1}	Randolph and Rogers, 1997
η	Mortality rate of attached ticks	0.035 day^{-1}	Randolph and Rogers, 1997
λ	Semisaturation term in the tick functional response	10 cattle ha^{-1}	Assumption
β	Transmission rate of infection from hosts to ticks	0.08271 ha day^{-1}	Medley *et al.*, 1993; O'Callaghan *et al.*, 1998
ε	Transmission efficiency from recovered hosts to ticks	0.009035	O'Callaghan *et al.*, 1998
σ	Transmission rate of infection from ticks to hosts	0.005591 day^{-1}	O'Callaghan *et al.*, 1998
γ	Reproductive rate of susceptible and recovered hosts	0.0009772 day^{-1}	Bebe *et al.*, 2003
ω	Natural mortality rate of hosts	0.000788 day^{-1}	Reynolds *et al.*, 1996
ρ	Additional mortality coefficient due disease	1.8869	Gitau *et al.*, 1999
ϑ	Recovery rate of hosts	0.004087 day^{-1}	Gitau *et al.*, 1999

i.e. the tick's adaptation mechanisms to seasonally variable climates that can produce a delay in the stage duration (Randolph, 1997). For a temperature of 25°C, the durations are obtained from Kettle (1995), Branagan (1973) and Mr. M. Kimondo (International Centre of Insect Physiology and Ecology, Nairobi, personal communication) and reported in Table 1.

Mortality rate of detached (μ) *and attached* (η) *ticks*. The mortality of detached ticks is subdivided into two components, i.e. the mortality during resting and the mortality during questing. We obtain from Table 1 in Randolph and Rogers (1997) the stage-specific finite mortalities per day $\zeta_E^r = 0.02$, $\zeta_L^r = 0.01$, $\zeta_N^r = 0.00475$, $\zeta_N^r = 0.0175$ for egg and resting larva, nymph and adult stages, respectively. Table 1 in Randolph and Rogers (1997) also provides estimates of the stage-specific finite mortalities $\zeta_L^q = 0.06$, $\zeta_N^q = 0.03$, $\zeta_A^q = 0.01125$, for ticks questing as larvae, nymphs and adults, respectively. These values are in close agreement with the mortality reported by Pegram and Banda (1990). Mortality due to drought is disregarded. We equal the mortality of all the functional states apart from questing to the mortality of resting states. From data on finite mortality rate we calculate the per-capita daily mortality

$$\mu_E^r = -\ln\left(\zeta_E^r\right) = 0.0202 \qquad [\text{day}^{-1}];$$
$$\mu_L^r = -\ln\left(\zeta_L^r\right) = 0.0101 \qquad [\text{day}^{-1}];$$
$$\mu_L^q = -\ln\left(\zeta_L^q\right) = 0.0619 \qquad [\text{day}^{-1}];$$
$$\mu_N^r = -\ln\left(\zeta_N^r\right) = 0.00476 \qquad [\text{day}^{-1}];$$
$$\mu_N^q = -\ln\left(\zeta_N^q\right) = 0.0619 \qquad [\text{day}^{-1}];$$
$$\mu_A^r = -\ln\left(\zeta_A^r\right) = 0.0177 \qquad [\text{day}^{-1}];$$
$$\mu_A^q = -\ln\left(\zeta_A^q\right) = 0.0113 \qquad [\text{day}^{-1}].$$

Under the assumption of a relative abundance of ticks in each functional state of each biological stage proportional to the state duration, and considering the eggs as part of the resting larvae, the stage-specific mortalities for larvae, nymphs and adults are

$$\mu_L = \left\{\mu_E^r D(E) + \mu_L^r\left[D(L_f) + D(L_m)\right] + \mu_L^q D(L_q)\right\} / \left[D(E) + D(L_f) + D(L_m) + D(L_q)\right] = 0.0358 \quad [\text{day}^{-1}];$$
$$\mu_N = \left\{\mu_N^r\left[D(N_f) + D(N_m)\right] + \mu_L^q D(N_q)\right\} / \left[D(N_f) + D(N_m) + D(N_q)\right] = 0.0216 \quad [\text{day}^{-1}];$$
$$\mu_A = \left\{\mu_A^r\left[D(A_f) + D(A_p) + D(A_o)\right] + \mu_A^q D(A_q)\right\} / \left[D(A_f) + D(A_p) + D(A_o) + D(A_q)\right] = 0.0163 \quad [\text{day}^{-1}].$$

