Spatial & temporal abundance of Rhipicephalus gertrudae (ACARI, Ixodidae) along a degradation gradient along the Lower Kuiseb river/Namibia

Diplomarbeit
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Contents

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Abstract

Abundance and distribution of the tick species Rhipicephalus gertrudae in two distinct areas along the ephemeral Kuiseb river, Namib-Naukluft Park, Namibia were determined by flagging vegetation over two sampling periods, late spring 1993 and winter 1994. The study area included a wilderness area and an area used for domestic stock farming. Vegetation type and surface cover were quantified along the sampling transects and related to tick abundance by using various regression models and cluster analysis. It was found that tick abundance was strongly defined by these two vegetation parameters, a result particularly discernable within the farming area where degradation of the ground vegetation is generally high. Ground vegetation improves gradually with distance within a 3,5 km radius of water points.

R. gertrudae were active throughout the survey period. Total tick abundance was higher in late spring, the hot season, than in winter, when it is generally colder.

The diurnal activity of R. gertrudae was studied under natural conditions to investigate how this tick species relates to environmental conditions such as daily climatic fluctuations and host availability in the Kuiseb. The Kuiseb's riparian forest is relatively mild climatically although it crosses the Central Namib Desert, one of the most arid regions in southern Africa. Tick activity was significantly related to air temperature and relative humidity and reached its peak in the late afternoons when host activity is greatest.

1. CHAPTER ONE

Introduction

Ticks are important arachnid ecto-parasites of vertebrates, and can directly impact host fitness (Lehmann, 1993) or act as vectors for a large number of diseases. They are one of the most important external parasites of animals and in certain areas can constitute a limiting factor to successful stock farming (Howell et al., 1978).

1.1. Classification, life history & biology of ticks

Ticks belong to the class Arachnida and together with the mites they comprise the order Acarina. Three families, Argasidae, Nuttalliellidae and Ixodidae, are distinguished and all families occur in southern Africa. Members of the three families differ markedly in appearance, habits and life histories. Little is known about the tick family Nuttalliellidae, which includes only one species. Eighty-three species of ixodid ticks (hard ticks) occur in southern Africa (Walker, 1991) and five argasid species (soft ticks) are described for South Africa (Howell et al., 1978). The life cycles of the latter two families are similar, comprising egg, larval, nymphal and adult stages. The number of nymphal instars varies among the Argasidae, but is only one in the Ixodidae. Soft ticks only feed for a few hours at a time and most developmental stages change their host between blood meals. The life cycle of a typical ixodid tick is as follows:

The fed female drops off her host, lays a batch of several thousand eggs somewhere on the ground and dies. Minute six-legged larvae hatch and attach to a suitable host. The larvae moult into nymphae which in turn feed and moult into adults. The adults mate on the host, where the males often remain for months before they die. Most ixodid ticks feed on three different hosts, not necessarily conspecific. A few species no longer require multiple hosts and require only one or two hosts.

Argasid ticks are generally known to occupy arid habitats, where they are often found in rock crevices or burrowed in the top layers of soil. Here they await their hosts, which they primarily detect by odour (CO_2) or vibration. They have the ability to withstand extremely high temperatures and low humidity level. In contrast, the juvenile stages of ixodid ticks are prone to desiccation and are therefore dependent on adequate climatic or microclimatic conditions, the latter provided through ample vegetation. Host-finding strategies range from stationary ambush to active hunting behaviour. Questing ticks generally climb up vegetation and await their hosts at suitable height.

1.2. Ticks in the Kuiseb

Ticks from the Kuiseb delta region were already recorded by Galton (1890), who wrote: "... we employed ourselves in picking bush tics from our persons, for the bushes swarmed with them." In general ticks are known to occur in the Kuiseb area and local inhabitants as well as visitors often mention their presence. Tilson (1977) recorded Palewinged starlings feeding on ticks picked off klipspringers in the Kuiseb canyon, although the tick species was not determined. During a tick census carried out by Brain and Bohrmann (1992) along the lower reaches of the Kuiseb Canyon large numbers of the tick species Rhipicephalus gertrudae were collected and one specimen of Hyalomma merginatum rufipes was recorded for the study area. From some areas along the river, all much closer to the coast, soft ticks of the species Ornithodoros savignyi (the sand tampan) were recorded near human settlements (Zeidler, pers. obs., 1992). Apart from these findings, not much is known about ticks in the area.

However, studies on the Chacma baboons (Papio ursinus) resident in the lower reaches of the Kuiseb river in the central Namib desert, Namib-Naukluft Park, revealed that tick infestation reduced the reproductive success of the baboons substantially by contributing to neonatal deaths of at least 43% of all infants (Brain & Bohrmann, 1992; Lehmann, 1993). A comparison of tick numbers yielded by (a) baboons, who inhabit the so called wilderness area in the upper reaches of the lower Kuiseb and (b) domestic stock present in the further downriver regions showed that tick infestation of livestock was much lower and never reached more than 5% of the numbers carried by baboons. Two inspected adult male baboons carried more than 400 adult ticks, whereas domestic stock at no time yielded more than 20 adult ticks per animal (Brain & Bohrmann, 1992). This result raised the question why larger herbivores, the main hosts of the prevailing tick species R. gertrudae (Walker, 1991), carried significantly less ticks than members of a wild group of baboons, a mammal species never before recorded as host for this tick.
To elucidate this controversial finding, the study presented in this thesis was carried out. As basis for this research the following null hypothesis was formulated: There is no difference in tick abundance between the wilderness area and the degraded area.

1.3. Main objectives

In order to test this null hypothesis, the following main objectives were determined:

(1a) To assess tick abundance during late spring and winter in two distinct areas of the Kuiseb, one where livestock were present and one where livestock were absent.

(1b) To assess vegetation cover and plant species richness in the two areas.

(2) To assess diel activity patterns displayed by the tick Rhipicephalus gertrudae in the Kuiseb.

2. CHAPTER TWO

Tick Abundance

2.1. Introduction

For many tick species habitat requirements such as host availability and suitable microclimatic conditions are extremely important for survival (Oliver, 1989). Some tick species are known to show sensitivity to extremes of environmental conditions such as temperature and vegetation density (Fourie et al., 1992). The development and host-seeking stages of most tick species are dependent on a humid microclimate for their success. Eggs and larvae are considered to be the stages most vulnerable to desiccation (Arthur, 1962; Randolph, 1993). Adequate microclimatic conditions can be provided by vegetation. Destruction of vegetation successfully reduces development of ticks (FAO, 1984).

The presence of suitable habitat conditions is also crucial for many of the vertebrate hosts. Since the different instars of ticks often feed on different hosts, habitat requirements can be diverse.

The ephemeral Kuiseb river, with its dense riparian woodland, provides favourable habitat conditions for a number of organisms (Seely et al., 1985), but the impact of livestock farming on the lower section of the Kuiseb results in destruction of vegetation and thus microhabitats (Gabriel, 1993). Vegetation and animal communities are probably influenced by this impact. Since ticks rely on both these environmental factors, their abundance or absence may reflect disturbances in the habitat.

A sampling design was created to determine tick abundance and species richness in two distinct areas: the area used by livestock; and the wilderness area.

Structure and composition of the vegetation was monitored to assess if tick numbers were related to (a) the type of vegetation (plant species composition) at each sampling site and (b) the fractions of vegetation versus substratum (ground, sand, dry wood debris) representing a measure for surface cover.

2.2. Area & Habitat

2.2.1. The Namib Desert & the Kuiseb

The hyperarid Namib desert stretches along the south western coast of Africa (Fig. 2.1) and is a relatively temperate desert with sporadic rainfall events (Seely, 1987). The climatic conditions are moderate for a desert area, with little seasonal temperature variation (Lancaster et al., 1984). Fog forms regularly along the coast (Pietruszka & Seely, 1985) and drifts up to 100 km inland, providing an alternative source of moisture (Seely, 1987).

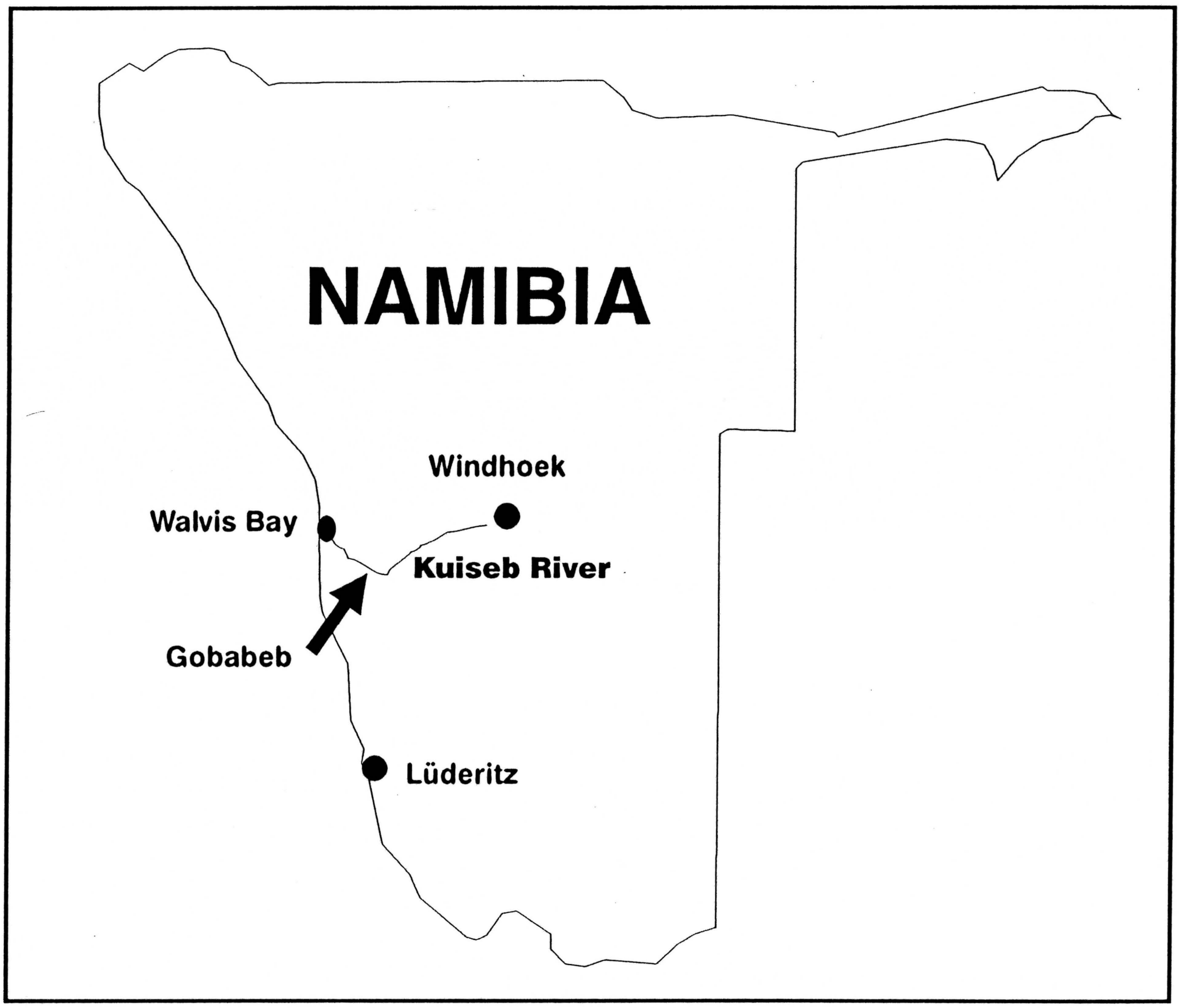


Figure 2.1: The Namib Desert stretches along the south-western coast of Africa. Namibia is the most arid country south of the Sahara. The ephemeral Kuiseb river crosses the central Namib where the Desert Ecological Research Unit of Nambia (DERUN) at Gobabeb is situated .

The ephemeral Kuiseb river is approximately 440 km in length (Stengel, 1964), extending from near Windhoek (22°40'S, 16°50'E) to the coast at Walvis Bay (23°10'S, 14°30'E). Through its constant underground waterflow and sporadically occurring floods, the Kuiseb supports dense forest vegetation. This river forms a linear oasis, which bisects the Central Namib Desert and separates the southern Namib Sand Sea and the gravel plains in the north (Fig. 2.2).

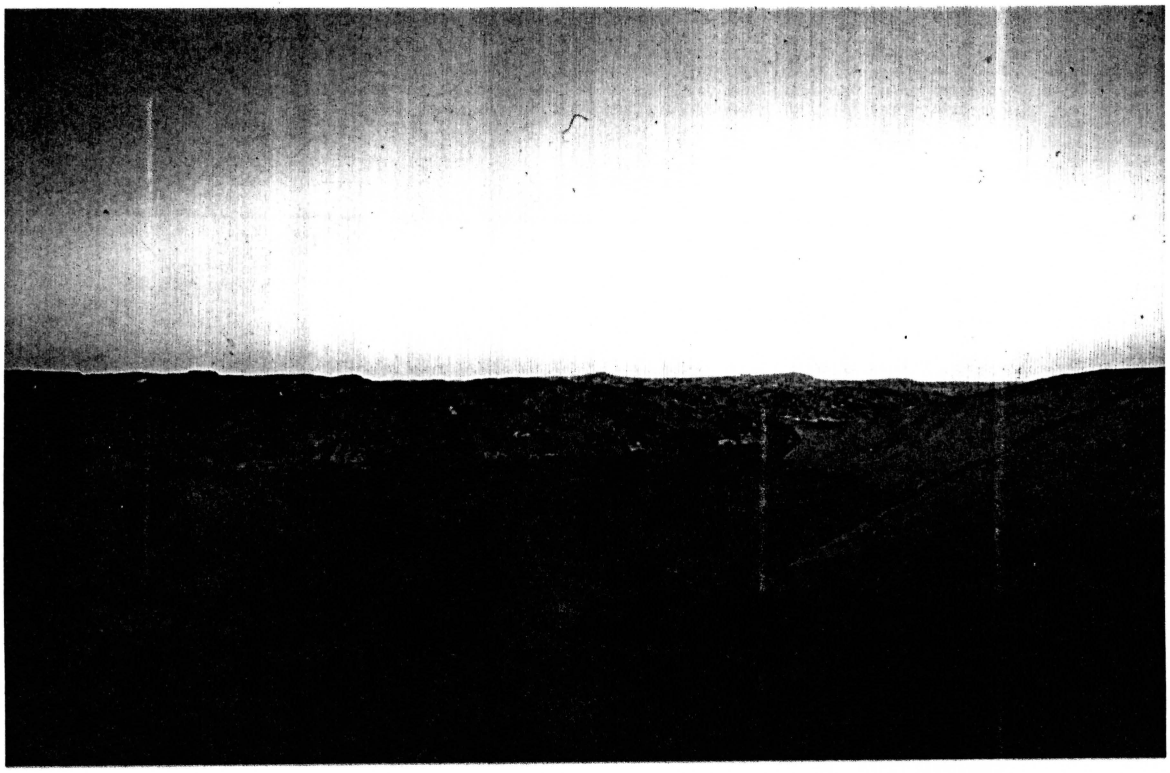


Figure 2.2: The constant underground waterflow of the Kuiseb supports the growth of a dense riparian forest vegetation.

The river provides shelter, food and limited water resources for a variety of animals, allowing even some non-desertic or partially adapted species to extend their range into the true desert (Seely et al., 1981). The river forms a connecting bridge to inland populations. Under aperiodic extreme conditions the Kuiseb acts as a last resort or refuge on a daily or seasonal basis (Hamilton et al., 1977).

Within the borders of the Namib-Naukluft Park, approximately the upper 150 km of the Kuiseb river are a proclaimed wilderness area, and human use is prohibited. The lower reaches of the Kuiseb, stretching towards the coast, are occupied by humans. The Topnaar, an indigenous group of Nama-speaking People, have inhabited the banks of the river for at least 300 years as nomads (Budak, 1977). Today they maintain small settled farms with large numbers of livestock (Seely et al., 1981).

2.2.2. Vegetation

The vegetation along the lower reaches of the river is dominated by perennial woody plant species such as Acacia erioloba, Faidherbia albida, Tamarix usneoides, Euclea pseudebenus, Salvadora persica, and two different Ficus spp., F. cordata and F. sycomorus. Indigenous and alien plant species such as Argemone ochroleuca, Datura innoxia, D. stramonium, Flaveria bidentis, Nicotiana glauca, Ricinus communis and Zygophyllum simplex occur in the riverbed and flood plains of the river. Individuals of these species often persist for several years. A variety of annual plant species establish themselves along the river channel after a flood and die off as the moist conditions near the surface drop (Seely et al., 1981; Theron et al., 1980). Therefore, this vegetation changes in cycles triggered by the flood events.

