Spatial and temporal distributions of parasites: can wild and domestic ungulates avoid African tick larvae?

M. DE GARINE-WICHATITSKY[1,2]*, T. DE MEEÛS[2], J.-F. GUÉGAN[2] *and* F. RENAUD[2]

[1] *CIRAD-EMVT, Centre International de Baillarguet. Programme ECONAP, Projet 'Santé et Environnement', B.P. 5035, 34032 Montpellier Cedex 1, France*
[2] *CNRS/IRD UMR 9926, Centre d'Etude sur le Polymorphisme des Micro-Organismes. Equipe: 'Evolution des Systèmes Symbiotiques'. IRD, 911 Avenue Agropolis, B.P. 5045, 34032 Montpellier Cedex 1, France*

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SUMMARY

Infestation of a new host is a crucial stage in the life-cycle of parasites, and the possibility that hosts avoid infesting contact depends, in part, on the predictability of infestation risk. Immature free stages of ticks (Acari, Ixodidae) have limited mobility and survival in the vegetation and strongly depend on host behaviours for their infestation. We studied spatial and temporal distributions of the larvae of 2 major groups of African tick species in a ranch in Zimbabwe. No difference in the abundance of *Rhipicephalus evertsi evertsi* larvae was found among vegetation types and during most of the seasonal cycle, and no reliable indicator of their presence on a given site was identified. *Rhipicephalus appendiculatus/Rhipicephalus zambeziensis* larvae are mainly found during the cool dry season, in vegetation types situated close to permanent water holes or dominated by *Acacia* trees, which provide key forage resources for ungulates; and several indicators of their presence were identified. For both tick groups, spatial and temporal distributions of the larvae result in an optimized contact with ungulate hosts: *R. e. evertsi* larvae are unpredictable and thus unavoidable by hosts, whereas *R. appendiculatus/R. zambeziensis* larvae are predictable but also unavoidable because they are associated with key-resources for ungulates.

Key words: ecology, infestation risk, parasite life-cycle, *Rhipicephalus* spp., tick distribution, ungulates.

INTRODUCTION

The infestation of a new host is a crucial stage in the life-cycle for all parasites (Kennedy, 1975; Schmid Hempel & Tanner, 1990). This can be achieved through four different modes as stated by Combes (1995): direct transmission by contact, transmission by consumption, transmission by vector and transmission by active free stage. For the large majority of ectoparasites, and ticks are no exception, transmission by active free stage is the most common solution adopted (Combes, 1995). But this mode of transmission is risky in that it exposes the free stages to various constraints outside the host, not the least of which is the imperative need for finding a host in an inhospitable environment to accomplish their life-cycle (Kennedy, 1975).

Threatened by all sorts of parasites which seek to exploit them, hosts have evolved a wide range of adaptations to prevent initial parasite infection and subsequent proliferation (Sheldon & Verhulst, 1996). Among the diversity of weapons elaborated by the host, including costly and complex immune responses, behaviours of hosts that may reduce or prevent contact with parasites are a first line of defence (Hart, 1994; Nelson, Keirans & Bell, 1975). Indeed, if beneficial to host fitness, such behavioural patterns should be strongly selected (Hart, 1990).

Can hosts avoid parasites? As stated by Moore (1995) there have been few investigations analysing the possibility of direct avoidance of parasites by hosts. Interestingly, the question appears crucial for some parasites which have limited migratory abilities and which rely on host behaviour to achieve infesting contact. Cases of hosts avoiding, or reducing contact with potential sources of parasites have been described in various situations (Hart, 1990; Lozano, 1991). For instance, grazing herbivores have evolved a tendency to avoid foraging near recently dropped faeces as a mean of reducing infestation from faecal-borne parasites (Michel, 1955; Hart, 1994 for review).

The characteristics of the free stages of ixodid ticks vary according to species, but a constant pattern is a reduced mobility of immature stages (Rechav, 1979), which also have specific micro-habitat requirements (Oliver, 1989). For the species *Rhipicephalus evertsi evertsi* for example, the larvae move very short distances from the site where engorged females laid the eggs (Gray, 1961; Rechav, 1979). The success of infestation of the ticks depends thus more on the movements of their hosts than on their own movements (Morel, 1981; Rechav, 1979). The free stages must be 'at the right place at the right

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* Corresponding author: CIRAD-EMVT. Prg. ECONAP. B.P. 5035, 34032 Montpellier Cedex 1, France. Tel: +33 04 67 61 58 00. Fax: +33 04 67 59 37 98. E-mail: degarine@cirad.fr

time' to maximize their chances of infesting a host (Barnard, 1989; Oliver, 1989). The detection of a host by a parasite-free stage and the efficiency to infest this host are also important for the accomplishment of the life-cycle, but the parasite distribution in time and space dictates the likelihood of contact with potential hosts. Sustainability of parasite life-cycles and degree of transmission will be enhanced if infesting free stages orientate towards host preferred habitats (Pike, 1990).

In this paper we describe the results of a study undertaken on a mixed game/cattle ranch in Zimbabwe, during which the variations in the abundance and the spatial distribution of the immature free stages of 2 groups of species of ticks (*Rhipicephalus appendiculatus*/*R. zambeziensis* and *R. e. evertsi*) were monitored. These parasitic arthropods have similar host preferences and the seasonal distributions of their larvae in the vegetation are analysed in terms of parasite niche segregation and predictability of host infestation. Then, we emphasize the consequences of such larval distributions on habitat use and avoidance behaviours by ungulate hosts in order to minimize tick infestations.