The population stage structure (*E+L*):*N*:*A* can be considered equal to 100:5:1, these values are close to the average population stage-structure of *R. appendiculatus* as reported by Punyua *et al.* (1986) and Randolph and Rogers (1997).

The mean tick mortality rate is finally calculated on the basis of weighted contribution of each stage

$$\mu = \frac{1}{106}\mu_L(100) + \mu_N(5) + \mu_A(1) = 0.035 \qquad [\text{day}^{-1}]. \qquad [2]$$

Tick population state structure. The assumption of a stable-state structure, the survivorship function $f(\mu, t) = \exp(-\mu t)$ with the constant mortality μ estimated in eqn. [2], and the durations in Table 1 allow the calculation of the probability $p(i)$ for a generic individual to be in the *i-th* state ($i = 1, 2, 3, \ldots, 11$)

$$p(i) = \frac{\int_{t=0}^{t=i} f(\mu,t) - \int_{t=0}^{t=i-1} f(\mu,t)}{\int_{t=0}^{t=11} f(\mu,t)} \quad \text{with} \quad \int f(\mu,t) = \int \exp(-\mu x)dx = -\frac{\exp(-\mu x)}{\mu} \qquad [3]$$

where t_0 is the beginning of the egg stage, t_i is the time interval between t_0 and the end of the state i, t_{11} refers to the end of the adult ovipositing state A_0. From the probability $p(i)$ the proportions of eggs, larvae, nymphs and adults are calculated. The estimates for eggs, larvae and nymphs are in close agreement with Randolph and Rogers (1997) data, while a higher proportion of adults are obtained. Note that in the estimation procedure the egg stage is included into the larval stage.

Tick fecundity rate (φ). Randolph and Rogers (1997) reported a total fecundity (Φ) of 3000 eggs laid by a female during the lifespan, while other authors refers to a Φ between 2000 and 5000 (Sutherst, 1985; Short *et al.*, 1989). These papers and others show a high variability in the fecundity. By taking into account a total fecundity of $\Phi = 3500$ and a sex ratio of $\zeta = 0.5$ (Randolph, 1997), we obtain the average per capita fecundity rate for the tick population

$$\varphi = \frac{\Phi}{D(A_0)} r(A_0) r(W) \xi = 3.9691 \quad [\mathrm{day}^{-1}]. \qquad [4]$$

where the duration of the ovipositing adult stage $D(A_0)$, the proportion of ovipositing adults $r(A_0)$ and of feeding ticks (on-host) $r(W)$ with respect to the total population are obtained from Table 1.

Since oviposition depends on a blood meal, only engorged individuals represented by W in [1a] are reproducing.

Tick attachment rate (α). In the case under study, attachment occurs once in each mobile stage after a period of questing. Estimates of the attachment rates for larvae, nymphs and adults are equal to the per capita daily probability to leave the questing state. For an average individual in the population the tick attachment rate is

$$\alpha = \frac{1}{D(L_q)} r(L_q) + \frac{1}{D(N_q)} r(N_q) + \frac{1}{D(A_q)} r(A_q) = 0.014033 \quad [\mathrm{day}^{-1}] \qquad [5]$$

where $r(L_q)$, $r(N_q)$, and $r(A_q)$ are the proportions of questing larvae, nymphs and adults in the total population.