2.2.3. Mammals

Mammals play a major role as hosts in the lifecycle of ticks. About 40 mammal species are associated with the Kuiseb (Stuart, 1975). Larger animals, such as spotted hyena (Crocuta crocuta), jackal (Canis mesomelas), chacma baboons (Papio usrsinus), steenbok (Raphicerus campestris) and klipspringer (Oreotragus oreotragus) occur along the river and are recorded as hosts for ticks. Tilson (1977), for example, observed pale winged starlings (Onychognathus nabouroup) picking ticks from klipspringer in the Kuiseb canyon; the tick species was not determined. Brain (1993) reported high tick burdens carried by baboons living along the river and a study by Brain & Bohrmann (1992) identified almost exclusively R. gertrudae occuring in the baboons range. Rarely the ticks in the area were reported to attach to humans.

Larger mammal densities along the Kuiseb are considered to be relatively low (van Wyk et al., 1985) but no recent data are available.

The interaction of these animals with their environment is of crucial importance in terms of tick biology, since they form a major part of the habitat. Interactions between the larger herbivorous mammals and the vegetation were studied by Hamilton et al. (1977). Briefly, they state that gemsbok (O. gazella) are present in the Kuiseb Canyon at any time of the year and are concentrated there in search of alternative fodder when desertic vegetation in the dunes declines. Other wild herbivores feed on the riparian forest vegetation on a regular basis (Cloete, 1983; Tilson, 1980), but browsing and grazing impact on the vegetation is negligible. Smaller mammals such as rodents rely on the dense forest vegetation as source of food and shelter (Christian, 1977). herbivorousmammals such as rodents rely on the dense forest vegetation as source of food and shelter (Christian, 1977).

Domestic animals in the lower Kuiseb regions include goats, sheep, donkeys and cattle, all of which feed extensively on the vegetation. Vegetation at ground level is severely denuded and a well-defined browse line is established in the area used by livestock. The degradation of the vegetation is strongly related to goat impact through browsing and trampling (Gabriel, 1992; Gabriel, 1993). This impact is particularly discernable within 3,5 km of water points.

2.2.4. Study sites

A 50km range along the Kuiseb river, within the Namib-Naukluft Park, was delineated as the study area. This area was chosen to represent: (A) the area used by livestock which hosts large populations of domestic stock and shows signs of degradation due to overgrazing and trampling; and (B) the so-called wilderness area where only game is present and which shows little or no browsing impact on the vegetation. Area A and area B overlap and livestock may move into the wilderness area occasionally.

In the two areas six study sites in each (n=12) were chosen for tick sampling. These locations were not selected at random. In order to be able to compare changes in tick numbers per study site over an extended time period I used the same sampling sites in the upriver regions as Brain and Bohrmann in their 1991 survey (Brain & Bohrmann, 1992). They selected areas with similar plant cover, plant species composition and physical features - characteristics they assessed visually. Downriver sites were established following Gabriel (1993), who quantified the impact of stock within the area used by livestock. He found that the impact diminished with increasing distance from water points. The present study considers whether such a gradient could also influence tick abundance. Based on these reflections and on the results of a preliminary survey (see 2.3.3), the following study sites were established:

Table 2.1: Location of the study sites (n=12)

Area A: Livestock area

Area	Distance from Gobabeb (km)	location
A1	0,0	Gobabeb compound well
A2	3,5	3,5km radius Gobabeb compound well
A3	8,9	Natab I well
A4	12,4	3,5km radius Natab well
A5	23,0	Homeb well
A6	26,5	3,5km radius Homeb well (Brain 2km)

Area B: Wilderness area

Area	Distance from Gobabeb (km)	location
B1	32,1	Brain 7,6km, Little fig tree
B2	33,9	Brain 9,4km, Bad bend
B3	37,9	Brain 13,4km, Gully camp
B4	41,9	Brain 17,1km, Big fig tree
B5	46,9	Brain 22,1km, Gorob confluence
B6	49,2	Brain 24,4km, Sarib (Hurabis/Warthog)

A map allocating the study sites is provided in figure 2.3.

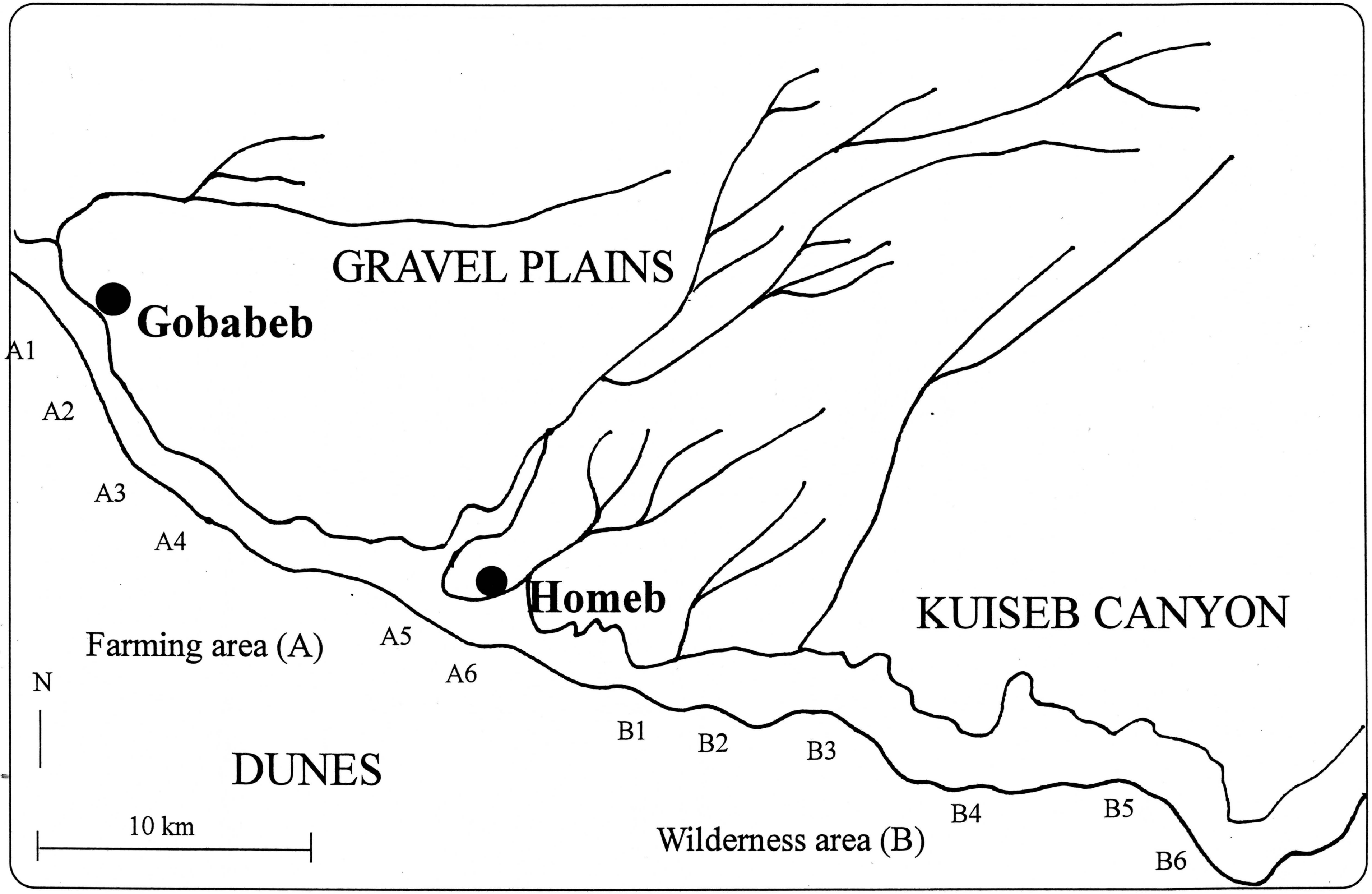


Figure 2.3: Map of the 12 study sites along the lower Kuiseb including a farming area (A) and a wilderness area (B).

2.3. Materials and Methods

2.3.1. Climatological data

During all sampling periods minimum and maximum temperatures in the shade were recorded, using standard thermometers. At the end of sampling at each site humidity was measured with a psychrometer. The percentage of clouds covering the sky at the time of observation was estimated.

Monthly climatological data such as average minimum and maximum temperatures and rainfall recorded at Gobabeb weather station are presented in table 2.2 and give a general indication of climatological conditions in the region.

Table 2.2: Climatological data obtained from the first order weather station at Gobabeb (August 1993 - August 1994).

Mean temperatures at Gobabeb (8/93-8/94) in C°, Rainfall in mm

Month	*Max*	*Min*	*08:00*	*14:00*	*20:00*	*Rain*
Aug 93	9.8	26	10.6	24.3	19.6	-
Sep 93	13.7	33.9	15	32.8	25.5	-
Oct 93	12.2	30.8	13.9	28.5	22.8	-
Nov 93	12.8	30	14.5	27.9	22.7	0.5
Dec 93	14.7	32.2	16.8	30.4	24.6	6.9
Jan 94	14.7	29.7	15.7	27.6	23.8	3.0
Feb 94	16.5	31.8	17.3	30	26.3	1.4
Mar 94	14.6	32.3	15.4	30.2	25.7	-
Apr 94	16.3	32.6	17.1	30.8	25.1	4.5
May 94	16	32.5	16.7	31.7	24.8	-
Jun 94	10.7	26.7	11.7	25.2	19	2.0
Jul 94	11.3	27	12.2	26.2	20	0.2
Aug 94	10.5	28.2	11.6	26.5	20.7	-

2.3.2. Vegetation survey

Vegetation presence/absence was recorded along 20 m randomly chosen tick sampling stretches (see 2.3.3) by laying out a 20m tape measure and noting each plant species covering a minimum of 1m along the stretch (Fig. 2.4). Each meter of substratum and its nature, i.e. ground/sand/dry wood debris, was indexed.

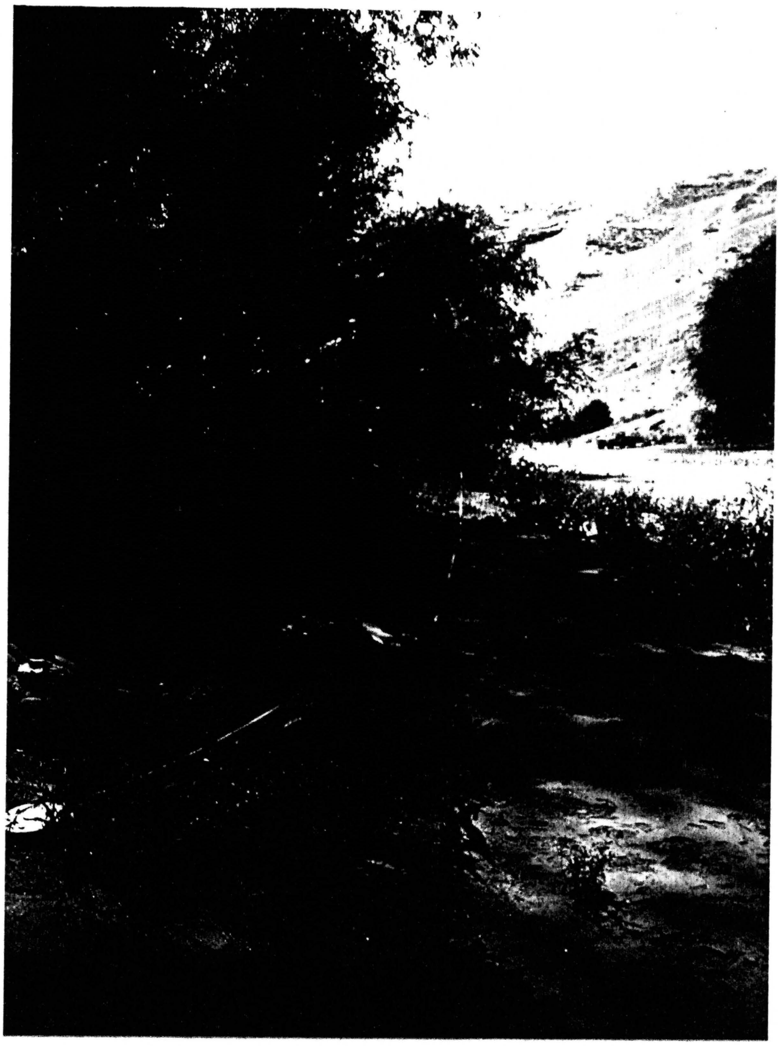


Figure 2.4: A 20 m transect was measured and collected for ticks along first order animal paths. All plant species and substratum characteristics covering a minimum of 1 m of the transect were recorded to assess if tick numbers found were related to particular vegetation features.

The vegetation and surface characteristics of each sampling site were recorded over the entire study period.

2.3.3. Preliminary tick survey

In August 1993 a preliminary tick survey was implemented to assess tick abundance, distribution and species richness along an approximately 50 km linear range of the Kuiseb stretching from Gobabeb to Sarib, thus including the wilderness area as well as the area used by livestock. Six study sites were chosen, each measuring approximately 500 m by 200 m. Ten randomly chosen runs of 20 m each were sampled. Ticks were collected by dragging a $1m^2$ flag (mauve-coloured towel) attached to one end of a 1,6 m wooden stick at a slow, constant walk over shrub vegetation ("flagging") (Brain & Bohrmann, 1992) up to approximately 1m in height, a technique that mainly collects questing ticks from the vegetation (Fig. 2.5.). Ticks were removed by hand and all ticks obtained from the flag were preserved in 70% Methanol for counting and identification. Expert advice on identification was provided through the Onderstepoort Veterinary Institute, Pretoria, South Africa.

Figure 2.5: At a slow constant walk a $1m^2$ towel fitted onto a 1,6m stick was dragged over the ground vegetation up to approximately 1m height to collect ticks off the vegetation. At the end of each 20m transect ticks were picked off the cloth and counted.

A simple spotcheck-like study was designed to assess whether more ticks were to be found at the demarcation line of the vegetation or amidst the vegetation. At study sites B1, B2 and B3, three areas were selected randomly and two 1m² plots were measured. One plot was always established at the edge of the vegetation and the other about 1,5m within the thicket. The vegetation and the ground were thoroughly examined for ticks and the tick numbers obtained at inward and outward lying plots compared.

The results obtained through these preliminary observations served as basis for the actual study, which will be introduced in the following paragraphs.

2.3.4. Sampling method

Sampling was conducted over two time periods covering late Spring 1993 (October & November 1993) and Winter 1994 (June & July 1994), to assess seasonal variation in tick abundance. Tick abundance was determined by the same tick collecting method ("flagging") used in the preliminary survey. In accordance with the results of the same, final study sites were selected (n=12, see 2.2.4) and the sampling design modified. Due to the fact that most ticks were found taking up questing position at the edge of the vegetation (see 2.4.1), stratified random sampling (Mühlenberg, 1993) was applied, restricting sampling to frequented animal paths. In contrast to the preliminary survey, it was decided to carry out non-destructive sampling, releasing all ticks after counting at the end of each transect.

In the wilderness area, 500m were measured along each side of the river channel, the river channel representing a first order game path. The vegetation along the channel is dense and only few gamepaths cut through it.

Since the paths used by domestic animals are not restricted to the course of the river channel, sampling took place over a much broader area, measuring 500m by 200m across the river.

2.3.5. Tick recovery and identification

To gain a reliable picture of the tick species richness obtained through the sampling design, the preliminary survey was replicated in June 1994 and all ticks identified under the microscope.

At the end of each 20m run, the ticks attached to the cloth were removed, counted, identified, sexed and released at the point of capture.

2.3.6. Statistical analyses

All data was analyzed using Number Cruncher Statistical System software (NCSS 5.03/5.3, Hintze, 1992). All data sets were tested for normal distribution and appropriate statistical tests were performed.

Preliminary survey

Tick numbers found at the edge of vegetation were compared to tick numbers obtained from plots admidst the thicket by using the Mann-Whitney two-sample test.

Vegetation survey

The numbers of plant species in the distinct areas A and B were compared for each sampling date using two-sample t-test (two-tailed). Only plant species which were recorded at least 5 times were considered in the calculations.

Similarities in plant species composition between the study sites for (a) the entire survey period and (b) each sampling month were revealed by cluster analysis and visual inspection of the resulting dendrograms. Cluster analysis as a statistical procedure is explained in detail below, under paragraph "Cluster analysis". Since data within each study site was extremely heterogenous, similar analyses were performed for selected study sites on the transect level.

The vegetation presence/absence data obtained from each study site were summed and expressed as vegetation/substratum ratio within areas A and B for each sampling month.

Two-sample t-test (two-tailed) was applied to compare the total amount of vegetation present in areas A and B during each sampling period.

In order to detect study sites with similar vegetation/substratum ratios, cluster analysis was performed as described below for plant species composition.

Tick abundance

Total and monthly tick abundance was compared between the wilderness area and that used by livestock using the Mann-Whitney two-sample test. Tick abundance within each of the study areas was investigated in detail for the entire study period and each sampling date using the Kruskal-Wallis test, with calculations of the Kruskal-Wallis multiple comparison z-values. The same test was used to detect seasonal changes in tick abundance.

Cluster analysis was used to detect similarities in tick abundance between the study sites.

Vegetation & Tick abundance

A possible association between tick abundance and plant species composition or surface/vegetation ratio was assessed for each month using multiple regression analyses. Data for plant species composition analyses were reviewed and species which were present but which covered less than 5m within the entire study area were excluded.
In a two variable cluster analyses model both tick abundance and vegetation/surface ratio were considered.