STUDY AREA AND METHODS

Study site

This work was conducted in an extensive ranch (Kelvin Grove Ranch, Agricultural and Rural Development Authority) located in the highveld of Zimbabwe (Mashonaland west province; 18° 36′ 08″ –18° 43′ 24″ S lat. and 30° 00′ 16″–30° 05′ 57″ E long.). The ranch is situated between 1100 and 1180 m in altitude, and the average annual rainfall is around 650 mm. Three major seasons occur (Norval, Walker & Colborne, 1982; Fritz, de Garine-Wichatitsky & Letessier, 1996): wet season (November–April); cool-dry season (May–July); and hot-dry season (August–October). The total surface of the ranch is 9400 ha, divided into 30 paddocks of approximately equivalent size. The vegetation of the ranch is a wooded savanna to woodland, with 4 major communities: 'Miombo' woodland (*Brachystegia* spp. and *Julbernardia globiflora*), 'Mopane' woodland (*Colophospermum mopane*), 'Terminalia' bush savanna (*Terminalia sericea*), and some patches of 'Acacia' bush savanna on richer soils (*Acacia nilotica* and *Dichrostachys cinerea*) (Fritz *et al*. 1996). One additional vegetation type was also identified in relation to permanent waterholes (dams and permanent pools in rivers), corresponding to shaded vegetation close to permanent waterholes (regardless of dominant tree species) and the open area (usually bare soil because of frequent trampling by stock and game) immediately surrounding the drinking places. A vegetation map was established using aerial photograph and ground truthing (Fritz *et al*. 1996).

Cattle, *Bos indicus* (mainly Brahman and Afrikander) and *Bos taurus* (mainly Simmental) and cross-breds, are raised extensively for the purpose of meat production. Five herds, corresponding to the different age classes (weaners, 2 herds of heifers, steers and breeding cows) are moved between the 30 paddocks available (approximately 300 ha each) according to the availability of grazing and water. The herds are dipped with acaricides on a weekly basis during the rainy season and every fortnight during the dry season.

Wild ungulate species encountered include impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*) and Burchell zebra (*Equus burchellii*). These herbivores range freely over the whole area of the ranch, as they easily jump over cattle fences. The biomass represented by these wild ungulate species is equivalent to the biomass of cattle in the ranch (Fritz *et al*. 1996). These wild ungulates are occasionally shot for meat and trophy hunting.

Methods

Tick sampling was done using a classical 'drag sampling method' similar to that described by Short & Norval (1981) and by Mooring, Mazhowu & Scott (1994). The operator pulls a 1·0 × 0·6 m white flannelette cloth (replaced when worn out or torn, 3 pieces of the same cloth were used during the course of the study) along a 100 pace long transect in the vegetation (equivalent to 62·5 ± 5·1 m). The drags collect host-receptive ticks, mostly immature stages, which climb on the flag and are then removed using forceps and preserved in 70 % ethanol for further identification in the laboratory. For 1 year, every week, each vegetation type available in the paddock occupied by a given herd was sampled, resulting in 350 sites sampled between April 1995 and May 1996. Tick sampling was performed between 06.00 and 18.00 h, with 3 replicates per site. In all vegetation types, care was taken by the operator during the transect to ensure a permanent contact between the cloth and the grass layer where the larvae are known to quest. Short & Norval (1981), Mooring *et al*. (1994) and several other authors used the same tick sampling technique in similar vegetation types of Zimbabwe and they made no mention of variable efficiency according to vegetation structure.

A total of 6032 larvae of ticks were collected during 1050 transects. The 2 most abundant groups of tick species are *R. appendiculatus*/*R. zambeziensis* (3679 larvae) and *R. e. evertsi* (2024 larvae) and the identifications were carried out under a binocular dissection microscope, in collaboration with the staff of the Veterinary Research Laboratory Tick Unit (Harare, Zimbabwe). A set of randomly chosen specimens was also sent for cross-identification to Professor I. G. Horak (Faculty of Veterinary Science, University of Pretoria, South Africa). The identification of *R. e. evertsi* larvae does not pose a serious problem, but we did not distinguish between the larvae of *R. appendiculatus* and the closely related species *R. zambeziensis*, which are morphologically very similar (Walker, Norval & Corwin, 1981). The two species will be referred hereafter as a *R. appendiculatus*/*R. zambeziensis* complex, because of the similarities in the biology of the two species and in their host preferences (Walker *et al.* 1981; Norval *et al.* 1982). *R. e. evertsi* is a 2-host tick, widespread in subsaharan Africa, whose larvae frequently infest wild and domestic ungulates but also lagomorph and other small mammals (Hoogstraal, 1956; Londt & Van Der Bijl, 1977; Minshull, 1981). *R. appendiculatus* and *R. zambeziensis* are both 3-host ticks whose larvae are found most frequently on wild and domestic ungulates but also on other small and medium size mammals (Hoogstraal, 1956; Norval *et al.* 1982). Larvae of *R. e. evertsi* and *R. appendiculatus* not only have similar host preference, but they also attach preferentially to the same site (ears) on these ungulate-hosts, although the first species is usually found deep inside the ear, whereas *R. appendiculatus* larvae are usually found attached to the margins of the ears.

Site characteristics

In order to understand the distribution of tick larvae in time and space, we first described the variations of abundance according to season and vegetation type. We then attempted to characterize the presence/absence of tick larvae on a given site, according to several groups of parameters likely to influence their local abundance. A list of all parameters recorded is presented in Table 1, along with the statistical analysis performed.