Tick detachment rate (δ). Detachment occurs once in each mobile stage at the end of feeding period. Estimates of attachment rates for larvae, nymphs and adults have been set equal to the per capita daily probability to leave the feeding state (Table 2). For an average individual in the population the tick detachment rate is

$$\delta = \frac{1}{D(L_f)} r(L_f) + \frac{1}{D(N_f)} r(N_f) + \frac{1}{D(A_f)} r(A_f) = 0.06487 \quad [\mathrm{day}^{-1}] \qquad [6]$$

where $r(L_f)$, $r(N_f)$, and $r(A_f)$ are the proportions of feeding larvae, nymphs and adults in the total population.

Semi-saturation term in the tick functional response (λ). The semi-saturation term in the functional response represents the tick density at which the attachment rate equals 50% of the maximum. Tentatively, the semi-saturation density has been set to $\lambda = 10$. This value is supported by observations made in the literature. Accordingly, the attachment probability $\alpha = 0{,}014033$ in eqn. [5], a plausible mean cattle density of 1 ha^{-1} and a life span of 166 days result to an attachment success of 21%. This value is in agreement with the values reported by Byrom and Gettinby (1992).

Transmission rate of infection from hosts to ticks (β). Medley *et al.* (1993) give an estimate of the probability of disease transmission from cattle hosts to ticks dependent on the status of the host. For primary/acute infected animals (that both die or survive) the transmission rate is $\beta_i = 0.1151$ per day. For recovered and carriers animals, $\beta_r = 0.0023$ per day. Given the modality in which the transmission of infection is modelled in the equations [1c] and [1d], we consider β as transmission rate of infection from primary/acute infected animals to ticks. Since only larvae and nymphs are susceptible to receive the pathogen from the cattle host, we follow O'Callaghan *et al.* (1998), working on the epidemiology of heartwater (*Cowdria ruminantium* infection), and assume that the rate of larval infection is 0.625 times the rate nymphal infection. For the transmission of the *T. parva* infection, we tentatively use a coefficient of 0.700 and calculate the transmission rate of infection from hosts to ticks

$$= \frac{\beta_i \times 0.700 \times L + \beta_i \times N}{L + N + A} = 0.08271 \qquad [\mathrm{day}^{-1}]. \qquad [7]$$

Following O'Callaghan *et al.* (1998), we consider the probability of a larval infection during feeding on carriers equal to 1/10 to the probability of nymphal infection. This enables us to calculate the average rate of transmission $\varepsilon\beta$ for larvae and nymphs feeding on recovered and carriers as

$$\sigma_N = \frac{h_N}{\phi\, D(N_f)}, \quad \sigma_A = \frac{h_A}{\phi\, D(A_f)} \qquad [8]$$

from which the proportion of infectious recovered cattle $\varepsilon = 0.009035$ can be derived.

Transmission rate of infection from ticks to hosts (σ). O'Callaghan *et al.* (1998) obtained the transmission rates for the *Amblyomma hebraeum* Koch heartwater system. We relied on their work rather than on Medley *et al.* (1993) because Medley *et al.* (1993) do not provide any data on tick age structure. Nevertheless, the per capita rate of infection for the *R. appendiculatus* / ECF system given in eqn. [9] by Medley *et al.* (1993) is similar to the one obtained in our work. O'Callaghan *et al.* (1998) provide the probabilities $h_N = 0.8$ and $h_A = 0.9$ that an infectious nymph and an infectious adult transmit the *Cowdria ruminantium* infection to the cattle host. Here, the stage-specific rates of *T. parva* infection transmission are calculated on the basis of the work by Ochanda *et al.* (1996) who observed that the sporogony occurs during 2-3 days in nymphs, 3-4 days in females and in irregular periods in males. Sporogony occurs only during the first period of feeding times. To obtain the estimate for the transmission rate of infection from ticks to hosts σ, previously used the MS thesis of Vesperoni (2005), ϕ is set to 0.6156. Accordingly, the stage-specific transmission rates of infection from nymph and adult ticks to hosts are

$$\sigma_N = \frac{h_N}{\phi\, D(N_f)},\quad \sigma_A = \frac{h_A}{\phi\, D(A_f)}$$

allowing the calculation of the average daily per capita transmission rate from ticks to hosts as

$$\sigma = \frac{\sigma_N N + \sigma_A A}{L + N + A} = 0.005591\ [\text{day}^{-1}]. \qquad [9]$$