Cluster analyses

To evaluate the null hypothesis, similarities between the individual study sites were investigated in detail, from tick abundance patterns to plant species composition and vegetation/substratum ratios by applying hierarchical cluster analysis (NCSS, 1992; Sokal & Rohlfs, 1981; Norton-Griffiths et al., 1975). The results are displayed in dendrograms. In this study single linkage, also known as nearest neighbour clustering, was performed and the similarities between the individual study sites were measured with Euclidean distance, the cut-off point was constantly set at 1.0. Resulting groups were clustered together when members were more similar to each other in tick abundance, vegetation features or a combination of these than they were to members of other groups. Statistical validity was not specifically tested for the clustering but the results for tick abundance were compared with the respective results obtained through the Kruskal-Wallis procedures (see 2.3.4).

2.4. Results

2.4.1. Preliminary tick survey

The results of the spot-check assessing whether more ticks would be found at the edge of the vegetation suggest that significantly more ticks are found at the demarcation line than in thethicket (Mann-Whitney, P<0,05)(Tab. 2.3).

Table 2.3: Spot check: Where do the ticks sit on the vegetation? At the edge or in the thicket? Significantly more ticks were found at the edge of the vegetatio

Edge	Thicket
B1 = 37	B1 = 0
B2 = 20	B2 = 0
B3 = 6	B3 = 1

2.4.2. Vegetation analysis

Plant species composition

Plant species richness differs significantly between area A, where numbers of species are lower, and area B, where numbers of species recorded are higher during all months of the survey (P<0,05; t-test) (Tab. 2.4).

Table 2.4: Total number of plant species found along the sampling transects in area A (farming area) versus B (wilderness area) during the individual months.

	Oct 93	*Nov 93*	*June 94*	*July 94*
Area A	17	16	12	9
Area B	23	21	17	19

The dendrograms obtained from the cluster analysis comparing plant species composition at the study sites (Fig. 2.6) suggest that, under a temporal aspect, overall plant species composition is more diverse in October and November (late spring) than in June and July (winter). Thus comparison of the individual sites is more complex for the late spring samples. It was found that study sites A1 and B6 differ substantially from most other sites throughout the survey. Plant species composition at site A6 seems to be more comparable to most B sites while B3 shows closer relations to most A sites.

The dendrograms obtained on the transects level for the selected study sites are included in the appendix and they will not be considered in much detail here. However, more similarities in plant species composition along the examined transects were found in area A than in area B. Seasonal changes cannot be determined unequivocally.

Cluster Analyses: Plant Species Composition

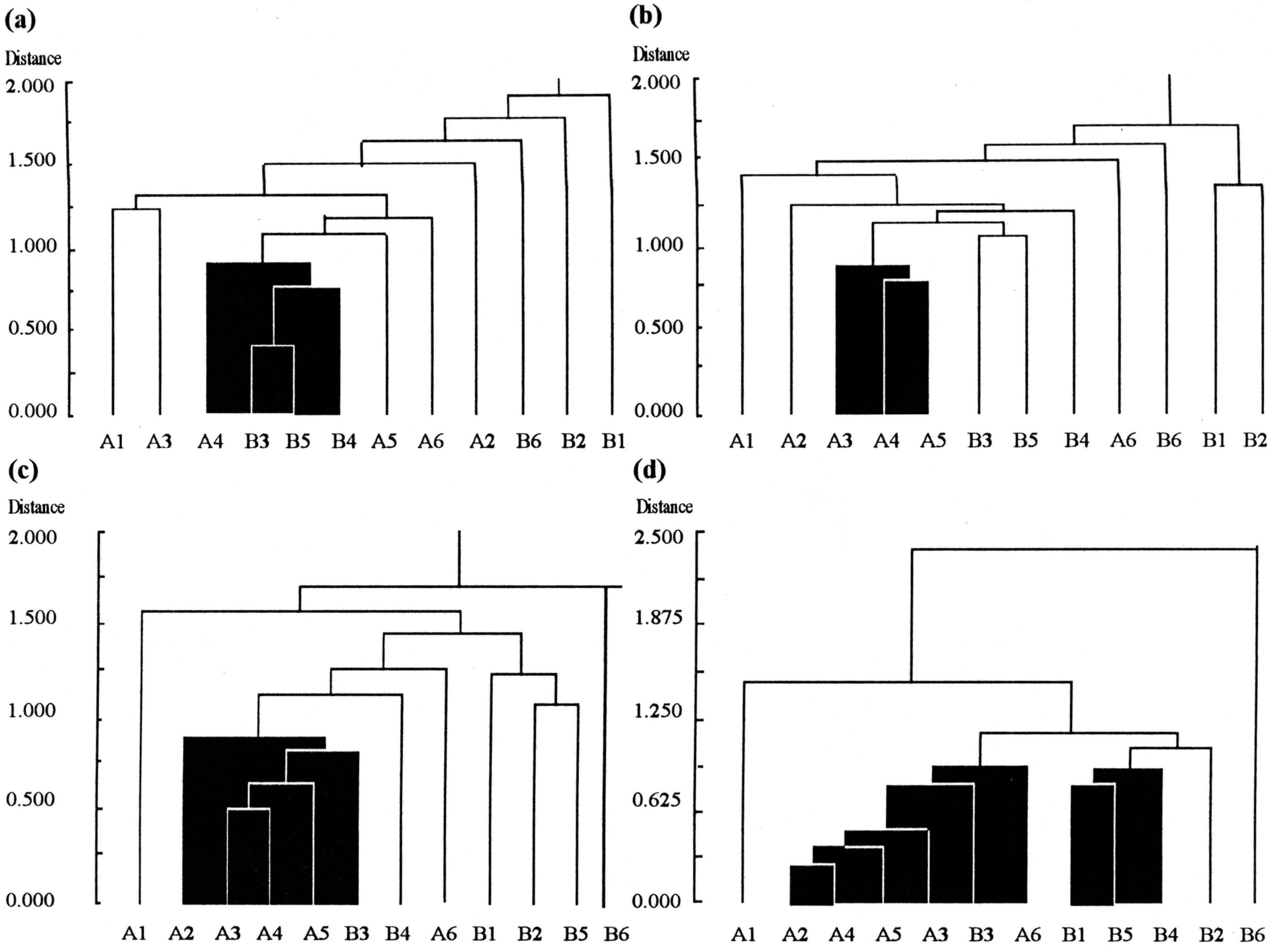


Figure 2.6: Dendrograms obtained for the clustering analyses of the plant species composition at the 12 study sites for the individual months (a) October 1993, (b) November 1993, (c) June 1994 and (d) July 1994. Sites which were similar in vegetation composition are grouped together.

Vegetation/substratum ratio (surface cover)

The vegetation/substratum ratios in areas A and B obtained for the individual sample months are illustrated in figure 2.7. The proportion of near-surface vegetation recorded is significantly higher in area B (wilderness area) (Fig. 2.8) than to area A (area used by livestock) (Fig. 2.9).

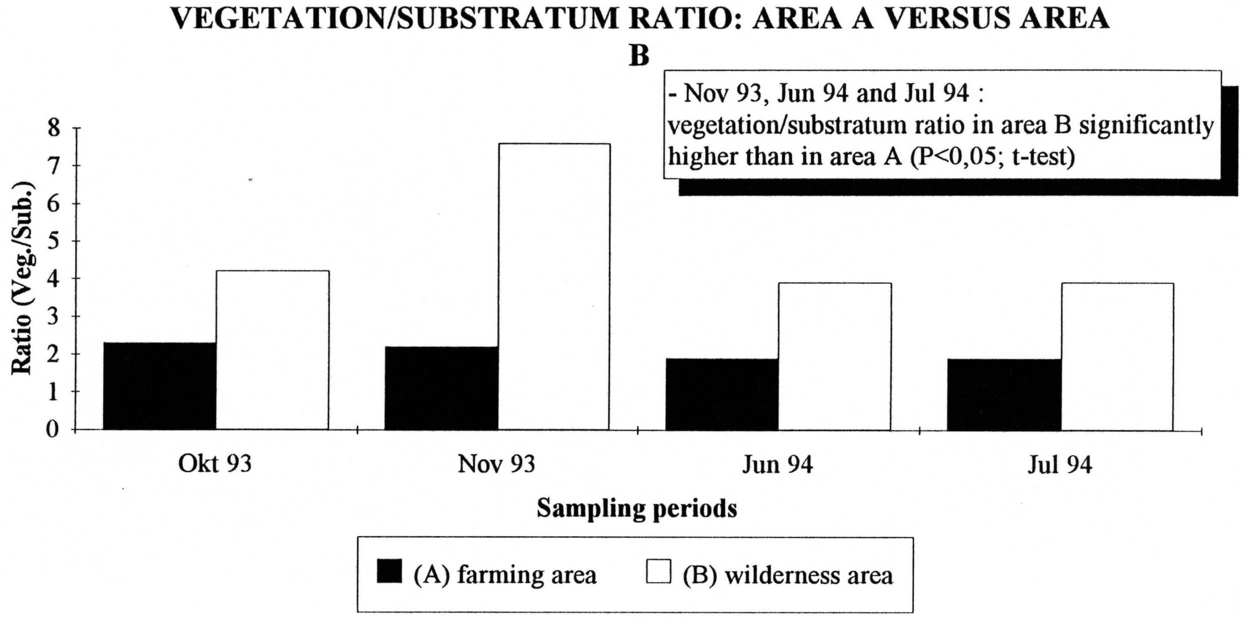


Figure 2.7: Vegetation/substraum ratio compared between the farming area (A) and the wilderness area (B). The proportion of vegetation is constantly higher in area B.

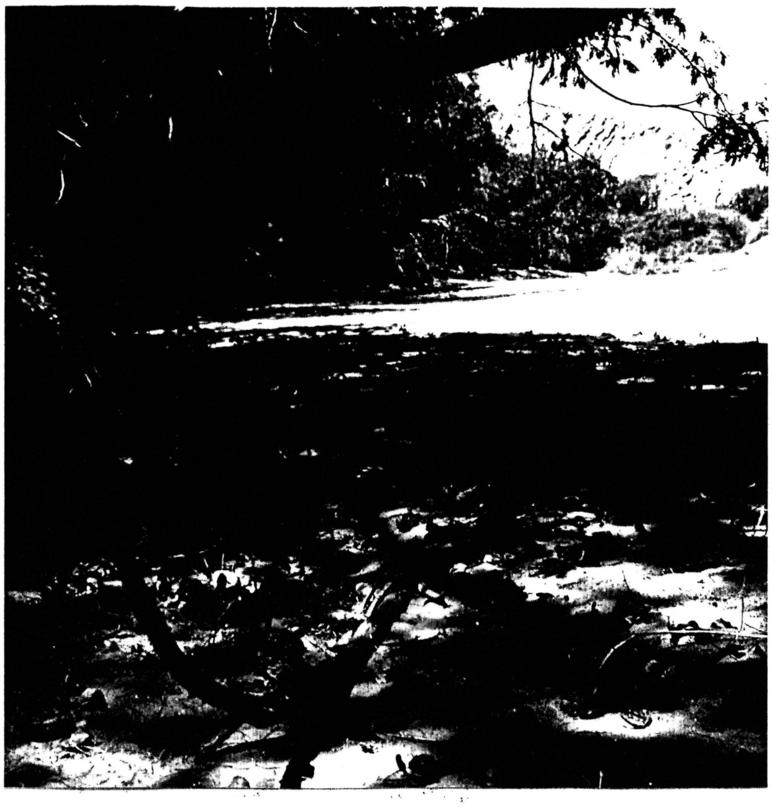


Figure 2.8: Photograph of vegetation along the Kuiseb river channel in area B (wilderness area). Faidherbia albida pods are lying on the ground, overall the ground vegetation is intact.

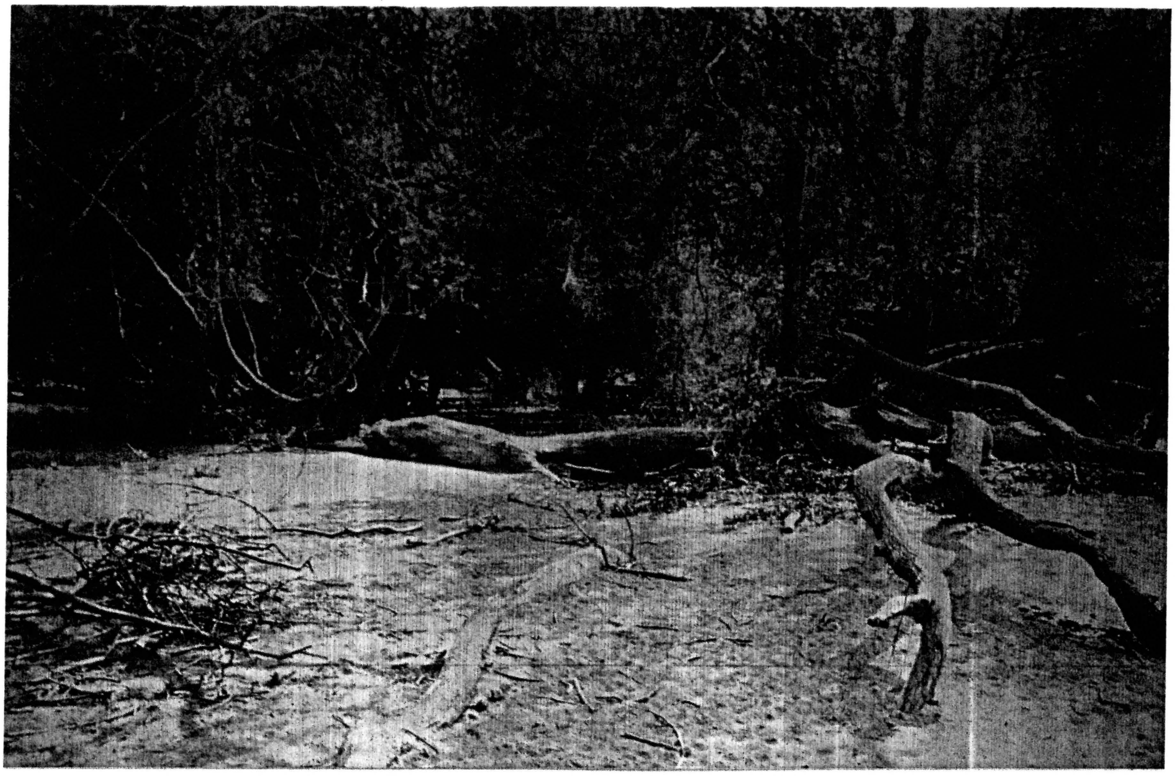


Figure 2.9: Photograph of the vegetation along the Kuiseb river in area A (farming area). Mostly barren sand and dry wood debris cover the ground. The vegetation is degraded by browsing and trampling.

Altogether, area B has a significantly higher proportion of vegetation surface cover than area A ($P<0,05$; t-test).

The comparison of the vegetation/substratum ratios within the individual months reveals significant differences between area A and area B for November 1993, June 1994 and July 1994 respectively ($P<0,05$; t-test). In October 1993 no significant difference in the ratio was found ($P>0,05$, t-test).

Cluster analysis was performed for the entire survey period as well as for the single months. In the resulting dendrograms, study sites with similar surface cover ratios were grouped together. Examination of the combined data set (Fig. 2.10) indicates that sites A2, A3, A5 form a group well distinguishable from the remaining heterogenous sites. A1 stands out as very different, linking on a high level with the other groups. It is striking that sites A4 and A6 differ fundamentally from the other A sites and they show great congruency with the B sites. This result is not as clear if considered on the monthly basis, but trends are detectable (Fig.2.11).