The physiognomy of the vegetation, in particular the shade which it provides and the air currents within the plants, has a major influence on the microclimatic parameters at a given site, and thus in turn on the survival of tick larvae (Londt & Whitehead, 1972; Branagan, 1973; Rechav, 1979; Short, Floyd & Norval, 1989). Important characteristics include the abundance of trees and shrubs as well as several parameters related to the herbaceous layer such as mean height or grass layer continuity. In addition, the specific composition of the herbaceous layer is likely to influence the survival or the abundance of tick larvae (Hassan, Dipeolu & Malonza, 1994; Mwangi, Hassanali & Essuman, 1995) and we assessed the percentage of coverage of major herbaceous species at each site. Final analyses retained the 22 most abundant species (represented in more than 5% of the sites sampled) or groups of morphologically similar species, among a total of 90 species identified in the area during the course of the study. Lastly, the abundance of tick larvae on a site is also related to the frequency of use by the hosts on which the female ticks engorged and from which they dropped before laying the eggs. Spoors and droppings of wild and domestic ungulates are good indicators of animal abundance (e.g. Jachmann & Bell, 1984; Koster & Hart, 1988), and we used these indicators to estimate the frequency of use of the sites by wild and domestic ungulates (cattle, greater kudu, impala, wildebeest and zebra).

Statistical analysis

The frequency distribution of tick larvae is highly skewed, containing many zeros and few extreme data, as frequently seen with such parasitic data (Crofton, 1971; Petney, Ark & Spickett, 1990; Gregory & Woolhouse, 1993). To overcome the consequences of this overdispersion on statistics, we unsuccessfully fitted our data with Poisson and negative binomial distributions (Sokal & Rohlf, 1981; Gregory & Woolhouse, 1993), before using a Box–Cox transformation according to the recommendations made by Sokal & Rohlf (1981). The data transformation with the parameters calculated ($\lambda = -2$ for *R. appendiculatus*/*R. zambeziensis* and $\lambda = -1$ for *R. e. evertsi*) gave satisfactory results, with the residuals controlled after a two-way ANOVA (season and vegetation) having a random distribution. Unplanned mean comparisons were carried out using Scheffé test according to the recommendations made by Day & Quinn (1989).

We then checked for parameters which could constitute good ‘indicators of tick larvae presence’ and which were likely to be used by ungulates as proximate factors to avoid infested sites. We used 2 complementary methods to classify non-infested (0 larvae/transect) and infested sites (>0 larvae).

(1) Logistic regression (LR), after backward stepwise selection of significant variables (Norusis, 1997). Following SPSS 8.0 procedure, the variables in the backward elimination procedure are selected if the regression coefficients calculated are significantly different from 0, with a cut-off value of 5% (Wald statistic). When no variable could be removed from the logistic model, the procedure was finished. For each tick species, variables selected by the backward stepwise procedure are used simultaneously in a minimal model of LR (for the whole of the seasons and for the cool dry season separately) to predict the presence/absence of larvae on sites. Percentage variables were transformed using arcsine transformation and categorical variables were coded using ($n-1$) indicator variables, where n is the number of modalities for each variable (Norusis, 1997). The χ^2 calculated on the difference of -2 Log Likelihood (-2LL) for the model including all selected variables compared to a constant indicates the overall significance of the model and Nagelkerke R^2 indicates the overall proportion of the variability explained by the model (Norusis, 1997).

Table 1. Description of explanatory variables for tick larvae abundance and types of statistical analysis used (see Methods for details)

	Explanatory variable		
Type of parameter	Description	Number of modalities (transformation)	Statistical method (software used)
Vegetation type	'Mopane', 'Brachystegia', 'Terminalia', 'Acacia' water hole	5 modalities	2-way ANOVA after Box–Cox transformation (SPSS 8.0 and GLIM 3.77)
Season	Rainy season, cool dry season, hot dry season	3 modalities	
Vegetation physiognomy	Tree abundance	4 classes of abundance	(1) Logistic Regression (SPSS 8.0) & (2) Artificial Neural Networks (Matlab 4.0)
	Bush abundance	4 classes of abundance	
	Grass abundance	4 classes of abundance	
	Mean grass height	4 classes: 0–10; 10–20; 20–50; >50 cm 5 modalities	
	Grass layer continuity % forbs, dried grass, green grass	% of grass layer (arcsinus transf.)	
Species composition of grass layer	23 major species (or group of species morphologically similar)	% of grass layer (arcsinus transf.)	(1) and (2)
Wild and domestic ungulate abundance	Droppings of cattle, impala, kudu, wildebeest and zebra	5 modalities	(1) and (2)