Host mortality in absence of disease (ω). O'Callaghan *et al.* (1998) reported a natural mortality rate Ω of 0.25 year^{-1} for domestic livestock in commercial beef enterprises in Zimbabwe. The natural mortality refers to all other causes other than heartwater and thus includes also culling. From this we obtain the daily mortality rate ω as

$$\omega = -\frac{1}{365}\ln(1-\Omega) = 0.000788 \qquad [\text{day}^{-1}]. \qquad [10]$$

Noteworthy, the natural mortality reported by O'Callaghan *et al.* (1998) is similar to the culling rate reported for example for European cattle kept for beef production in Nebraska (Azzam *et al.*, 1990) and for Boran breeds in Africa (Trail *et al.*, 1986). The estimated mortality rate is in close agreement with the data reported by Bebe *et al.* (2003).

Fecundity rate of susceptible and recovered hosts (γ). From Bebe *et al.* (2003) we obtain an estimate of the age of first calving of 2.8 years which correspond to $t_C = 1022$ days, that is close to the value of 900 days reported by Reynolds *et al.* (1996). Babe *et al.* (2003) also provide an estimate of the parity of cows kept in free-grazing farms $\gamma_p = 2.6$ and a mean reproductive period of $t_R = 1357$ days, and a proportion of cows in a herd ξ_h of 0.51. Thus, the fecundity rate per day for uninfected cattle is

$$\gamma = \xi_h \frac{\gamma_p}{t_R} = 0.0009772 \qquad [\mathrm{day}^{-1}]. \tag{11}$$

In eqn. [1e] is assumed that infected cattle does not reproduce, hence no estimation of fecundity in infected animals is required. This restrictive assumption and the ECF effect on cattle mortality, described in the next paragraph, should be considered in the below proposed model extension.

Additional mortality coefficient of hosts (ρ). Gitau *et al.* (1999) reported a great heterogeneity in ECF morbidity and mortality, even at low spatial scales, in different agro-ecological zones and grazing systems in Kenya. From Gitau *et al.* (1999) we derive an average percentage of 22.5% per year of cattle that died from ECF from those initially diagnosed with clinical ECF which corresponds to a daily mortality rate $\psi_E = 0.0006983$. The total mortality ψ_T in infected cattle is

$$\psi_T = -\ln[(1-\psi_E)(1-\omega)] = \rho\omega$$

from which we obtain the additional mortality coefficient for sick animals

$$\rho = \frac{\psi_T}{\omega} = 1.8869 \qquad [\mathrm{day}^{-1}]. \tag{12}$$

The heterogeneity becomes even greater if other investigations are taken into account. For example, Moll *et al.* (1986) observed a mortality of 0 and 2.6% in six months, Medley *et al.* (1993) took into account the natural history of infection and included a mortality rate of 0.25 per day in their model. In other studies, mortality rates between 1% and 30% per year have been reported (Irvin, 1985). This variability can partially be explained by differences in resistance to *T. parva* among cattle breeds and in the strain of parasites as represented by the parameter *b* in eqns. [1f, 1g], and by the magnitude of the infected tick challenge considered by the dynamics in our model [eqn. 1d]. Nevertheless, great differences remain and should receive due attention by epidemiologists and veterinarians. Obviously, these differences have important implications for the planning and targeting of ECF control programmes (Gitau *et al.*, 1999).