Cluster Analyses: Vegetation/Substratum Ratio

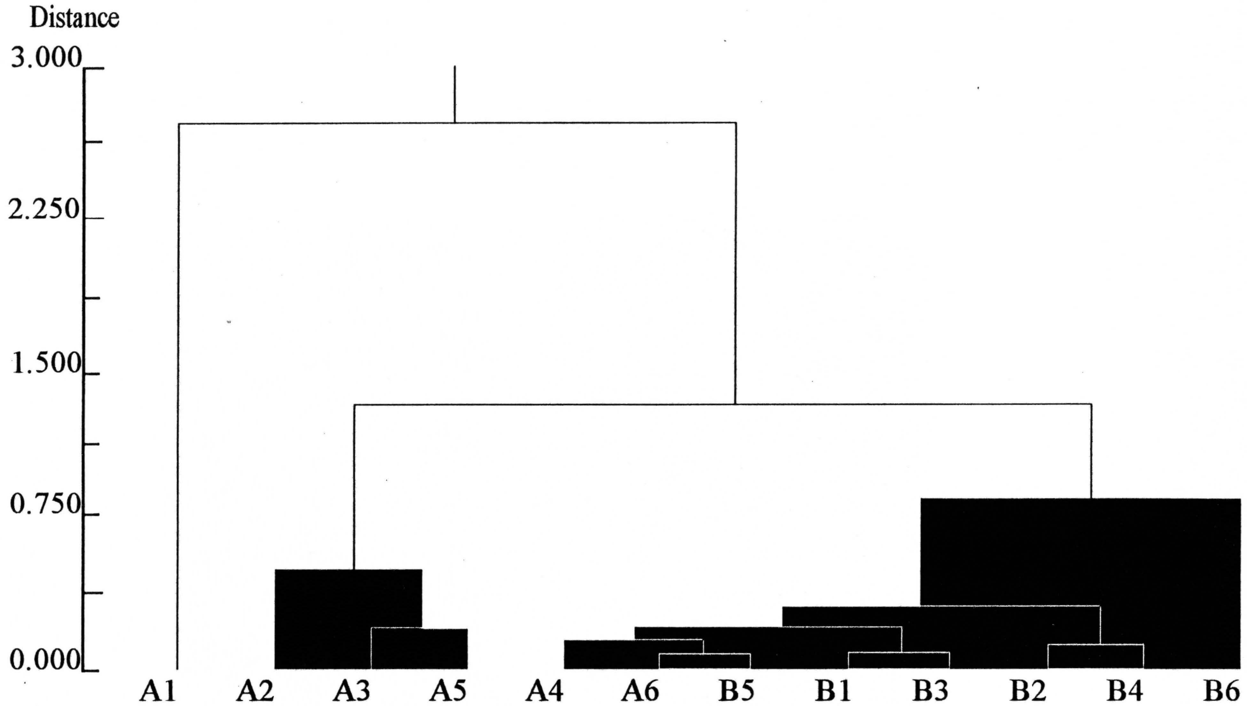


Figure 2.10: Dendrogram obtained for the clustering analysis of the vegetation/surface ratio at the 12 study sites for the entire study period. Sites with similar surface cover ratios are grouped together. Three main groups are suggested by this clustering. Site A1 stands solitary.

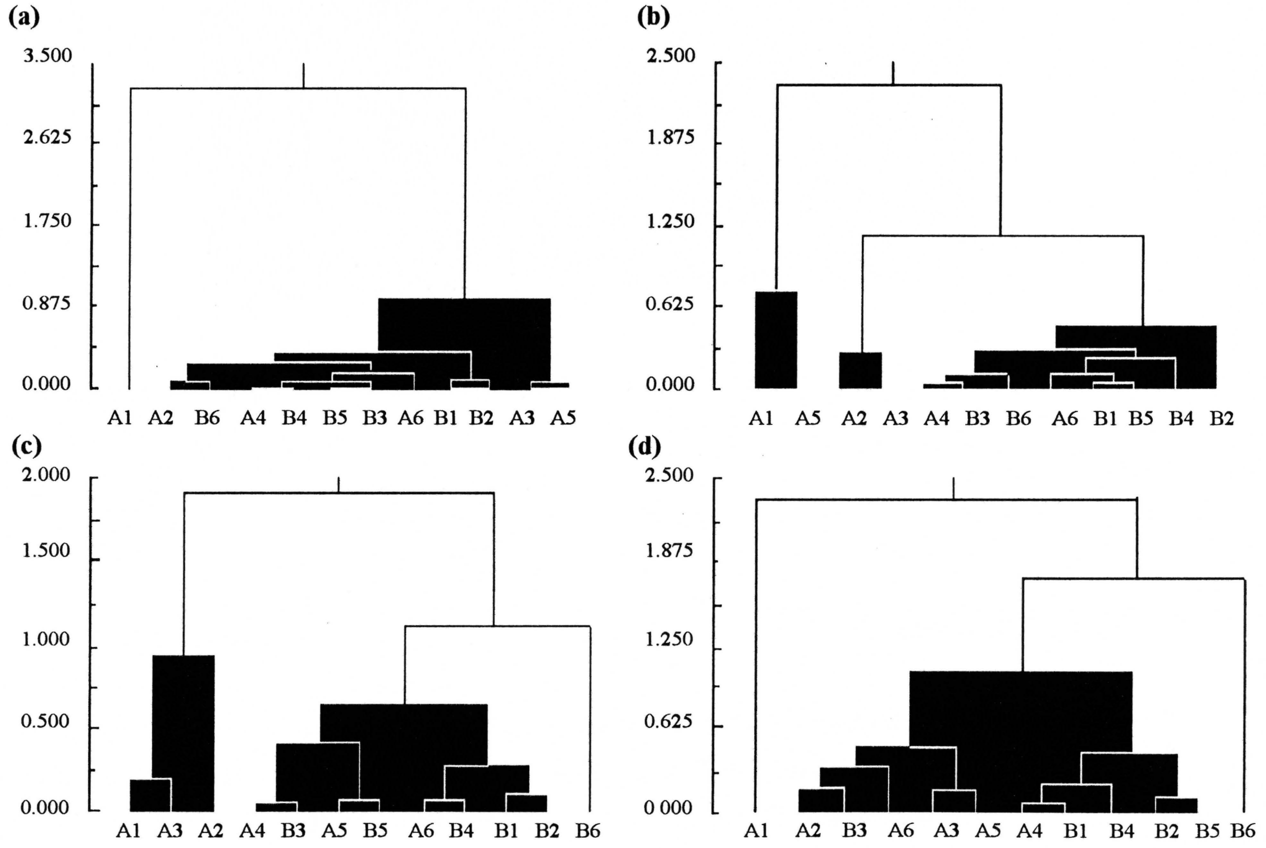


Figure 2.11: Dendrograms obtained by cluster analyses of vegetation/substrate ratio at the 12 study sites for the individual months (a) October 1993, (b) November 1993, (c) June 1994 and (d) July 1994.

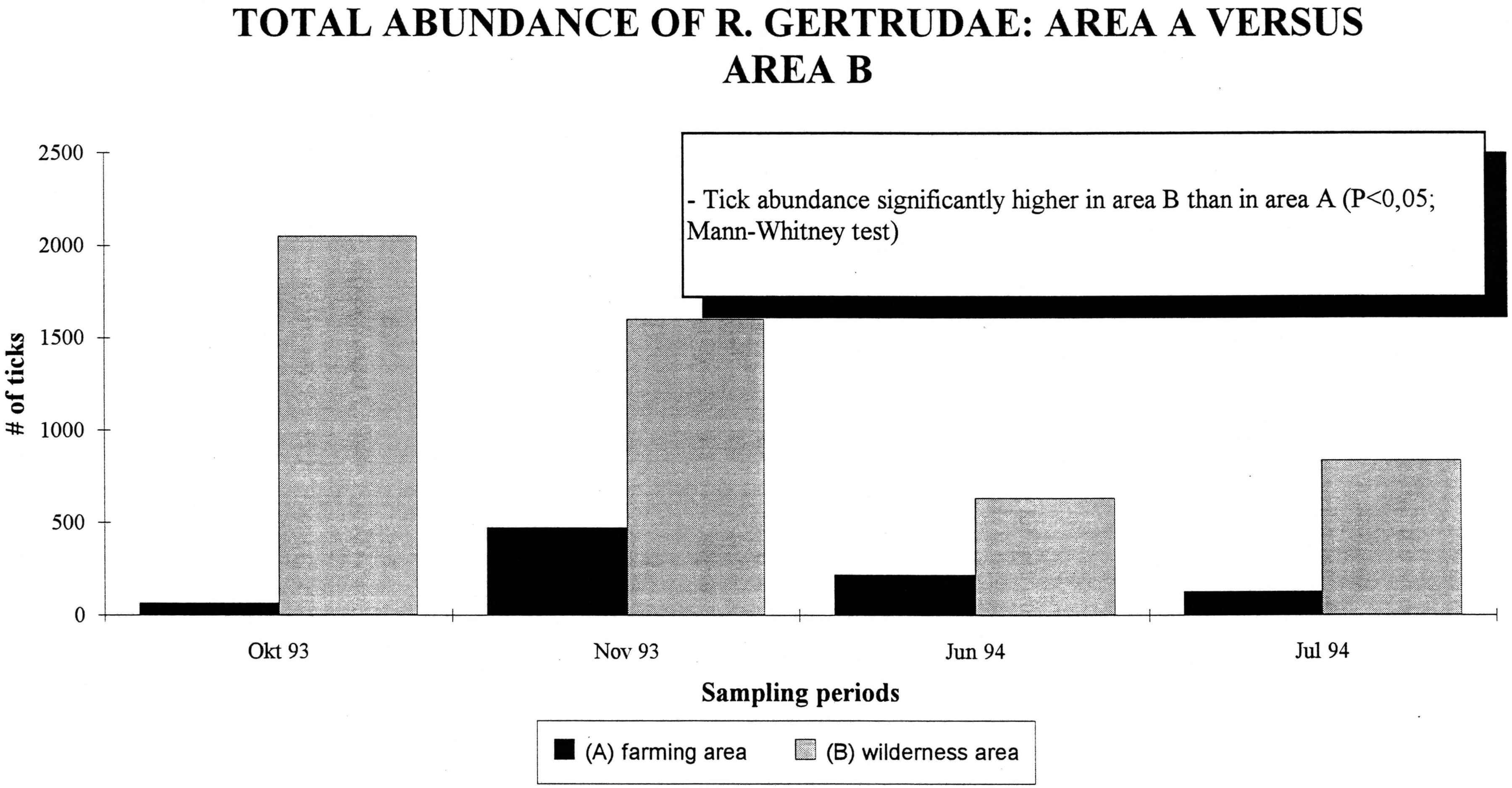
2.4.3. Tick species richness

All ticks found during this study were identified as adult Rhipicephalus gertrudae (Fig. 2.12).

Figure 2.12. Photograph of R. gertrudae in questing position on the vegetation awaiting passing hosts.

2.4.4. Seasonal changes

Comparing total tick numbers found in the entire area over the four months of sampling, no seasonal fluctuations were observed (P>0.05; Kruskal-Wallis). Examining the data for areas A & B independently, a significant difference in tick numbers between the months November 1993 and June 1994 was found for area B (P<0,05; Kruskal-Wallis) (Fig. 2.13).



- Tick abundance significantly higher in area B than in area A (P<0,05; Mann-Whitney test)

Figure 2.12: Tick abundance during the individual months sampling compared between (A) degraded area and (B) wilderness area. Tick numbers in area B are continously higher than in area A.

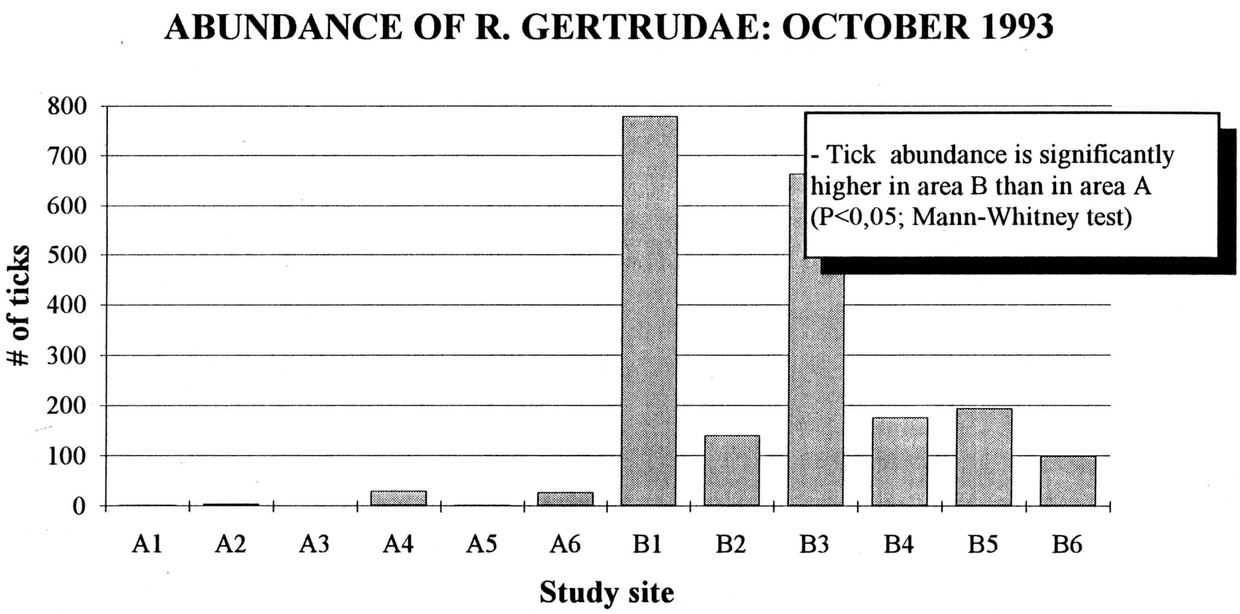
2.4.5. Tick abundance

The absolute numbers of ticks found at the 12 study sites for the sampling periods are presented in table 2.5 , which also includes summarized descriptive statistics. Tick numbers illustrated in figures 2.14 - 2.17. The graphs show the heterogenous distribution of the data. As shown in table 2.5, tick numbers found per study site fluctuate from zero (study site A1) to 780 (study site B1) within the same month (October 1993). Range and standard deviation are high at each study site. Examination of the coefficient of variation suggests a general trend towards lower and more homogenous values for samples from area B than from area A.

Table 2.5: The total number of ticks obtained through flag sampling for each study site are given for the individual sampling periods. The standard deviation of each sample is included. The range is indicated in brackets.

Sampling period	*A1 tick#s (range)*	*Stddv*	*A2 tick#s (range)*	*Stddv*	*A3 tick#s (range)*	*Stddv*
Oct 93	2 (0-1)	0.4	5 (0-2)	0.7	0	0
Nov 93	0	0	6 (0-3)	1.1	22 (0-13)	4.4
Jun 94	0	0	10 (1-5)	1.6	11 (0-3)	1.3
Jul 94	1 (0-1)	0.3	10 (1-3)	1.3	18 (0-8)	2.7
Sampling period	*A4 tick#s (range)*	*Stddv*	*A5 tick#s (range)*	*Stddv*	*A6 tick#s (range)*	*Stddv*
Oct 93	30 (0-25)	7.8	2 (0-2)	0.6	27 (0-9)	3.3
Nov 93	131 (0-58)	17.1	6 (0-3)	1.3	308 (0-110)	34.1
Jun 94	22 (0-5)	1.6	5 (0-3)	1.1	169 (0-79)	25.2
Jul 94	17 (0-10)	3.1	5 (0-3)	1	76 (0-21)	7.6

Sampling period	*B1 tick#s (range)*	*Stddv*	*B2 tick#s (range)*	*Stddv*	*B3 tick#s (range)*	*Stddv*
Oct 93	780 (0-199)	85	139 (0-49)	15.7	664 (5-292)	91.5
Nov 93	599 (2-162)	62.3	88 (0-32)	8.9	285 (5-85)	23.8
Jun 94	166 (0-58)	17.9	77 (0-33)	11	87 (0-20)	6.3
Jul 94	278 (3-84)	29	92 (0-33)	1	136 (0-43)	14.9
Sampling period	*B4 tick#s (range)*	*Stddv*	*B5 tick#s (range)*	*Stddv*	*B6 tick#s (range)*	*Stddv*
Oct 93	176 (0-53)	16.8	193 (0-78)	23.7	99 (0-48)	14.1
Nov 93	167 (1-63)	18.7	397 (1-121)	38.3	67 (1-11)	2.9
Jun 94	140 (0-98)	30	93 (0-31)	10.4	69 (0-24)	7.8
Jul 94	201 (0-121)	37.6	98 (0-27)	10.3	31 (0-8)	2.8



- Tick abundance is significantly higher in area B than in area A (P<0,05; Mann-Whitney test)

Figure 2.14: Tick abundance data obtained from flag sampling in October 1993.

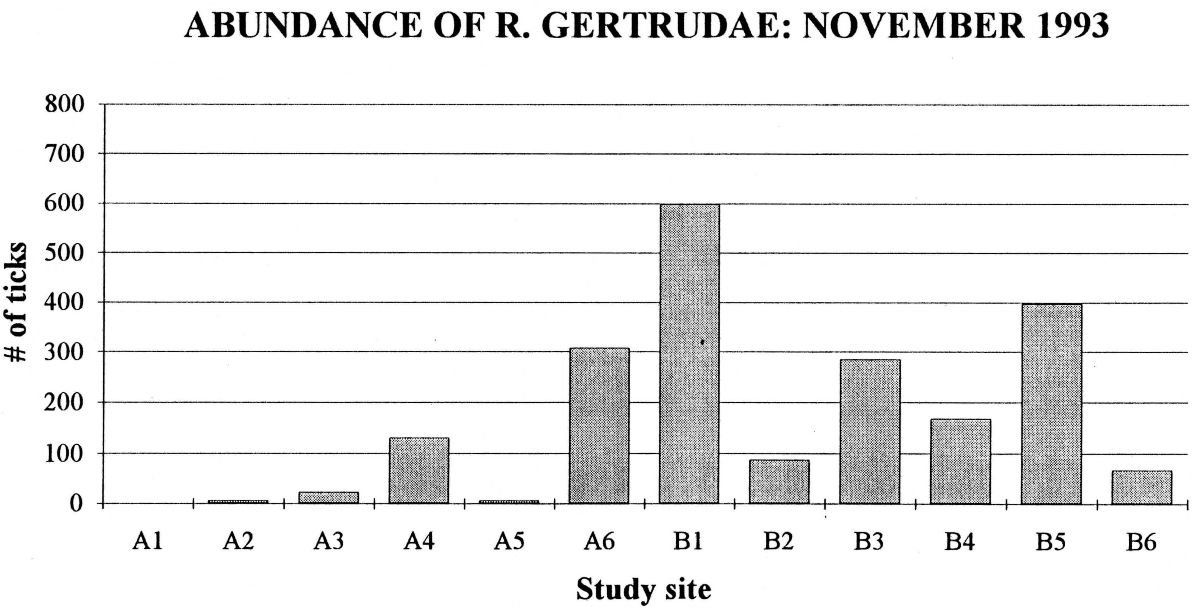


Figure 2.15: Tick abundance data obtained from flag sampling in November 1993.