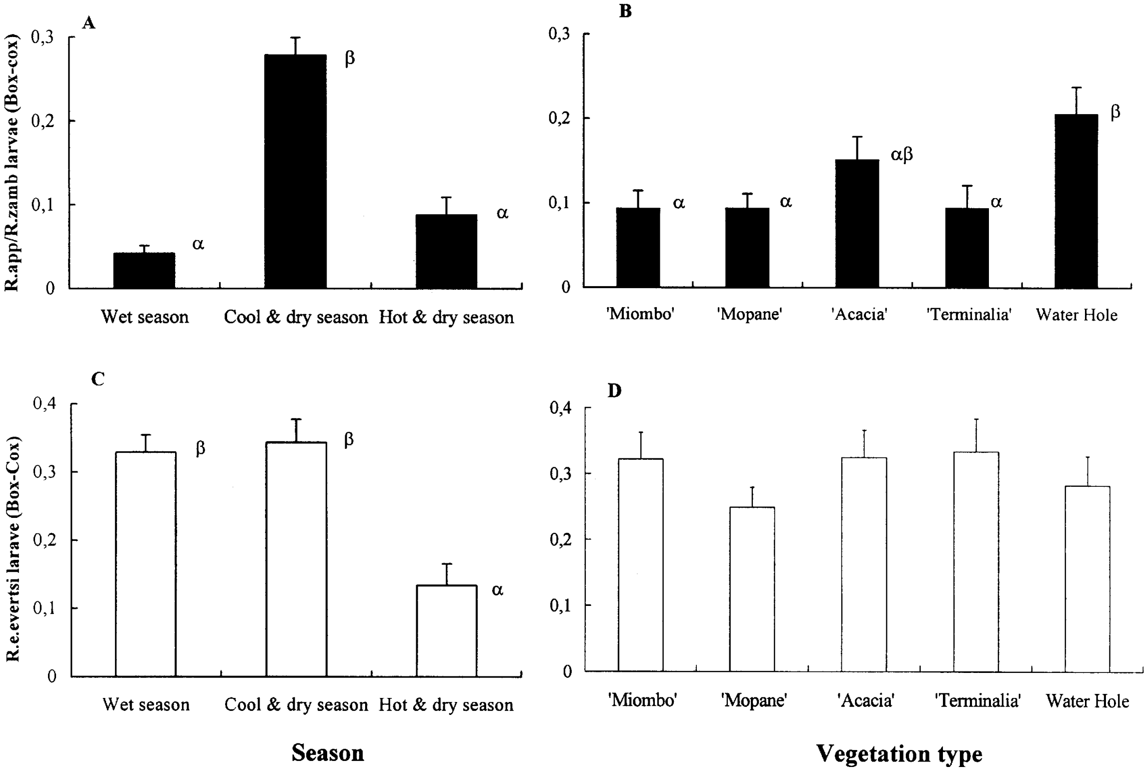

Fig. 1. Spatial and temporal variations in the abundance of *Rhipicephalus appendiculatus/R. zambeziensis* (R.app/R.zamb, ■) and *R. e. evertsi* (R.e.evertsi, □) larvae in Kelvin Grove ranch. Mean number of larvae per transect (error bars denote S.E.) after Box–Cox transformation (see text for results of two-way ANOVA; Scheffé test at 5%, α and β indicating homogeneous subsets). (A) Seasonal variations of *R. appendiculatus/R. zambeziensis* larvae; (B) abundance of *R. appendiculatus/R. zambeziensis* larvae in the main vegetation types; (C) seasonal variations of *R. e. evertsi* larvae; (D) abundance of *R. e. evertsi* larvae in the main vegetation types.

(2) Classification with artificial neural networks (ANN) (Edwards & Morse (1995) for review). Using the same variables selected by LR with an additional random variable (random number between 0 and 1), we classified all sites sampled for tick larvae during the whole seasonal cycle. This random variable was

Table 2. Indicator variables for the presence/absence of *Rhipicephalus appendiculatus*/*R. zambeziensis* and *R. e. evertsi* larvae, all seasons included (between April 1995 and May 1996)

(Logistic Regression (Norusis, 1997) with explanatory variables previously selected by backward stepwise selection (see Methods for details).)

	R. appendiculatus/*R. zambeziensis* ($n=312$)				*R. e. evertsi* ($n=326$)			
	−2 Log Likelihood		χ^2	*P*	−2 Log Likelihood		χ^2	*P*
Model	265·04		124·848	0·0001	402·04		47·993	0·0001
Nagelkerke R^2	0·462				0·183			
	Selected variables*	D.F.	Wald	*P*	Selected variables	D.F.	Wald	*P*
Explanatory variables	A.cong	1	4·91	0·0267	Seta.sp	1	7·91	0·0049
	E.cap	1	2·32	N.S.	S.sang	1	5·38	0·0204
	O.amer	1	4·36	0·0368	Z.gloch	1	1·90	N.S.
	S.cordi	1	2·85	N.S.	GRABU	4	7·65	N.S.
	Seta.sp	1	0·54	N.S.	IMPANC	3	8·36	0·0392
	GRGRE	1	22·58	0·0001	Constant	1	0·24	N.S.
	GRABU	4	9·33	N.S.				
	GRHEI	1	16·00	0·0001				
	BOVANC	3	6·45	N.S.				
	BOVREC	3	4·72	N.S.				
	IMPANC	3	0·86	N.S.				
	KUDREC	3	0·68	N.S.				
	ZEBREC	2	0·12	N.S.				
	Constant	1	0·01	N.S.				
	Observed	Predicted (%)			Observed	Predicted (%)		
Classification (cut-off 0·50)								
0 larvae	213	184 (86)			154	89 (58)		
>1 larvae	99	54 (55)			172	121 (70)		
Overall		(76)				(65)		
Classification (cut-off 0·75)								
0 larvae	213	156 (73)			154	20 (13)		
>1 larvae	99	16 (16)			172	40 (23)		
Overall		(55)				(18)		

* A.cong, *Aristida congesta*; E.cap, *Eragrostis capensis*; O.amer, *Ocinum americana*; S.cordi, *Sida cordifolia*; S.sang, *Schizachyrium sanguineum*; Set.sp, *Setaria* spp.; Z.glo = *Zornia glochidiata*; BOVREC, cattle recent droppings; BOVANC, cattle old droppings; IMPANC, impala old droppings; KUDREC, kudu recent droppings; ZEBREC, zebra recent droppings; GRABU, grass abundance; GRHEI, grass height; GRGRE, % green grass; D.F., degrees of freedom; probabilities (*P*): N.S., $P>0·05$.

inserted in the database representing a factor that had no influence upon the tick abundance. This helps to assess the stochasticity of the distribution and the validity of the contributions of the other variables (Ball, Palmer-Brown & Mills, 1999). The specifications of the ANN used are as follows: the first layer comprised 6 input neurons for *R. e. evertsi* and 15 input neurons for *R. appendiculatus*/*R. zambeziensis*; the hidden layer had 5 neurons and the last layer had 2 neurons which corresponds to the presence/absence of tick larvae. The training of the network was performed using a back-propagation algorithm (Rumelhart, Hinton & Williams, 1986). We used a jacknife (leave-one-out) procedure to isolate a training set of sites ($n-1$ sites) and an independent test set (1 site), repeated for each observation in turn. In each run, the model was first adjusted with the training set and then used to predict the presence or absence of ticks in the test set (Mastrorillo, Lek & Daubs, 1997). Ten runs were performed for each analysis in order to assess the contribution of each variable (±S.D.) to the prediction. The maximum number of iterations was set to 500.