Recovery rate of hosts (ϑ). As a consequence of the ECF infection, Gitau *et al.* (1999) reported a finite mortality rate of 22.5 % per year (see previous paragraph), meaning that 77.5% of initially infected individuals have recovered within a year at the rate ϑ

$$\vartheta = \frac{1}{365} \ln(1-0.775) = 0.004087 \qquad [\mathrm{day}^{-1}]. \tag{13}$$

This rate is lower than $\vartheta = 1/15 = 0.06667$ reported by Medley *et al.* (1993) who relied on their understanding of the natural history of the infection. Considering the important role of the recovery process, high priority should be given to a reliable estimation of

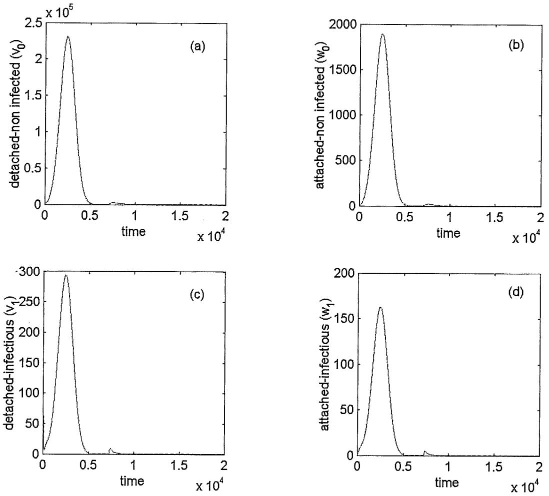

Figure 2: Time [days] evolution of the initial stage of tick population dynamics (20000 days). The abundance [individuals hectare^{-1}] of detached non infectious ticks v_0 (a), attached non infectious ticks w_0 (b), detached infectious ticks v_1 (c) and attached infectious ticks w_1 (d) are obtained as solution of the system (1a -g). Initial conditions have been chosen equal to zero, except for $h_0(0) = 1$, and $v_0(0) = v_1(0) = 200$. The results have been obtained with reference to the set of parameters in Table 2.

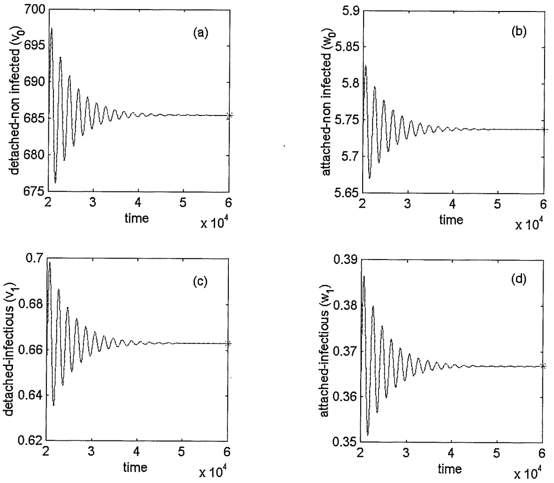

Figure 3: Time [days] evolution of tick population dynamics for large time periods (from 20000 time units to equilibrium). The abundance [individuals hectare^{-1}] of detached non infectious ticks v_0 (a), attached non infectious ticks w_0 (b), detached infectious ticks v_1 (c) and attached infectious ticks w_1 (d) are obtained as solution of the system (1a -g). Initial conditions have been chosen equal to zero, except for $h_0(0) = 1$, and $v_0(0) = v_1(0) = 200$. The results have been obtained with reference to the set of parameters in Table 2.

(ϑ) in future epidemiological studies. Noteworthy, our model allows the possibility of modifying the rate of recovery by the resistance coefficient b in eqns. [1f, 1g].