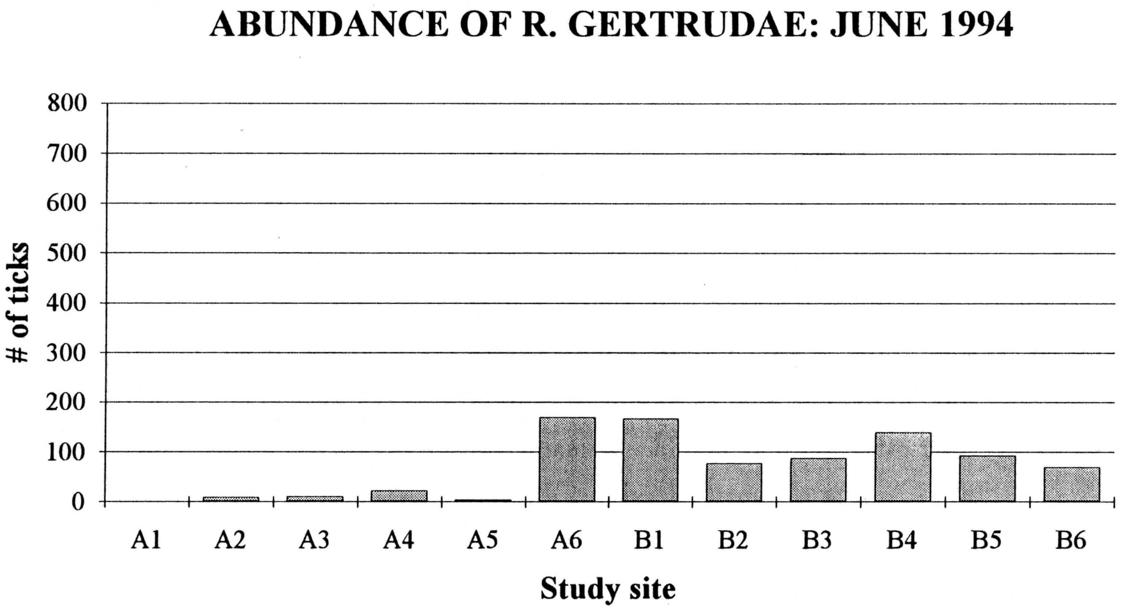
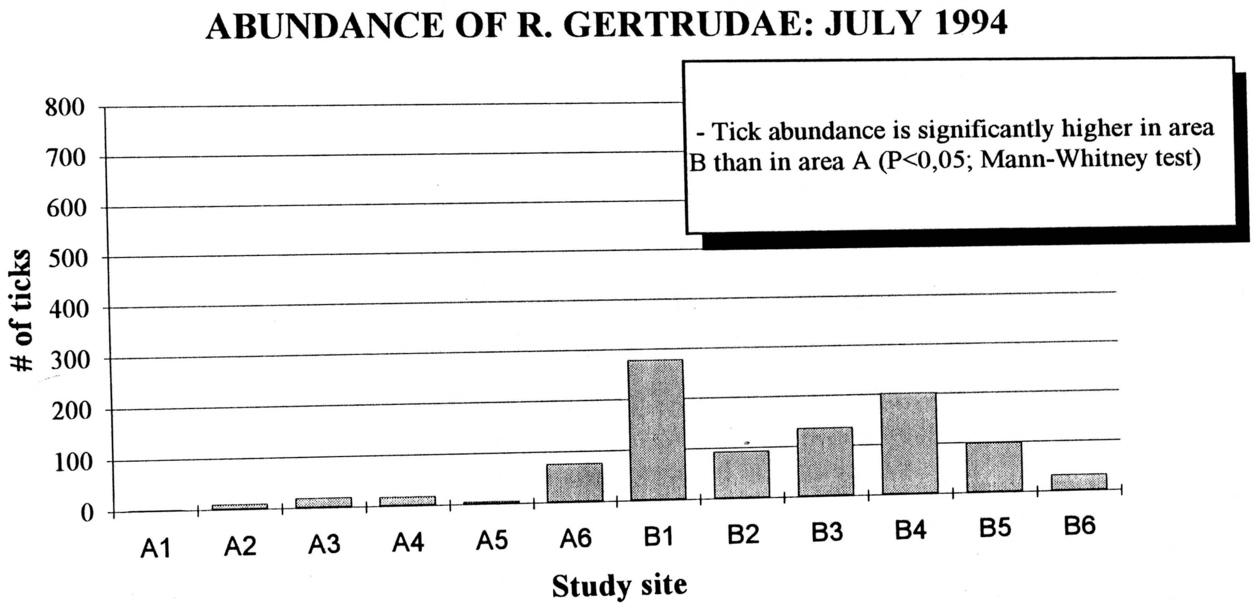


Figure 2.16: Tick abundance data obtained from flag sampling in June 1994.



- Tick abundance is significantly higher in area B than in area A (P<0,05; Mann-Whitney test)

Figure 2.17: Tick abundance data obtained from flag sampling in July 1994.

Collectively, the total number of ticks counted in area B was at least five times greater than in area A, a calculation statistically verified on a significance level of P<0,05-(Mann-Whitney two-sample test) (Fig. 2.10).
In all four months ticks found in area B (wilderness area) outnumbered ticks in area A (area used by livestock) (Figs. 2.14 - 2.17). These values for tick abundance were statistically significant for the periods October 1993 and July 1994 (P<0,05; Mann-Whitney two-sample test).
On the basis of these results the null hypothesis stating that there is no difference in tick abundance between the wilderness area (B) and the degraded area (A) is to be rejected.

Besides the unambiguous differences in tick abundance revealed for area A versus area B, tick distribution within each of these areas was examined. Within area A, study sites A1 to A6 differed significantly in tick numbers for each individual month as well as for the entire period (P<0.05, Kruskal-Wallis). Area A6 stands out as sustaining higher tick numbers than the remaining A-sites, a similar but, not so unequivocal, result can be detected for area A4 (Tab. 2.6 - 2.10).
Within area B tick distribution proves to be more homogenous among the various study sites. B1 was identified as having significantly more ticks than study sites B2 and B6 (P<0.05; Kruskal-Wallis) (Tab. 2.6). Comparing tick abundance within area B for the individual months (Tab. 2.7 - 2.10) reveals that, in addition to study site B1, B3 also carries higher tick numbers than other study sites, significantly so in the months of October and November 1993. During the months of lower tick abundance (June and July 1994) tick numbers obtained from the individual study sites within area B do not differ significantly, except between area B1 and B6 in July. Area B6 varies substantially from the other areas, habouring low tick numbers.

Inspection of the dendrogram obtained from the cluster analysis for the entire survey period (Fig. 2.18) reveal that some individual study sites out of area A have tick abundances more similar to study sites in area B than to study sites in the same area. This is particularly apparent for A4 and A6, each clustering in groups with B sites. A6 is part of a group which carries high tick numbers (B4, B5, B3); A4 combines with B6 and B2 - sites with comparatively lower tick abundance. The latter group is close to sites A1, A2, A5 and A3, all of which share the characteristic of carrying low tick numbers.

The dendrograms for the individual months are presented in figure 2.19.

Table 2.6: Kruskal-Wallis multiple comparison z-values indicating significant differences in total tick abundance at the individual study sites

	A1	A2	A3	A4	A5	A6
A1	...	...	...	S	...	S
A2	...	...	...	...	...	S
A3	...	...	...	...	...	...
A4	S	...	...	...	S	...
A5	...	...	...	S	...	S
A6	S	S	...	...	S	...

	B1	B2	B3	B4	B5	B6
B1	...	S	...	...	...	S
B2	S	...	...	...	...	...
B3	...	...	...	...	...	...
B4	...	...	...	...	...	...
B5	...	...	...	...	...	...
B6	S	...	...	...	...	...

Table 2.7: Kruskal-Wallis multiple comparison z-values indicating significant differrences in tick numbers at the individual study sites in October 1993

	A1	A2	A3	A4	A5	A6
A1	...	...	...	...	...	S
A2	...	...	...	...	...	...
A3	...	...	...	...	...	S
A4	...	...	...	...	...	...
A5	...	...	...	...	...	S
A6	S	...	S	...	S	...

	B1	B2	B3	B4	B5	B6
B1	...	...	...	...	...	S
B2	...	...	S	...	...	...
B3	...	S	...	...	...	S
B4	...	...	...	...	...	...
B5	...	...	...	...	...	...
B6	S	...	S	...	...	...

Table 2.8: Kruskal Wallis multiple comparison z-values indicating significant differences in tick abundance at the individual study sites for November 1993.

	A1	A2	A3	A4	A5	A6
A1	...	...	...	S	...	S
A2	...	...	...	S	...	S
A3	...	...	...	S	...	S
A4	S	S	S	...	S	...
A5	...	...	...	S	...	S
A6	S	S	S	...	S	...

	B1	B2	B3	B4	B5	B6
B1	...	S	...	...	...	S
B2	S	...	S	...	...	...
B3	...	S	...	...	...	S
B4	...	...	...	...	...	...
B5	...	...	...	...	...	S
B6	S	...	S	...	S	...

Table 2.9: Kruskal Wallis multiple comparison z-values indicating significant differences in tick abundance at the individual study sites for June 1994.

	A1	A2	A3	A4	A5	A6
A1	...	...	...	S	...	S
A2	...	...	...	...	...	S
A3	...	...	...	...	...	...
A4	S	...	...	...	S	...
A5	...	...	...	S	...	S
A6	S	S	...	...	S	...

	B1	B2	B3	B4	B5	B6
B1	...	...	...	...	...	...
B2	...	...	...	...	...	...
B3	...	...	...	...	...	...
B4	...	...	...	...	...	...
B5	...	...	...	...	...	...
B6	...	...	...	...	...	...

Table 2.10: Kruskal Wallis multiple comparison z-values indicating significant differences in tick abundance at the individual study sites for July 1994.

	A1	A2	A3	A4	A5	A6
A1	...	...	...	...	...	S
A2	...	...	...	...	...	S
A3	...	...	...	...	...	S
A4	...	...	...	...	...	S
A5	...	...	...	...	...	S
A6	S	S	S	S	S	...

	B1	B2	B3	B4	B5	B6
B1	...	...	...	...	...	S
B2	...	...	...	...	...	...
B3	...	...	...	...	...	...
B4	...	...	...	...	...	...
B5	...	...	...	...	...	...
B6	S	...	...	...	...	...

Cluster Analyses: Tick Abundance

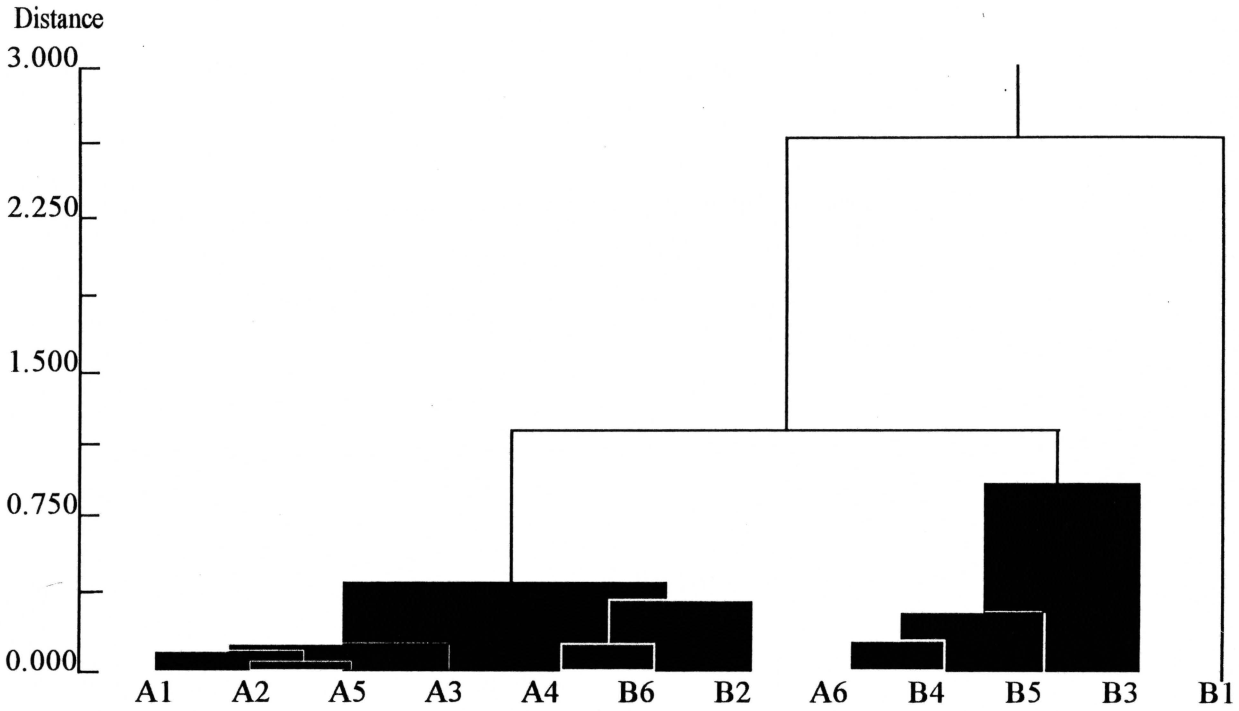


Figure 2.18: Dendrogram obtained for the clustering analysis of tick abundance at the 12 study sites during the entire study period. Sites with similar tick numbers are grouped together. Two main groups are suggested. Site B1 stands seperated.

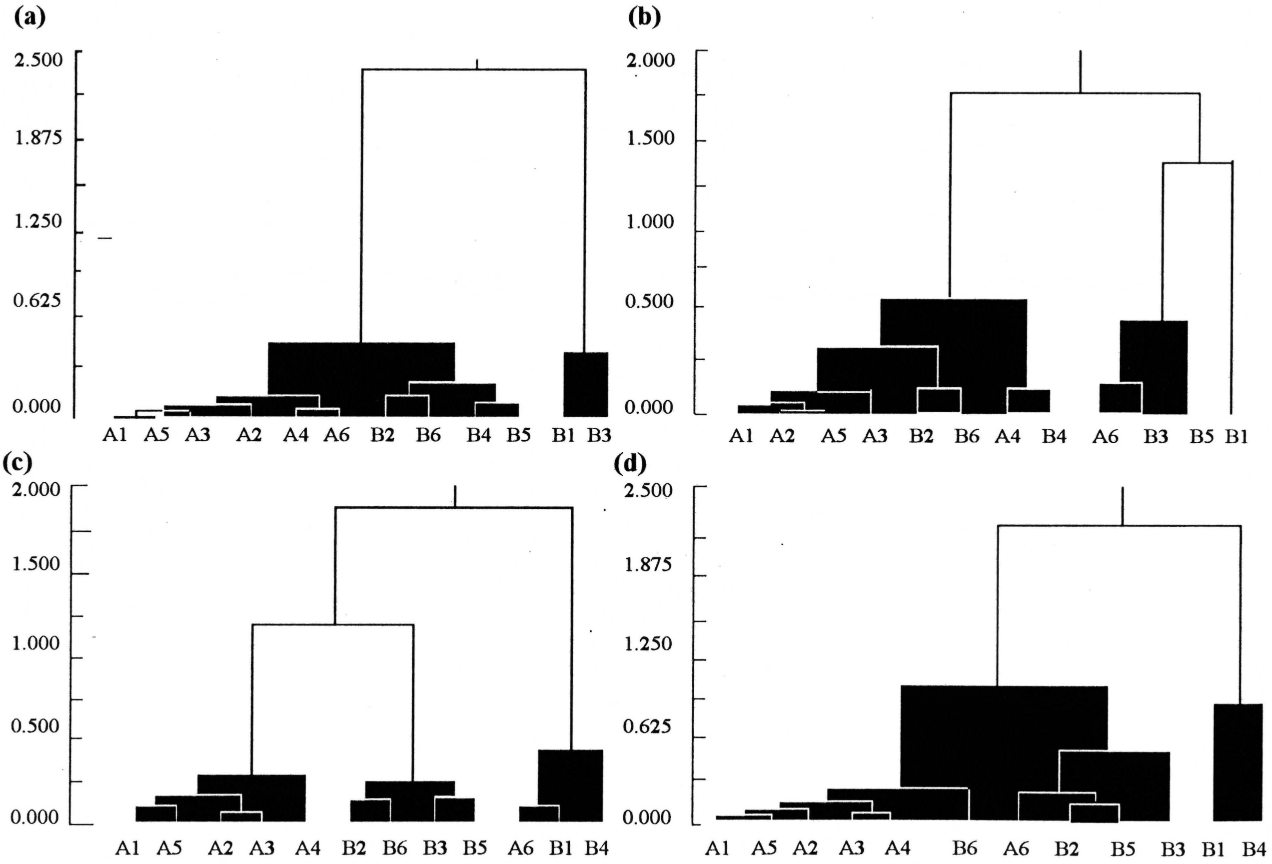


Figure 2.19: Dendrograms obtained by cluster analyses of tick numbers at the 12 study sites for the individual months (a) October 1993, (b) November 1993, (c) June 1994 and (d) July 1994.