The various statistical procedures used (as well as a description of the variables and softwares used) are summarized in Table 1.

RESULTS

Spatial and temporal distribution of tick larvae

The effects of season and vegetation type on the abundance of tick larvae (two-way ANOVA after Box–Cox transformation, and Scheffé test at 5%, homogeneous subsets indicated in Fig. 1) were different according to the group of tick species considered (Fig. 1). *R. e. evertsi* has a significant decrease in the number of larvae found during the

Table 3. Contribution of selected indicator variables and a random variable to the prediction of presence/absence of *Rhipicephalus appendiculatus/R. zambeziensis* and *R. e. evertsi* larvae, all seasons included (April 1995 to May 1996)

(Results of Artificial Neural Network analysis indicate the mean contribution (% of contribution ± S.D.) of each variable to the prediction of the model (10 runs for each species).)

R. appendiculatus/R. zambeziensis ($n=312$)		*R. e. evertsi* ($n=326$)	
Selected variables*	Contribution % (± S.D.)	Selected variables	Contribution % (± S.D.)
RAND	7·47 (±1·04)	RAND	19·78 (±7·09)
A.cong	7·29 (±0·81)	Seta.sp	14·03 (±1·89)
E.cap	6·81 (±1·51)	S.sang	23·41 (±3·66)
O.amer	10·28 (±1·25)	Z.gloch	6·34 (±2·36)
S.cordi	7·69 (±0·97)	GRABU	24·34 (±2·56)
Seta.sp	5·05 (±1·64)	IMPANC	13·87 (±8·36)
GRGRE	16·12 (±1·90)		
GRABU	4·21 (±1·61)		
GRHEI	14·86 (±1·86)		
BOVANC	5·69 (±1·37)		
BOVREC	3·93 (±1·50)		
IMPANC	2·29 (±0·97)		
KUDREC	7·92 (±1·33)		
ZEBREC	2·53 (±1·47)		

* See legend Table 2 for variable names; RAND, Random variable (continuous between 0 and 1). S.D., Standard deviation.

hot dry season, whereas this number is relatively constant between the rainy season and the cool dry season ($F_{2,345}=11·579$, $P<0·0001$). *R. appendiculatus/R. zambeziensis* larvae present a very clear peak of abundance during the cool dry season, few individuals being encountered apart from this period ($F_{2,345}=69·425$, $P<0·0001$).

In Kelvin Grove ranch, the abundance of *R. appendiculatus/R. zambeziensis* larvae appears to be significantly influenced by the type of vegetation in which measurements were taken (Fig. 1B). There are significantly more ticks in the vegetation close to permanent water holes, and to a lesser extent in the type of vegetation dominated by *Acacia* spp., than in all the other types of vegetation ($F_{4,343}=3·081$, $P=0·016$). By contrast, the number of *R. e. evertsi* larvae does not present a significant difference according to the type of vegetation ($F_{4,343}=0·849$, $P>0·05$).

No significant interaction was found between seasonal effect and vegetation type for either species ($F_{8,339}=1·179$, $P>0·05$ for *R. appendiculatus/R. zambeziensis* and $F_{8,339}=1·221$, $P>0·05$ for *R. e. evertsi*).

Indicators of tick larvae presence

Among the 3 categories of variables described previously (physiognomy of the vegetation, botanical composition of the herbaceous layer and ungulate abundance), we selected those which might have a significant effect on the presence of tick larvae. The selection was carried out on the whole data set collected during the seasonal cycle using LR stepwise backward procedure (Norusis, 1997).

By LR, the backward procedure retains 3 variables (abundance of herbaceous, average height of the herbaceous layer and percentage of green grass) as having an effect on the probability of presence of *R. appendiculatus/R. zambeziensis* larvae. By contrast, only 1 variable (abundance of herbaceous) is retained in the model to predict the presence of *R. e. evertsi* larvae. Among the 22 herbaceous species considered, 5 species/groups of species (*Aristida congesta*, *Eragrostis* spp., *Ocimum americanum*, *Setaria* spp. and *Sida cordifolia*) for *R. appendiculatus/R. zambeziensis* and 3 herbaceous species/groups of species for *R. e. evertsi* (*Setaria* spp., *Schyzachirium sanguineum* and *Zornia glochidiata*) were selected. Lastly, 4 variables (old and recent droppings of cattle, recent droppings of kudu and zebra and old droppings of impala) are retained to predict the presence of *R. appendiculatus/R. zambeziensis*, whereas only 1 indicator is identified for *R. e. evertsi* (old droppings of impala).

Once the significant variables had been selected, we introduced them into a model (LR or ANN) aiming at determining the probability that a site is infested by tick larvae. The first model is established on the whole data set, including all seasons, in an attempt to investigate the existence of permanent

Table 4. Indicator variables of presence/absence of *Rhipicephalus appendiculatus*/*R. zambeziensis* and *R. e. evertsi* larvae, during the cool dry season (May 1995 to August 1995)

(Logistic Regression (Norusis, 1997) with explanatory variables previously selected by backward stepwise selection (see Methods for details).)