Numerical simulations. The dynamics obtained using the set of parameters in Table 2 that fulfill all the conditions for the existence and stability of the coexistence equilibrium are illustrated in Figures 2-5 where the x-axis is measured in days. The high capacity of the detached tick population to increase or decrease is demonstrated in Figure 2 where large changes in tick numbers occur in the first phase lasting about three years. Figure 3a-d shows the decreasing fluctuations of the tick population density that approaches the equilibrium after a relatively long time period of 20000 days. At the equilibrium, the density of detached non-infected ticks is more than 100-fold higher than the number of attached non infected ticks (3a vs. 3b), while the equilibrium level of attached non infected ticks is only 15-fold higher than attached infectious ticks (Figures 3b vs. 3d). Interestingly, the density of detached infectious ticks is only two times the density of attached infectious ticks (3c vs. 3d).
Figure 4 depicts the population fluctuation of susceptible, infected and recovered cattle. The equilibrium density of cattle is reached after passing through an initial phase of wide population fluctuations and occurs at the same time as ticks reach their equilibrium (Figure 4 vs. 2) Figure 5 shows the population fluctuations after time 2000 to illustrate the asymptotic stability that results. The density of recovered cattle (h_2) at the equilibrium is higher than the density of susceptible (h_0) and infected and infectious (h_1) cattle (Figure 5). Noteworthy, the density of infectious cattle at equilibrium is only about 11% of the total cattle population.

DISCUSSION

The various cattle breeds in Africa exhibit different levels of resistance to ticks and ECF (Fivaz *et al.*, 1989; Norval *et al.*, 1991; Norval *et al.*, 1992; Ali and De Castro, 1993; Ndungu *et al.*, 2005). The here described model primarily refers to European breeds but the inclusion of the coefficients a, b e c in system [1a-g] paves the road for an analysis of resistance in the epidemiology of ECF. Of particular practical relevance will be the influence of resistance on enzootic stability previously described as an epidemiological state wherein the clinical disease is scarce despite high infection rates (Norval *et al.*, 1992; Torr *et al.*, 2002).

The disease transmission model and lumped parameter estimation procedures are efficient instruments for making effective use of experience and a wide array of information including models, experimental data, observations, statistics available at national and international institutions as well as assessments by experts. The here presented procedures allow the evaluation of information consistency and the selection of data that result to satisfactory model predictions with respect to observations or assessments by experts. In the recovery rate of hosts (ϑ), for example, we found inconsistencies in the literature with profound influence on the dynamics of the system. Namely, Medley *et al.* (1993)

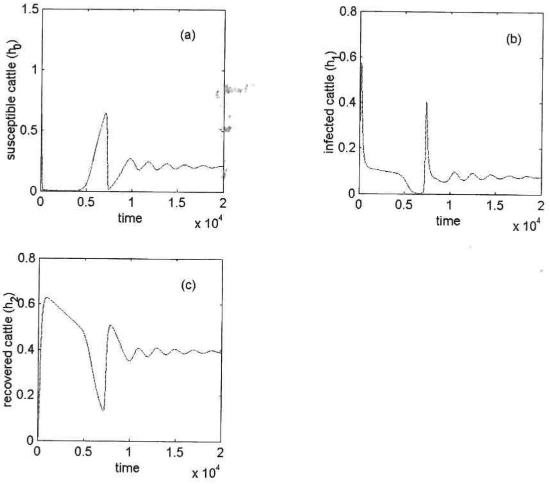

Figure 4: Time [days] evolution of the initial stage of cattle population dynamics (20000 days). The abundance [individuals hectare^{-1}] of susceptible h_0 (a), infected and infectious h_1 (b) and recovered h_2 (c) cattle are obtained as a solution of system (1a -g). Initial conditions have been chosen equal to zero, except for $h_0(0) = 1$, and $v_0(0) = v_1(0) = 200$. The results have been obtained with reference to the set of parameters in Table 2.