2.4.6. Vegetation & Tick abundance

Plant species composition

For each of the four sampling dates, the flagging results for the study sites were analyzed to determine if tick abundance was associated with plant species flagged. These tests provided evidence for such a relation for the months of October 1993 ($P=0{,}003$, $R^2=0{,}46$) and July 1994 ($P=0{,}005$, $R^2=0{,}3311$) (Tab. 2.11).

Table 2.11: Results of multiple regression analysis applied to detect if tick numbers sampled are related to the composition of the vegetation flagged.

Month	Prob. level	R sqared
Oct 93	0.003	0.46
Nov 93	0.152	0.2849
Jun 94	0.313	0.2083
Jul 94	0.005	0.3311

df= 119

Auto regression was performed with the same data set for each month. The proposed plant species combinations forming empirically optimal regression models are presented in table 2.12.

Table 2.12: Results from the autoregression function suggesting plant species associations which would give maximal empirical values for the regression model.

Month	Prob. level	R squared	Plant species suggested
Oct 93	0	0.3916	ID10, ID11,ID13
Nov 93	0	0.1439	ID3, dry wood, sand
Jun 94	0	0.1451	Salvadora, Zygophyllum, dry wood
Jul 94	0	0.3311	Creps.,Zygophyllum, Faidherbia pods

df= 119

Vegetatio/subtratum ratio (surface cover)

The multiple regression analyses used to investigate the possible relationships between tick numbers and vegetation/substratum ratios yielded inconsistent results. In November, June and July significant associations were revealed, but R squared values were relatively low (Tab. 2.13). In October no such significance was detected.

Table 2.13: Results from multiple regression analysis show relations between tick numbers sampled and the vegetation /substratum ratio flagged.

Month	Prob. level	R. sqared
Oct 93	0.146	0.0571
Nov 93	0.009	0.1102
Jun 94	0.045	0.0804
Jul 94	0.006	0.1004

Vegetation/substratum ratio data and tick abundance for the entire sample period were included as two variables in a cluster analyses model (Figs. 2.20 - 2.21). In comparison to the afore mentioned model which only includes the vegetation/substrate ratio some relations changed. A4, A6 and the B sites still differ substantially from area A1 and areas A2, A3, A5, but areas B1 and B3 can now be distinguished as separate entities. These results are not so obvious on a monthly basis, but trends remain.

2.5. Discussion

2.5.1. Seasonality

Sampling was restricted to two time periods and therefore the data obtained does not reflect full seasonal cycles but only selected events. Nevertheless the data sets can be used to interpret and discuss trends in seasonal changes in tick abundance.

Cluster Analyses: Vegetation/Substratum Ratio & Tick Abundance

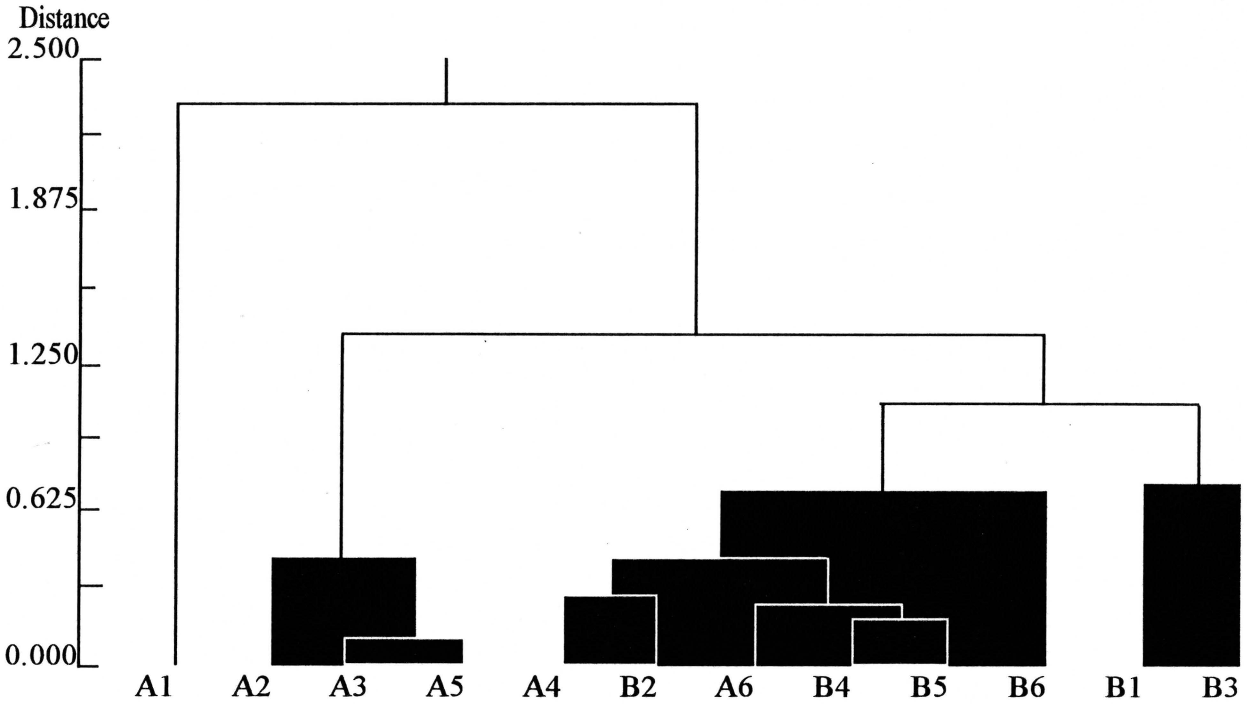


Figure 20: Dendrogram obtained for the clustering analysis of the combined factors vegetation/surface ratio and tick abundance at the 12 study sites for the entire study period. Sites which were similar in surface cover ratios and tick numbers are grouped together. Three main groups are suggested by this clustering. Site A stands solitary.

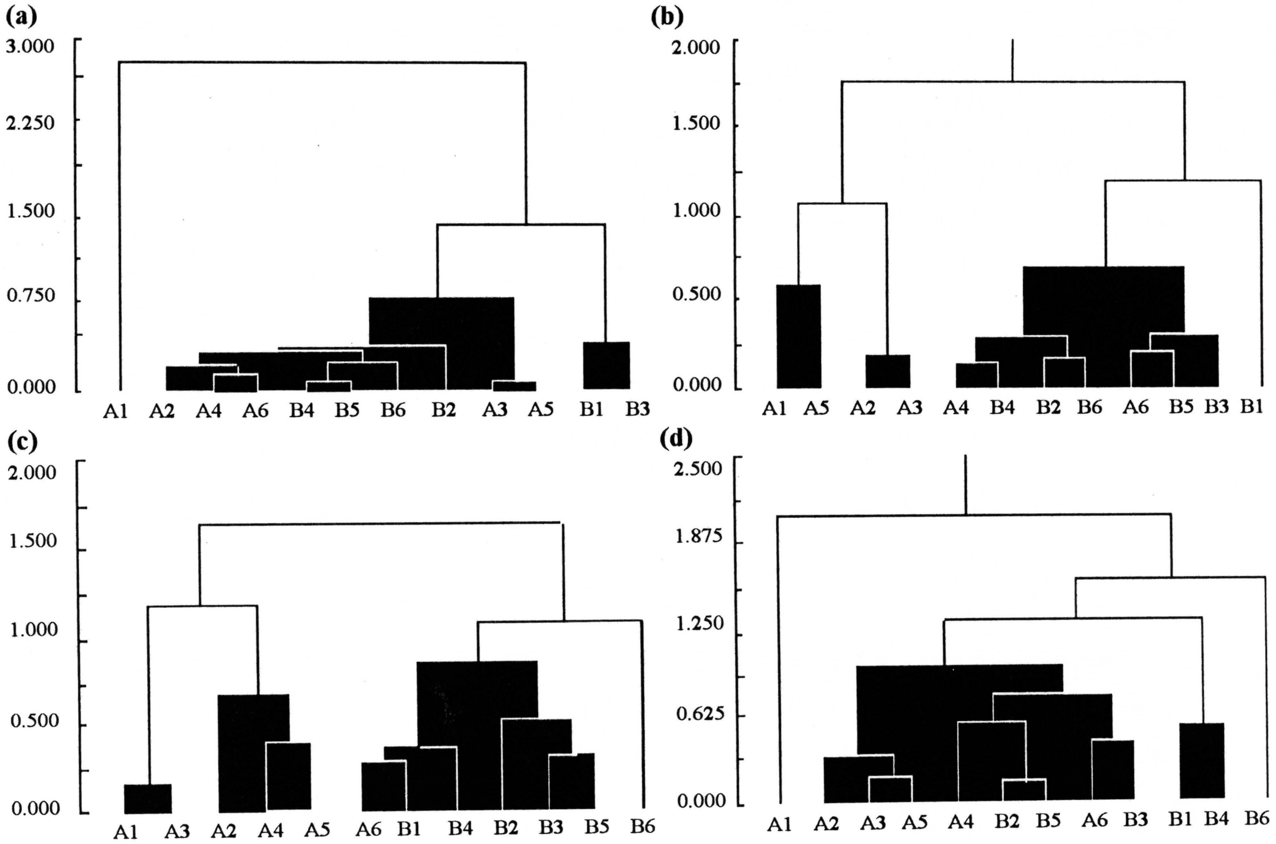


Figure 2.21: Dendrograms obtained by cluster analyses of vegetation/surface ratio and tick abundance at the 12 study sites for the individual months (a) October 1993, (b) November 1993, (c) June 1994 and (d) July 1994.

Langenhoven and Biggs (1984)[1] suggest that R. gertrudae in the Windhoek district are inactive during a period from April through October. In contrast, the results of this study show that adult R. gertrudae were never completely inactive during any of the sampling periods, although less abundant during winter. In general, inactivity can be interpreted as a response to changing environmental factors (Tauber et al., 1986), to survive through times of unfavourable conditions. In Namibia the climate is generally hot and wet during summer and cold and dry during winter. Considering desiccation as a major threat for tick survival, it seems clear that ticks show maximum activity during the wet season. That R. gertrudae in the lower Kuiseb region are abundant throughout the year may be related to the fact that the Kuiseb's vegetation is supported by a continous underground waterflow, maintaining a dense perennial and predominately evergreen vegetation. There is only a little seasonal variation in the vegetation and thus the riverine forest presents a relatively stable habitat.

Survival of ticks will be maximal if activity periods coincide not only with optimal climatic conditions but also host availability. Success will be greatest if the most favourable periods are occupied by the most vulnerable of all lifestages, the larvae (Randolph, 1993; Roger & Randolph, 1993). No data on temporal resource partitioning between the various lifestages of R. gertrudae are available, but some theoretical considerations suggest that host availability may be seasonal. When conditions become harsh in the desert areas surrounding the Kuiseb, animals take refuge in this linear oasis (Hamilton et al., 1977) and host numbers increase. On the other hand, some mammals, especially desert rodents, are known to go through times of aestivation, a behaviour displayed to escape unfavourable conditions (Louw & Seely, 1982). During such times they would therefore not be available as hosts for juvenile ticks.

Due to the fact that adult R. gertrudae are abundant throughout the entire year it can be speculated that the life cycle of the Kuiseb ticks is continuous and that many of the adult ticks which cannot find suitable hosts go through long times of starvation and are present for prolonged periods.

2.5.2. Vegetation & Tick abundance

Statistical analyses have shown that tick abundance along the lower Kuiseb is determined by the vegetation. Habitat features were assessed by determining the vegetation/substratum ratio at each study site as measure of surface vegetation cover and plant species richness and composi-

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[1] All ticks refered to as belonging to the Rhipicephalus carpensis group were later identified as R. gertrudae (Walker pers. com., 1994).

tion. It was anticipated that differences in vegetation features would be negligible within the wilderness area (area B) and that degradation within the area used by livestock (area A) would diminish gradually with increasing distance from stock waterpoints (Gabriel, 1993). The tick abundance data obtained showed obvious congruencies with the vegetation features at the individual sites.

Sites A4 and A6 have vegetation cover ratios more similar to the ratios in area B than within area A (Figs. 2.10 - 2.11). This corresponds with the finding that study areas A4 and A6 carry significantly higher tick numbers than the remaining A-sites. These two study sites represent less degraded stretches along the area used by livestock (Gabriel, 1993) and microhabitat destruction is limited. Evaluation of the vegetation data obtained for A1 categorises this study site as extremely degraded. With three ticks recorded, total tick abundance at this site was the lowest in the entire survey area.

The assumption that differences in vegetation features in area B would be negligible is to be rejected. Although overall vegetation ratios are higher and more homogenous in area B than in area A, plant species richness is greater and plant species composition extremely variable at the individual study sites within B. Tick abundance data is also more homogenous within area B. B6 differs substantially from all other sites by having the richest plant species composition and carrying the lowest tick numbers within area B. This finding may be a result of the strong associations detected between tick numbers and plant species composition of the stretches sampled.

Not all tick abundance data shows such strong congruencies with the vegetation data and interpretation is less clear. Site B1 stands out significantly, carrying the highest tick numbers at any time of observation. Yet, vegetation characteristics of B1 seem to be fairly similar to most other study sites within area B. One special feature can be considered to influence tick numbers at this site, as well as at site B4, where also high tick abundance was found: at each a figtree is established. Figtrees play an important role in the ecology of the Kuiseb. Their fruits are a welcome source of moisture for various animals, especially baboons which spend a considerable amount of time near these oases (Brain, 1993). Brain & Bohrmann (1992) found a strong correlation between the number of days baboons had spent in an area and tick numbers found at the respective places. Consequently it seems to be a reasonable assumption that host availability is a determinant of tick abundance. Whether this is true for other study sites carrying high tick numbers, as A6, B5 and B3 (Figs. 2.18 - 2.19), remains speculative. First of all, it is not clear which range of animals acts as hosts for <u>R. gertrudae</u> in the Kuiseb and secondly, no recent data on abundance and distribution of mammals in the Kuiseb is available. Both these aspects should be followed up in future research.

2.5.3. Patchiness of tick distribution

Distribution is the spatial aspect of abundance (Andrewartha & Birch, 1954). Tick distribution in the study area shows complex patterns of variation and patchiness, and these can be attributed to a variety of factors. Due to the tight relations between vegetation and ticks, the patchy vegetation along the Kuiseb will cause similar patchiness in tick distribution. Tick aggregations can also be induced by the hosts.. The tick species Ixodes neitzi for example was reported to locate its hosts by detecting glandular markings of klipspringer (O. oreotragus) on the vegetation (Rechav et al., 1978). Other antelopes such as steenbok also use chemical compounds for interspecific communication (Smithers, 1983). It can be speculated that R gertrudae have similar host detecting abilities as I.neitzi. Usually ticks react to odour, primarily to CO_2, and other stimuli. Steenbok as well as baboons are known to establish territories and they spend much time in specific areas. Well established sensory organs would allow the ticks to detect preference areas of hosts and they could direct their movement into such areas, where they would accumulate to await the hosts. Tick accumulation can be induced by means of intraspecific communication through the production of so-called assembly pheremones by individual ticks (Hamilton, 1992) to improve mating-success, host-allocation and exploitation of favourable microhabitats by large numbers of ticks. Such behavioural traits can influence patchy distribution of ticks substantially.

Most host species have established territories and frequently visit, for example, places like the area around the fig trees (see 2.5.3.). Engorged ticks drop off where the hosts move. Due to the reproductive strategies of hard ticks, the detached females lay several thousand eggs in one batch onto the ground. This may result in aggregation of developmental stages along the frequented animal paths.

2.5.5. Statement on the methodology

The flagging method applied favours the collection of adult ticks and results are often biased (Roger & Randolph, 1993). Larvae and nymphs are small in size and are therefore easily overlooked when picking ticks off the flag. In addition to this, spatial distribution of the juvenile stages may differ from the adults'. Juvenile ticks are most vulnerable to desiccation and they rely on suitable microclimatic conditions. This along with the need to contact intermediate hosts, may restrict the larvae and nymphs to living in the dense vegetation layers. These are not accessible through the collecting method applied. In future research it is therefore recommended that the methodology be reviewed.

3. CHAPTER THREE

Diel activity patterns of R. gertrudae

3.1. Introduction

Temporal and spatial congruencies in the activity patterns of ticks and their hosts are essential in ensuring contact (Fourie et al., 1993). Host-seeking behaviour of ticks is species specific. Some ticks take questing position on the tips of the surface vegetation and await passing hosts, some migrate up into the trees and let themselves drop when a host comes past. Still others respond to host stimuli by actively host-seeking (Fourie et al., 1993; Arthur, 1962).
The activity of ticks is influenced by a variety of biotic and abiotic factors, and their response to climatological and photoperiodical conditions restricts their locomotory actions (Duffy & Campbell, 1994; Gushi et al., 1975; Snyman et al., 1994) and therefore the possibility of tick-host contact.