	R. appendiculatus/*R. zambeziensis* ($n=98$)				*R. e. evertsi* ($n=102$)			
	−2 Log Likelihood		χ^2	*P*	−2 Log Likelihood		χ^2	*P*
Model	55·64		65·09	0·0001	122·10		14·42	n.s.
R^2 Nagelkerke	0·685				0·179			
	Selected variables*	d.f.	Wald	*P*	Selected variables	d.f.	Wald	*P*
Explanatory variables	A.cong	1	0·53	n.s.	Seta.sp	1	0·07	n.s.
	E.cap	1	2·54	n.s.	S.sang	1	5·04	0·0248
	O.amer	1	4·99	0·0255	Z.gloch	1	0·23	n.s.
	S.cordi	1	0·04	n.s.	GRABU	4	2·42	n.s.
	Seta.sp	1	0·74	n.s.	IMPANC	3	2·42	n.s.
	GRAV	1	3·42	n.s.	WATHOL	1	0·00	n.s.
	GRAB	4	2·86	n.s.	Constant	1	1·23	n.s.
	GRHEI	1	0·02	n.s.				
	BOVANC	3	3·01	n.s.				
	BOVREC	3	0·02	n.s.				
	IMPANC	3	0·60	n.s.				
	KUDREC	3	0·12	n.s.				
	ZEBREC	2	4·99	n.s.				
	WATHOL	1	4·59	0·0321				
	Constant	1	0·01	n.s.				
	Observed	Predicted (%)			Observed	Predicted (%)		
Classification (cut-off 0·50)								
0 larvae	30	21 (70)			40	20 (50)		
>1 larvae	68	60 (88)			62	47 (76)		
Overall		(83)				(66)		
Classification (cut-off 0·75)								
0 larvae	30	21 (70)			40	0 (0)		
>1 larvae	68	53 (88)			62	25 (40)		
Overall		(76)				(25)		

* See Table 2 for legend; WATHOL, water hole.

indicators of infestation risk. The second analysis consists in testing this model during the period of maximal abundance of the 2 groups of species, during the cool dry season only.

The results of LR models carried out on the whole data set are presented in Table 2. For the 2 groups of tick species, the variables included in the model significantly improve the predictions on larvae presence/absence ($\chi^2=124·848$, 25 d.f., $P=0·0001$ for *R. appendiculatus*/*R. zambeziensis*; and $\chi^2=47·993$, 10 d.f., $P=0·0001$ for *R. e. evertsi*). Although both models do not fit perfectly the data (−2 Log Likelihood have high values), the prediction is more accurate for *R. appendiculatus*/*R. zambeziensis* (Nagelkerke $R^2=0·462$; overall 76% of cases correctly classified) than for *R. e. evertsi* (Nagelkerke $R^2=0·183$; overall 65% of cases correctly classified). By merely adding 2 descriptive variables (season with 3 modalities and presence/absence of permanent water point), the performance of the model is greatly improved for *R. appendiculatus*/*R. zambeziensis* (−2LL decrease of 55·437 and Nagelkerke $R^2=0·606$), whereas it is not improved and remains poor for *R. e. evertsi* (−2LL decrease of 17·893 and Nagelkerke $R^2=0·237$). The differences between the 2 models are even more obvious if one considers a more drastic cut-off value of 0·75 instead of a conservative 0·50, since the model correctly classifies 55% of the sites for *R. appendiculatus*/*R. zambeziensis*, whereas only 18% are correctly classified for *R. e. evertsi*.

Results of ANN (10 runs for each group of tick), carried out on the same data with addition of a random explanatory variable (RAND) are presented in Table 3. The first comment which one can make relates to the mean contribution of the random variable to the predictions of the model. In the case of *R. e. evertsi*, none of the variables introduced in the model has a mean contribution significantly higher than RAND, even those which significantly contributed to the LR model. The contribution of RAND to the model is highly variable (19·8% ± 7·1)

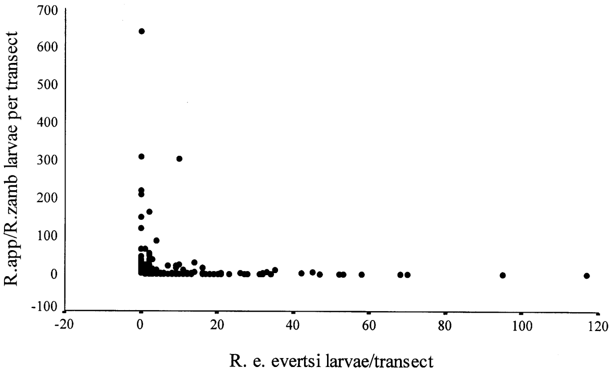

Fig. 2. Relationship between the number of *Rhipicephalus appendiculatus/R. zambeziensis* (R.app/R.zamb) larvae and the number of *R. e. evertsi* (R.e.evertsi) larvae collected per transect. A total of 437 sites were sampled, transects during which no larvae were collected were withdrawn from the analysis (see text).