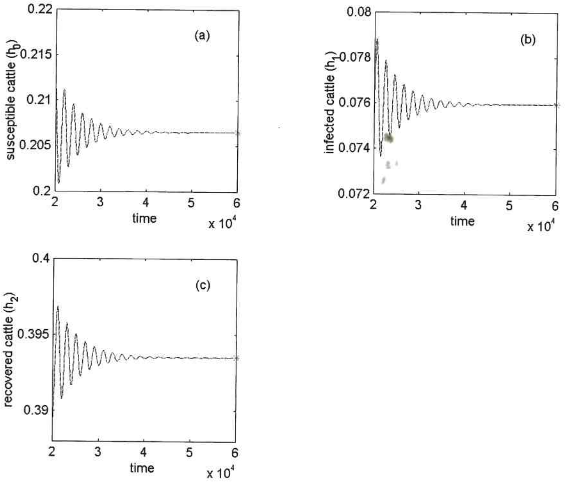

Figure 5: Time [days] evolution of cattle population dynamics for large time periods (from 20000 time units to equilibrium). The abundance [individuals hectare^{-1}] of susceptible h_0 (a), infected and infectious h_1 (b) and recovered h_2 (c) cattle are obtained as a solution of system (1a -g). Initial conditions have been chosen equal to zero, except for $h_0(0) = 1$, and $v_0(0) = v_1(0) = 200$. The results have been obtained with reference to the set of parameters in Table 2.

referred to Moll *et al.* (1986) and took into account the natural history of infection to get a much higher value than the one we obtained when relying on Gitau *et al.* (1999). The value for ϑ obtained from Gitau *et al.* (1999) (Table 2) appears to produce more satisfactory dynamic patterns (Figures 2 and 3) than an estimation of ϑ on the basis of the work by Medley *et al.* (1993).

The numerical simulation carried out to illustrate the dynamics resulting from the estimated parameters shows that the model satisfactorily represents the ECF epidemiology, adequately takes into account important components of more realistic and complex models, despite of model development on very restrictive assumptions, and serves as an entry point for model extensions that can efficiently be done in an adaptive management framework (Gilioli *et al.*, 2009). This framework is particularly appropriate for systems characterized by high complexity, i.e. systems composed of many parts which are coupled in a nonlinear fashion (Jørgensen, 2002). Gilioli and Baumgärtner (2007) described the application of epidemiological models and adaptive management procedures to navigating ecosocial systems towards enhanced sustainability.

CONCLUDING REMARKS

The disease transmission model and lumped parameter estimation procedures are efficient instruments for making use of experience and a wide array of information including models, experimental data, observations, statistics available at national and international institutions as well as assessments by experts. In many cases, there is conflicting information and selection of appropriate data for use in model parametrization is difficult. The here presented procedures allow the evaluation of information consistency and produce model predictions that correspond to observations or assessments made by experts.

The dynamic patterns produced by the model demonstrate its capability to adequately represent important components of more realistic and complex models, despite of model development on very restrictive assumptions. This indicates that the current model can be seen as an entry point into the development of more complex models that further deepen the insight into the spatio-temporal behavior of the tick-disease cattle system. The identification of elementary model components and the suggestions for model extension are considered as important qualities for guiding future activities aiming at research and management objectives. The adaptive management framework is particularly appropriate for further model development and provision of decision support (Gilioli and Baumgärtner, 2007).

In this work, we focus on European cattle with little resistance to ticks and ECF. The model structure, however, permits the evaluation of resistance types and paves the road for their consideration in integrated tick-disease management systems. Among the other model extensions under consideration is the substitution of constant model parameters by functions expressing their dependencies on environmental conditions including weather. Additional extensions may be derived from details of the tick life cycle, from the need to consider time-varying age structures (Randolph and Rogers, 1997), and from the movements of both cattle and wildlife influencing tick populations and disease transmission.

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Dr. Gianni Gilioli - Università Mediterranea di Reggio Calabria, Dipartimento di Gestione dei Sistemi Agrari e Forestali, Località Feo di Vito - 89122 Reggio Calabria (Italia), E-mail: gianni.gilioli@unirc.it.

Prof. Johann Baumgärtner - Dipartimento di Protezione dei Sistemi Agroalimentare e Urbano e Valorizzazione delle Biodiversità (Di.P.S.A.), Università degli Studi di Milano, Via Celoria 2, I-20133 Milano (Italy). E-mail: johann.baumgartner@unimi.it.

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