The objective of the study introduced in this chapter is to gain information about the diurnal activity patterns displayed by R. gertrudae in the Kuiseb habitat. The results not only provide an insight into the general ecology of this tick species, but also provide useful information for evaluating the data obtained in the abundance survey.

3.2. Material and Methods

The experimental site corresponds with study site B1 of the tick abundance study dealt with in chapter 2. Within this area three 1m² plots in which ticks could be easily detected were chosen along the vegetation edge bordering the river channel. The square zone was marked at its corners and all ticks present within this range at the time of observation were counted. None of the ticks were removed from the plot. Observations were carried out on an hourly basis over 24 hours in October and June and 72 hours in November. Twigs, plant leaves and ground were examined to include ticks in questing positions on the vegetation as well as ticks moving on the ground. These two characteristics were considered to reflect activity of the ticks. Ticks walking into the plot during the time of actual observation were not considered since these could have been attracted by the presence of the observer.
Climatological data including ambient air temperature and relative humidity were recorded hourly.

Three categories for reporting the mean percentage area of each plot exposed to shade, sunshine or a combination of these were established. Times of sunrise and sunset were marked separately. During the night a weak torch was used to facilitate counting.
The first 24-hour survey was established in October 1993 and repeated over a 72-h period in November 1993 and 24-h period in June 1994.

3.3. Statistical analyses

Tick data from the three individual plots were combined and analyzed for each sampling date. The numbers of ticks recorded were used as response variables in multiple regression analyses to evaluate whether there is a linear relationship with temperature, humidity or time of day, the independent variables used in the model.

Multiple regression analysis was used to determine whether sun or shade exposure of each plot related to tick numbers. Three exposure categories were established: (1) 100% shade, (2) 50% shade/ 50%sun and (3) 100% sun.

By applying Wilcoxon tests for matched pairs it was tested whether tick activity is triggered by sunset or sun rise. Tick numbers counted before and after the respective event were compared. For this purpose data from all sampling dates were combined.

3.4. Results

The diurnal activity pattern of adult R. gertrudae for the different survey dates and the corresponding climatological data are illustrated in Figs. 3.1 - 3.3. Visual inspection of the curves suggests that tick activity peaks in the late afternoon just before sunset. Ticks are active during the night, but less so than in the day.

The statistical analysis comparing tick numbers before and after sunrise and sunset reveals that these two events appear to induce a sharp difference in tick activity ($P<0,05$; Wilcoxon test for matched pairs). But there are other sharp changes as well which are not related to sunrise and sunset.

The multiple regression analyses performed to evaluate the possible associations of temperature, relative humidity or time of day with tick numbers for the various survey periods yielded almost consistent results for all the survey periods (Tab. 3.1).

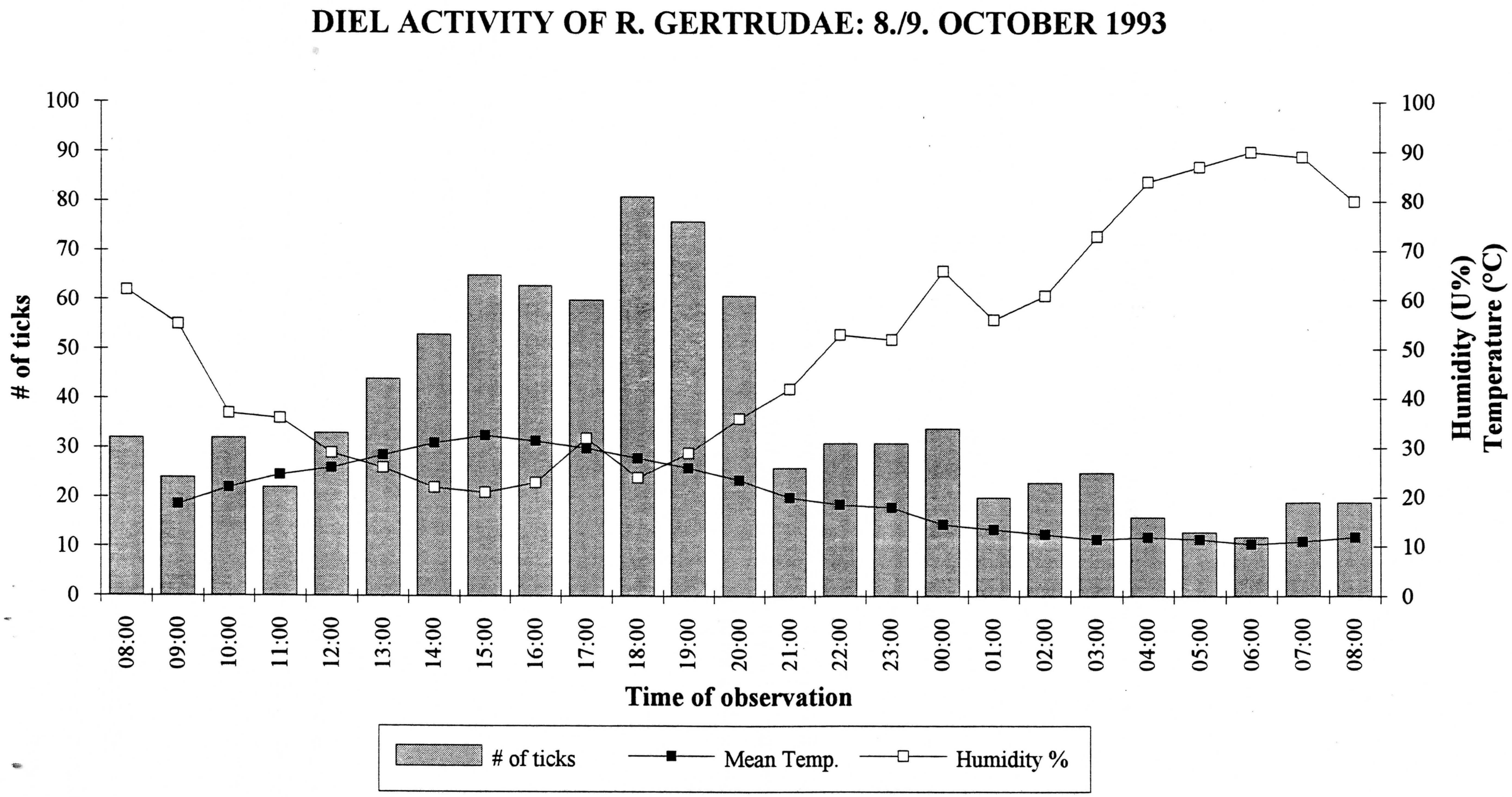

Figure 4.1.: Diurnal activity pattern of adult R. gertrudae in relation to ambient air temperature and relative humidity observed over a 24h period, Kuiseb river/Namibia, 8./9. October 1993.

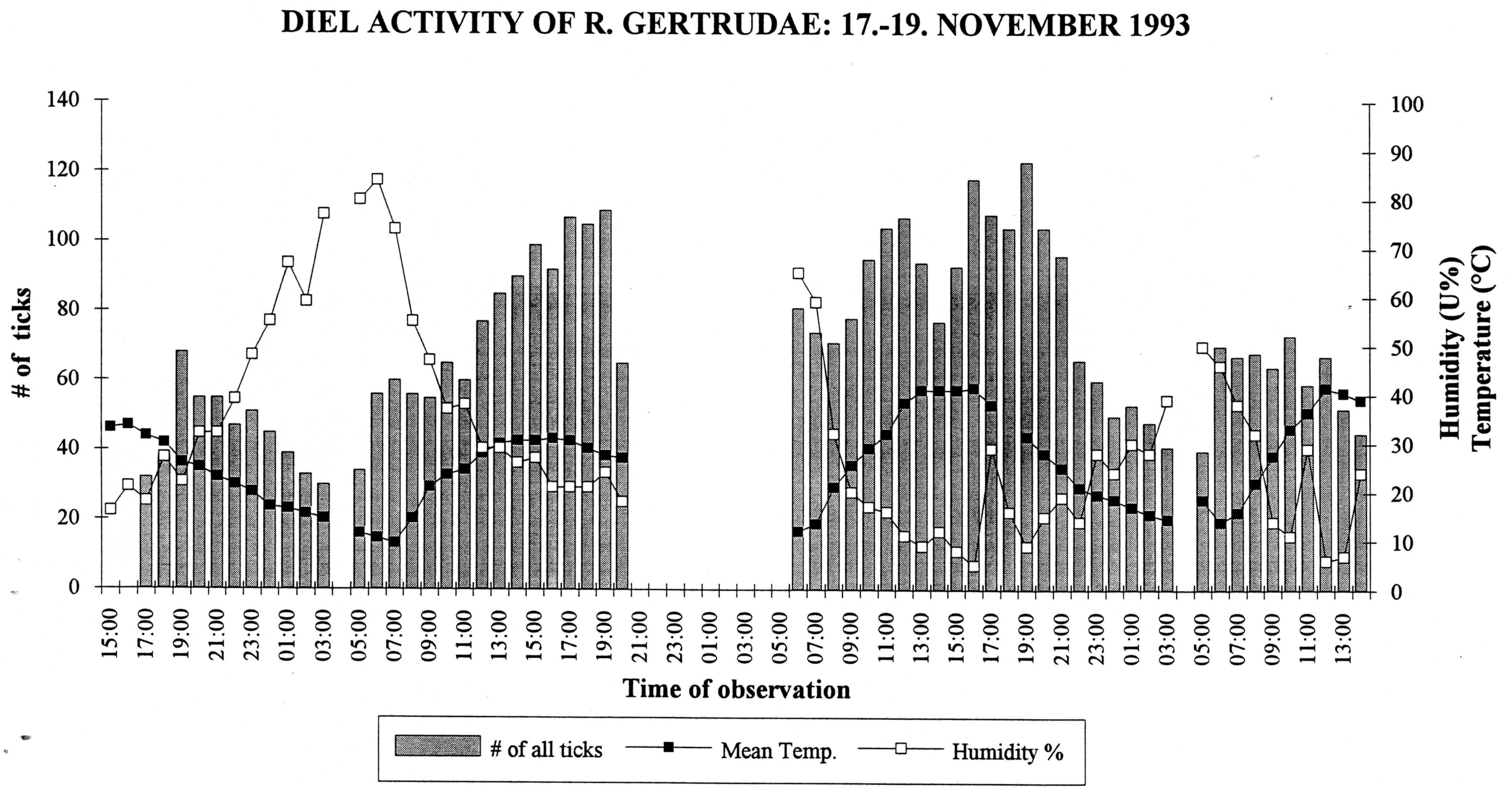

Figure 4.2.: Diurnal activity pattern of R. gertrudae adults in relation to ambient temperature and relative humidity observed over a 72h period, Kuiseb river/Namibia, 17.- 19. November 1993.

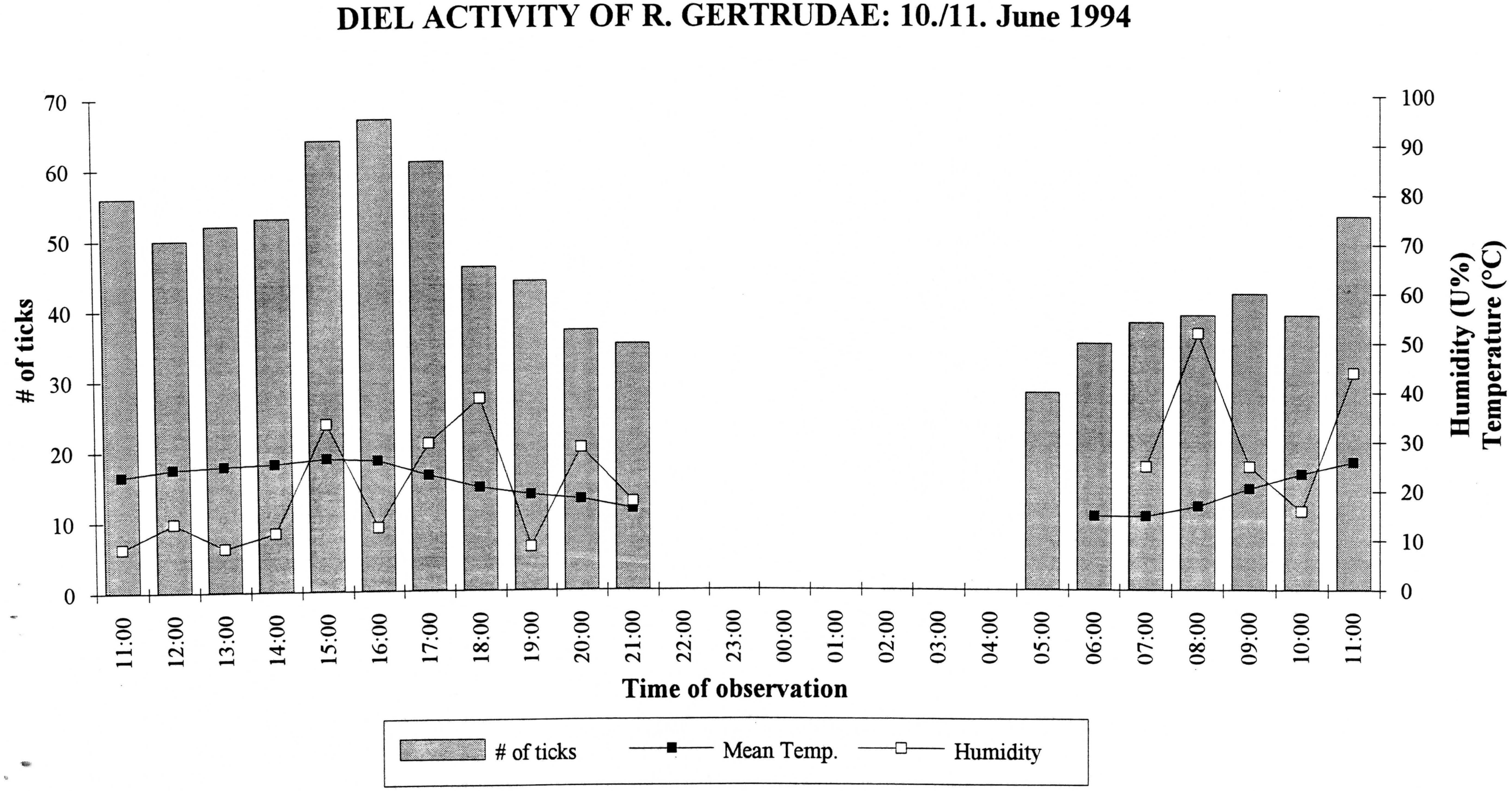

Figure 4.3.: Diurnal activity pattern of adult R. gertrudae in relation to ambient air temperature and relative humidity observed over a 24h period, Kuiseb river/Namibia, 10./11. June 1994.

Table 3.1: Results of multiple regression analyses applied to detect whether there is a linear relationship between tick numbers observed over a 24h or 72h period and temperature, humidity or both.

		Oct. '93 (df= 23)	Nov.'93 (df= 59)	June'94 (df= 16)
Temperature (^{2}C)	Prob. level R squared	0.0001 0.6717	0.0001 0.2695	0.0001 0.709
Humidity (U%)	Prob. level R squared	0.0001 0.6201	0.0001 0.3016	0.622 0.0178
°C & U%	Prob. level R sqared	0.0001 0.6728	0.0001 0.3118	0.0001 0.6813
Time	Prob. level R squared	0.001 0.3349	0.001 0.1837	0.176 0.1111

For all three months, temperature was positively associated with tick numbers ($P< 0,0001$). Relative humidity showed similarly strong, but negative relations for the months of October 1993 and November 1993 ($P< 0,0001$), but no such connection was revealed for the June survey. The models including both independent variables were all highly significant ($P<0,0001$), and had the highest R squared values (Oct.'93: $R^2= 0,6728$, Nov.'93: $R^2= 0,3118$, June '94: $R^2= 6813$). Time of day shows significant ties for the months of October and November ($P<0,001$) only and had the lowest R squared values (Oct.'93: $R^2= 0,3349$, Nov.'93: $R^2=0,1837$).

Results for the multiple regression analyses which were used to reveal possible relationships between tick numbers and exposure of the individual plot to sun or shade are given in Tabel 3.2. The results are very inconsistent. Associations between the variables were only found for three observations, two in November (plot I, $P<0,05$; plot II, $P<0,0001$) and one in June (plot II, $P<0,001$). The R squared value was higest in the latter observation ($R^2= 0,5208$).

Table 3.2: Results of multiple regression analyses applied to detect whether there is a linear relationship between tick numbers found within the plot, and the percentage of sun/shade exposure of the plot.