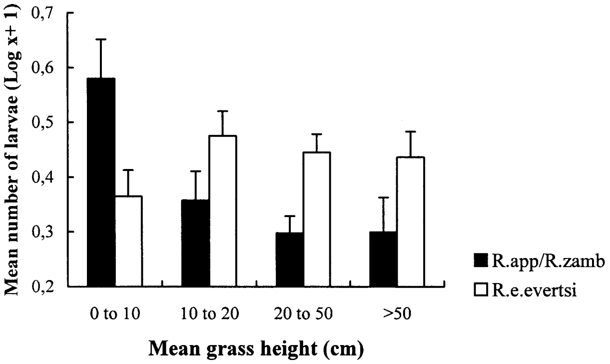

Fig. 3. Mean number of *Rhipicephalus appendiculatus/R. zambeziensis* (R.app/R.zamb, ■) and *R. e. evertsi* (R.e.evertsi, □) larvae according to estimated mean height of the grass layer (error bars denote S.E.). A total of 437 sites were sampled, transects during which no larvae were collected were withdrawn from the analysis (see text). Abundance values of larvae for both groups of ticks were log $(x+1)$ transformed in order to minimize effects of non-normality on calculations. Mean grass heights (in cm) were grouped into 4 classes: 0–10; 10–20; 20–50 and >50.

compared to other explanatory variables. In the case of *R. appendiculatus/R. zambeziensis*, 3 variables (O.amer, GRGRE and GRHEI) have a higher mean contribution to the model than RAND. These variables also significantly contributed to the LR model, except A.cong which had a significant contribution to the LR model and apparently not to the ANN model. All the remaining variables (except A.cong) did not contribute to the prediction of the LR model (Table 2).

The same explanatory variables used in the previous analysis, and an additional variable indicating the proximity of a water point, were used in a LR model intended to classify the sites sampled during the cool dry season (Table 4) according to the presence/absence of tick larvae. For *R. appendiculatus/R. zambeziensis*, the LR model significantly fits the data ($-2\text{LL}=55{\cdot}64$, $\chi^2=65{\cdot}09$, 26 D.F., $P<0{\cdot}0001$) and gives a good prediction (Nagelkerke $R^2=0{\cdot}685$), whereas the results are not significant for *R. e. evertsi* ($-2\text{LL}=122{\cdot}10$, $\chi^2=14{\cdot}42$, 11 D.F., $P>0{\cdot}05$).

With a cut-off value of 0·75, 78% of the sites infested by *R. appendiculatus/R. zambeziensis* larvae are correctly classified, whereas only 25% of the sites are correctly classified for *R. e. evertsi*. In addition to the variables described as 'permanent indicators' throughout the seasons, the variable indicating the proximity of permanent water point strongly improves the prediction for *R. appendiculatus/R. zambeziensis* larvae.

Niche segregation between larvae

Out of the total database, we selected the transects during which at least 1 larva of either group of species was collected, thus excluding unsuitable sites for the survival of tick larvae. As illustrated by Fig. 2, we observed a significant negative correlation between the number of larvae of a species and that of the other group of species (Spearman $r=-0{\cdot}497$, $n=437$, $P<0{\cdot}0001$). We also found on the same data set that *R. e. evertsi* larvae are more abundant in the sites where the grass is higher (Kruskal–Wallis, 3 D.F., $\chi^2=8{\cdot}2590$, $P=0{\cdot}0410$), whereas *R. appendiculatus/R. zambeziensis* are mainly met when the herbaceous layer is shorter (Fig. 3). This preference for short grass (Kruskal–Wallis, 3 D.F., $\chi^2=11{\cdot}07$, $P=0{\cdot}0114$) is to be taken into account with the fact that the areas located near the water points are often overgrazed.

DISCUSSION

The specificity of ticks is variable according to species (Hoogstraal & Kim, 1985; Oliver, 1989), not only by the range of host species infested, but also by the sites of attachment on these hosts. In spite of marked differences with regard to their biology (3-host versus 2-host cycle), *R. appendiculatus*, *R. zambeziensis* and *R. e. evertsi* have similar host preferences. Indeed, the larvae of these species preferentially infest large wild and domestic ungulates (Hoogstraal, 1956; Horak, Boomker & Spickett, 1992; Londt & Van Der Bijl, 1977; Norval, 1979), and occasionally they also infest small and medium-sized mammals. However, *R. appendiculatus* larvae are preferentially found attached to the margins of the ears whereas *R. e. evertsi* larvae and nymphs are found inside the external ear channel (Baker & Ducasse, 1967), and simultaneous infestations of the same host are not rare.

Studies carried out on the distribution of these ticks show that *R. appendiculatus* occurs most commonly in savanna or savanna woodland habitats and tends to be absent from open plains and dense forests (Lessard, L'Eplattenier & Norval, 1990; Perry, Lessard & Norval, 1990). More specifically, the immature stages are found in habitats with a tree or bush cover providing sufficient shade and a developed herbaceous layer (Londt & Whitehead, 1972; Norval & Perry, 1990). *R. e. evertsi* also occurs in drier areas (Londt & Whitehead, 1972; Norval & Perry, 1990) since it is more resistant to desiccation than *R. appendiculatus* (Fielden & Rechav, 1996).

Locally, the physiognomy of the vegetation, and particularly the characteristics of the grass layer, influence the free stages of the ticks (Rechav, 1979) since it is responsible for the microclimatic parameters within the vegetation (shade and air circulation) and thus the survival of the ticks (Gray, 1961; Londt & Whitehead, 1972). The results for our study show that the distribution of the larvae of these 2 species in the vegetation is indeed very different. *R. appendiculatus*/*R. zambeziensis* larvae are met almost exclusively in the vegetation close to permanent water holes, and to a lesser extent in the habitats dominated by thorn-bush (*Acacia* spp. and *Dichrostachys cinerea*). In addition, our results using 2 different statistical procedures indicate that several parameters are reliable indicators of the presence of these larvae: characteristics of the herbaceous layer (reduced height of the grass cover, high proportion of green grass), frequent use of the area by wild and domestic ungulates and the presence of several plant species often associated with overgrazing. This last statement contradicts previous studies since several authors have shown that *R. appendiculatus* tends to disappear from overgrazed areas (Norval *et al*. 1982; Perry *et al*. 1990). However, the vegetation situated close to permanent water points often tends to be overgrazed, and these associations result from the frequent occurrence of the larvae of this species close to water holes. This is confirmed by the high contribution of this variable (proximity of water hole) to the predictions of the models aiming at classifying infested/non-infested sites with *R. appendiculatus*/*R. zambeziensis* larvae. As opposed to that predictability, our study shows that in the same area the distribution of *R. e. evertsi* larvae is stochastic, with no reliable indicator of infestation risk, as indicated by the contribution of the random variable introduced in the ANN model. The larvae of these 2 groups of species do have separate niches, and the segregation between them seems to be enhanced by their differential preferences for grass layers with different heights (Londt & Whitehead, 1972).

Does the spatial and temporal distribution of the larvae of these 2 groups of species guarantee the infestation of the hosts? The probability of contact between a parasite infective stage and the host is the major factor which influences the growth, reproduction and development of ticks (Barnard, 1991; Oliver, 1989). The need for meeting with a host constitutes a selective pressure which strongly influenced the evolution of ticks, especially for the species which infest wandering vertebrates with extensive home ranges or occurring at low densities (Hoogstraal & Aeschlimann, 1982). Ticks infesting large ungulates thus adopted a reduction of the number of individual hosts required to accomplish their cycle. This limits the risks associated with the infestation of a new host (Hoogstraal & Aeschlimann, 1982; Hoogstraal & Kim, 1985; Oliver, 1989). For instance, *R. appendiculatus* and *R. zambeziensis* require 3 individual hosts in order to accomplish their life-cycle, whereas *R. e. evertsi* requires only 2 (larvae and nymphs feed on the same host). Interestingly, the larval, nymphal and adult stages of *Boophilus decoloratus*, another African tick frequently infesting wild and domestic herbivores, are completed on the same host. In the cases of *R. appendiculatus* and *R. e. evertsi*, several authors showed that the availability of hosts influences the development of the populations of these 2 species (Newson, 1979; Norval, 1979; Punyua & Hassan, 1992). The larvae are the most vulnerable stages of the development of ixodid ticks, for they are more sensitive to desiccation and survive less long in the vegetation than the nymphs or adults (Perry *et al*. 1990; Short & Norval, 1981). Their distribution in time and space is crucial since it conditions the probability of meeting with the hosts and the maintenance of the species.

Could ungulates avoid contact with tick larvae while foraging? The relationship between foraging behaviour of mammals and parasite avoidance has been mentioned by several authors (Hart, 1994; Keymer & Read, 1991; Lozano, 1991), but there is little experimental evidence of this phenomenon. Avoidance of infective nematode larvae by bovines through selective grazing away from recently dropped faeces has been described long ago (Michel, 1955). More recently, Sutherst, Floyd & Bourne (1986) also showed that cattle were able to avoid large clumps of *Boophilus microplus* larvae, another species of tick occurring in Australia. But the defences adopted by the hosts in response to parasitism depend on the predictability of the infestation (Harvell, 1990; Heeb, Werner & Kölliker, 1998). Cattle have adopted avoidance behaviours of nematode larvae because they are associated with fresh droppings easily noticeable in the pasture. In the same way, cattle avoid large clumps of *B. microplus* larvae when they can detect by eye large concentrations of ticks emerging from shelter onto grass tips. But, given the larval distributions we observed in Kelvin Grove, ungulate hosts cannot adopt such avoidance behaviours. If we consider the results presented in terms of evolutionary strategies, the tick species studied have larval distributions which guarantee the contact of some of the larvae with potential hosts, although these distributions are very different and result from complex interactions between biotic and abiotic factors (Barnard, 1991; Randolph, 1997). Indeed, as *R. e. evertsi* larvae occur in all types of vegetation during most of the seasonal cycle, ungulate hosts cannot adopt a sustainable strategy of habitat use which results in an avoidance of contact with these larvae. In addition, the lack of significant differences between the average number of larvae met in the various vegetation types does not make it possible to minimize the contact with *R. e. evertsi* larvae. The distribution of the larvae of this species in the environment is stochastic and none of the indicators we tested makes it possible to predict their presence on a given site.

R. appendiculatus and *R. zambeziensis* are potentially in a much more vulnerable situation with respect to a possible avoidance by the hosts, since the larvae are met mainly during the cool dry season and in 2 types of vegetation. But the hosts are facing a trade-off between the benefits of parasite avoidance and the costs associated with the exercise of the defensive behaviour (Hart, 1990, 1994). In the case of the avoidance of *R. appendiculatus* and *R. zambeziensis* larvae, the fitness cost would be prohibitive, since it consists of avoiding permanent water holes during the dry season and in reducing the use of acacia-dominated habitats, which provide key forage resources to most ungulate species during the dry season (Fritz *et al*. 1996). As stated by Hart (1994), the forage may be too poor for ungulates during unfavourable periods to allow them the luxury of always avoiding contact with potential sources of parasites.

We have seen that the spatial and temporal distribution of the larvae of the 2 groups of tick species is different. It must result from interactions between different strategies to come into contact with hosts, and complex abiotic and biotic processes. Unpredictable in the first case or predictable but associated with key resources in the second case, the spatial and temporal distribution of *R. e. evertsi* and *R. appendiculatus*/*R. zambeziensis* larvae 'avoids being avoided' by their common hosts.

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