		Oct. '93 (df= 24)	Nov.'93 (df= 60)	June'94 (df= 17)
Plot I	Prob. level	0.586	0.023	0.275
	R squared	0.0131	0.0850	0.0739
Plot II	Prob. level	0.413	0.9	0.0001
	R squared	0.0294	0.0003	0.5208
Plot III	Prob. level	0.086	0.0001	0.563
	R sqared	0.1225	0.2031	0.0214

3.5. Discussion

Before I start an extensive discussion of the activity patterns displayed by R. gertrudae under natural conditions, some critical review of the method applied must be undertaken. First of all the use of the term activity must be discussed in the context of this study. It was assumed that tick presence on the vegetation as well as vertical and horizontal migration represent activity. During the survey it became clear that some ticks spend all night on the vegetation, taking in a coiled up position which could be interpreted as a resting position. These ticks were always included in the counts since they reacted promptly when the observer approached the plot for the hourly census. Obviously the ticks were in a waiting mode, thus displaying host-seeking behaviour. It is difficult to draw a clear distinction between activity and resting behaviour of the ticks. In addition to this it remains absolutely speculative where the ticks are to be found when they are not visible in the plot and what kind of activity they perform in their absence.

To gain a better understanding of tick activity patterns displayed in their natural environment it would be a worthwhile endeavour to elaborate on the method applied. The method is considered to give a good indication for tick activity although its results may be biased in several ways. First of all the physical environment in the plot must allow easy detection of the ticks to assure that all ticks present are included in the counts. At night this might be a major problem. The use of a torch is necessary to facilitate correct counts but the unnatural light may influence tick activity, since light is known to be an important trigger for endogenous rhythms (More-Ede et. al., 1982). Although endogenous rhythms may have a major impact on the activity patterns of ticks as described in detail for insects by Saunders (1976), environmental stimuli are thought to be the dominant determinant of most behaviour in the natural environment (Enright, 1970). In the following discussion of the results for diurnal activity patterns displayed by R. gertrudae,the endogenous rhythms will therefore not be considered in much detail. However, a relation between tick abundance and time of day was revealed in the regression analyses and in the following paragraphs the possible influence of various environmental stimuli on the activity patterns will be discussed.

The diurnal activity cycle of R. gertrudae seems to be predominatly unimodal, with tick activity being greatest just before sunset (Figs. 3.1 - 3.3). The observation from 29 November 1993 indicates the possibility of a second activity peak in the late mornings which would express a bimodal activity cycle. To get concise results on this issue it would be necessary to monitor tick activity over longer time periods. It would be interesting to find out if an alternation of unimodal and bimodal activity can be triggered by environmental stimuli.

Although changes in activity are variable throughout and therefore not exclusively related to sunrise and sunset, light/dark changes at sunrise and sunset may be considered to act as cues for tick activity.

When the numbers of adult R. gertrudae were regressed against ambient air temperature and relative humidity[2], it was found that these two components explained a significant amount of the variation of the data. Inspection of the graphs presented in Figs. 4.1 - 4.3 reveals a similar course in changes of tick numbers and air temperature. Tick numbers reach their peak within 1 to 4 hours lag period around the maximum temperature. How long this lag period is seems to depend on the length of time period between temperature maximum and sunset. The activity maximum of the ticks always reaches its peak towards sunset.
Comparing the results of the October/November (late spring) observations with the June (winter) survey it seems that the amplitude of the graphs is much more strongly pronounced in the late spring samples. These distinct patterns in diurnal tick activity may be related to the extreme fluctuations in temperature during the October (Max 32,5°C, Min 10,5°C) and November (Max 41,5°C, Min 9,5°C) samples. In contrast to this overall temperatures during the June survey were more constant and the maximum temperature reached only 26,5°C (measurements of night temperatures are not available, but in general lowest temperatures occur in the early morning. In this

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[2] Louw & Seely (1982) discuss the relationship between ambient temperature, humidity ratio and saturation temperature. They show that with rising air temperature the capacity of the air to hold water vapour increases. It is the water vapour deficit of the air that determines the dessicating effect; temperature and humidity must therefore be evaluated as entirety.

sample the minimum temperature only reached 10°C at 5:00). Whether these differences in minimum and maximum air temperature fluctuations and corresponding fluctuations in tick activity between late spring and winter could represent seasonal trends remains speculative. The statement would not be supported by the climatological data obtained from Gobabeb weather station for the period of August 1993 to August 1994 (Tab. 2.2). Here summer temperatures are generally higher than winter temperatures, but the range between minimum and maximum temperatures remains similar. Whether or not these conditions are strictly comparable to the climate prevailing within the linear Kuiseb oasis needs critical review.

The above findings draw attention to the possible response behaviour of R. gertrudae to temperature. First of all some more general considerations on climatic preferences in this tick species shall be made. For example, ticks of the genus Rhipicephalus in Israel are known to relate well to hot environmental conditions (Feldman-Muhsam, 1981). In Namibia adult R. gertrudae were recorded from the Windhoek district as being active in the period between October and April (Langenhoven & Biggs, 1984), thus the hot but usually more rainy season. These findings can provide a guideline for the evaluation of results for diel activity preferences.

To better understand the circadian activity patterns displayed by R. gertrudae in the Kuiseb the special climatic conditions prevailing in this habitat must be considered. From the collected climatological data at the study sites it is clear that the ticks resist relatively extreme climatic conditions and this despite the fact that heat and low relative humidity enhance desiccation, a crucial point in tick survival (Randolph, 1993). Nothing is known about R. gertrudaes' physiology but energy exchange processes with the environment such as conduction, radiation, convection and evaporation will be important factors in tick survival under climatic conditions as encountered in the Kuiseb. The increasing numbers of ticks found during the hottest and driest period of the day leads to assume that dessication is not a primary problem for adult R. gertrudae in the Kuiseb. This finding may be partly explained by the fact that transpiration from the vegetation on which the ticks quest is highest under dry and hot conditions and may thus provide a suitable microclimate (Randolph, 1993). Not all plants on which the ticks sit provide such transpiratorial effects, as many ticks are000, for instance, found to quest from dry Flaveria bidentis stalks. These plants could provide other possibilities for escape from extremly unfavourable microclimatic conditions. Here ticks could climb to high elevations, where the microclimatic conditions may be more favourable than near the soil surface (Louw & Seely, 1982). These thoughts are merely speculative and indepth studies need to be pursued to find answers.

Although the results of the multiple regression analysis revealed a relationship between relative humidity and tick numbers in the October and November surveys, the possible influence of humidity on tick activity needs to be evaluated. No such relationship was detected for the June sample, where humidity levels fluctuated greatly but the activity cycle showed its "normal" form. As already discussed, low macroclimatic humidity conditions seem not to restrict activity of R.

gertrudae. Possibly they exploit adequate moisture sources by migrating into the dense vegetation layers where microclimatic conditions could be favourable. There are frequently high humidity values are frequently provided along the Kuiseb. When drifts inland from the coast (fog was recorded at the study sites at two occasions). Again most of the explanations are merely speculative and further research is needed to get consise answers.

It was anticipated that the diurnal activity pattern of the tick and host overlap to some extent to facilitate contact. How the tick data fits with the temporal and spatial presence of their hosts is still to be investigated. Some data are available on the daily activity cycles displayed by Chacma baboons (P. ursinus) (Brain, 1993), klipspringer (O. oreotragus) (Tilson, 1979) and steenbok (R. campestris) (Cloete, 1983) in the Kuiseb, all potential or expected hosts of R. gertrudae in the study area. Both baboons and steenbok spend most of the day in the Kuiseb river, following their various activities such as resting, feeding, moving etc.. The baboons leave the river in the evening and spend the night in their sleeping cliffs along the canyon wall. Klipspringer visit the riverine forest only for feeding, which typically takes place in mid-morning and in the late afternoon. Browsing activity of steenbok shows similar bimodal peaks. The baboons start feeding in the early mornings and spend the time until the late afternoon feeding in the shade along the river channel. Both steenbok and baboons are ultimately accessable for ticks throughout the day and steenbok also at night. The feeding times are considered to allow maximum contact between the waiting ticks and their hosts. The unimodal activity peak of R. gertrudae overlies the second peak displayed by the hosts and this could guarantee high evidence for successful attachment. Other environmental factors such as the slow increase in temperature in the morning may restrict the ticks from fully exploiting the first activity spell of the hosts. All these statements should be evaluated carefully and their relevance needs to be tested.

A more straightforward finding is that tick numbers observed in some plots were as much as twice as high in the afternoons compared to ticks found in the mornings.

4. Chapter Four

Conclusions

The research conducted in this project has revealed information regarding distribution and abundance of Rhipicephalus gertrudae by quantifying vegetation type and vegetation cover as the most important parameters restricting tick survival. This is the first detailed ecological study of this nature on the tick species R. gertrudae, which occurs over a wide range in southern Africa.

The results of the study indicate that the habitat conditions in the wilderness area of the lower Kuiseb are favourable for the survival of the tick species R. gertrudae. Its abundance within the entire study area, including wilderness and farming areas, seems to depend primarily on the complex interactions with vegetation, microclimate and hosts. Several behavioral and presumably physiological adaptations enable successful niche occupation of adult R. gertrudae in the Kuiseb.

Tick numbers in the area used by livestock are limited by the impact of domestic stock. Habitat degradation restricts survival of the vulnerable developmental tick stages. Trampling may destroy the ticks' eggs, which are mainly laid onto the ground.

The ability to adapt to a wide range of hosts could be accounted for as opportunistic reaction to limited herbivore host availability. The assumption that host limitation may act as evolutionary force is supported by the fact that host finding strategies displayed by R. gertrudae in the Kuiseb are diverse and can be described as opportunistic. They include seeking for hosts from vantage points and locomotory hunting.

5. Bibliography

ANDREWARTHA, H.G. & BIRCH, L.C., 1954. *The distribution and abundance of animals.* Chicago: The University of Chicago Press, pp.3-782

ARTHUR, D.R., 1962. *Ticks and diseases.* Oxford: Pergamon Press, pp.445

BIGGS, H.C. & LANGENHOVEN, J.W., 1984. Seasonal prevelance of ixodid ticks on cattle in the Windhoek district of South West Africa/Namibia. *Onderstepoort J. Vet. Res.* 51, 175-182.

BRAIN, C., 1993. *The eco-physiology of babbons living in the Kuiseb Canyon, Namibia.* PhD, University of the Witswatersrand, Johannesburg, South Africa.

BRAIN, C. & BOHRMANN, R., 1992. Tick infestation of baboons (Papio ursinus) in the Namib Desert. *Journal of Wildlife Diseases.* 28, 188-191.

BUDACK, K.F.R., 1977. The #Aonin or Topnaar of the Lower !Khuiseb Valley and the sea. *Khoisan Linguistic Studies.* 3.

CHRISTIAN, D.P., 1977. *Comparative demography and water metabolism in three Namib desert rodents (abstract).* PhD, Michigan State University, USA.

CLOETE, G., 1983. *Etho-ecological aspects of the steenbok (Rhaphicerus campestris Thunberg, 1811) in the Namib Desert, South West Africa.* MSc, University of the Orange Free State, Bloemfontein, South Africa.

DUFFY, D.C. & CAMPBELL, S.R., 1994. Ambient air temperature as a predictor of activity of adult Ixodes scapularis (Acari: Ixodidae). *J. Med. Entomol.* 31, 178-180.

ENRIGHT, J.T., 1970. Ecological aspects of endogenous rhythmicity. *Annual Review of Ecology and Systematics.* 1, 221-238.

FAO, 1984. *Ticks and tick-borne disease control - A practical field manual.* Rome: FAO, Food and Agriculture Organization of the United Nations, pp.621 (321 V2)

FELDMAN-MUHSAM, B., 1981. Some observations on the hibernation of Rhipicephalus sanguineus in Jerusalem. *Proceedings of a conference on "Tick Biology and Control", Rhodes University, Grahamstown, South Africa.* , 205-207.

FOURIE, L.J., HORAK, I.G. & VAN DEN HEEVEN, J.J., 1992. The relative host status of rock elephant shrews Elephantulus myurus and Namaqua rock mice Aethomys namaquensis for economically important ticks. *S.-Afr. Tydskr. Dierk.* 27, 108-114.

FOURIE, L.J., SNYMAN, A., KOK, D.J. et al., 1993. The appetence behaviour of two South African paralysis-inducing ixodid ticks. *Experimental & Applied Acarology.* 17, 921-930.

GABRIEL, M., 1993. *The impact of stock along a defined stretch of the Lower Kuiseb River, Central Namib Desert: A first attempt at quantification (abstract).* Diplom, University of Regensburg, Germany.

GALTON, F.R.S., 1890. *Narrative of an explorer in tropical South Africa.* London: Ward,Lock & Co.

GUOSHI, C., GUANGYUAN, C., FENGGENG, P.et al., 1975. Preliminary observations on the diurnal activity of Ixodes persulcatus Schulze in the Forest region of Tianshan Mountain, Xingjang, China. In: Griffiths, D.A.;.B., C.E. (eds.) *Acarology VI* (pp. 1204-1207). Chichester: Ellis Horwood Ltd.

HAMILTON III, W.J., BUSKIRK, R. & BUSKIRK, W.H., 1977. Intersexual dominace and differential mortality of Gemsbok Oryx gazella at Namib Desert waterholes. *Madoqua.* 10, 5-19.

HAMILTON, J.G.C., 1992. The role of pheromones in tick biology. *Parasitology Today.* 8, 130-133.

HINZE, J.L. (1984). Number Cruncher Statistical System (NCSS), Version 5.03 9/93. In Kaysville: Hintze.

HOWELL, C.J., WALKER, J.B. & NEVILL, E.M., 1978. *Ticks, mites and insects infesting domestic animals in South Africa. Part 1 Descriptions and biology.* Pretoria: Dept. agric. tech. Serv., pp.69

LANCASTER, J., LANCASTER, N. & SEELY , M.K., 1984. Climate of the central Namib Desert. *Madoqua.* 14, 5-61.

LEHMANN, T., 1993. Ectoparasites: direct impact on host fitness. *Parasitology Today.* 9, 8-13.

LOUW, G. & SEELY, M., 1982. *Ecology of desert organisms.* Essex, UK: Longman, pp.194

MEHLHORN, H. & PIEKARSKI, G., 1989. *Grundriß der Parasitenkunde* (3rd ed.). Stuttgart: Gustav Fischer Verlag (UTB), pp.407

MOORE-EDE, M.C., SULZMAN, F.M. & FULLER, C.A., 1982. *The clocks that time us.* Cambridge, Massachusetts: Harvard University Press, pp.448

MÜHLENBERG, M., 1993. *Freilandökologie* (3rd ed.). Heidelberg: UTB, pp.512

NORTON-GRIFFITHS, M., HERLOCKER, D. & PENNYCUICK, L., 1975. The patterns of rainfall in the Serengeti Ecosystem, Tanzania. *E. Afr. Wildl. J.* 13, 347-374.

OLIVER (Jr.), J.H., 1989. Biology and systematics of ticks (*Acari:Ixodida). Annu. Rev. Ecol. Stys.* 20, 397-430.

PIETRUSZKA, R.D. & SEELY, M.K., 1985. Predictability of two moisture sources in the Namib Desert. *South African Journal of Science.* 81, 682-685.

RANDOLPH, S.E., 1993. Climate, satellite imagery and the seasonal abundance of the tick *Rhipicephalus appendiculatus* in southern Africa: a new perspective. *Medicaland Veterinary Entomology.* 7, 243-258.

RECHAV, Y., NORVAL, R.A.I., TANNOCK, J.et al., 1978. Attraction of the tick Ixodes neitzi to twigs marked by klipspringer antelope. *Nature.* 275, 310-311.

ROGERS, D.J. & RANDOLPH, S.E., 1993. Distribution of tsetse and ticks in Africa: past, present and future. *Parasitology Today.* 9, 266-271.

SAUNDERS, D.S., 1976. *Insect clocks.* Oxford: Pergamon Press, pp.279

SEELY, M., 1985. Predation and environment as selective forces in the Namib Desert. In: Vrba, E.S. (eds.) *Species and speciation* (pp. 161-165). Pretoria: Transvaal Museum.

SEELY, M., 1987. *The Namib*. Windhoek: Shell Oil Namibia Ltd., pp.104

SEELY, M.K., BUSKIRK, W.H., HAMILTON III, W.J. et al., 1979/80-1980/81. Lower Kuiseb river perennial vegetation survey. *Journal XXXIV/XXXV, SWA Scientific Society.* , 57-86.

SMITHERS, R.H.N., 1983. *The mammals of the southern African subregion*, University of Pretoria, South Africa, pp. 736

SNYMAN, A., FOURIE, L.J., KOK, D.J. et al., 1994. Vertical migration of adult Ixodes rubicundus the Karoo paralysis tick (Acari: Ixodidae). *Experimental & Applied Acarology.* 18, 101-110.

SOKAL, R.R. & ROHLF, F.J., 1981. *Biometry,* (2nd ed.). United States: Freeman & Co., pp.859

STENGEL, H., 1964. The rivers of the Namib and their discharge into the Atlantic. Part I: Kuiseb and Swakop. *Scient. Pap. Namib Desert Res. Stn.* 22, 1-50.

STUART, C.T., 1975. Preliminary notes on the mammals of the Namib Desert Park. *Madoqua.* 4, 5-68.

TAUBER, M.J., TAUBER, C.A. & MASAKI, S., 1986. *Seasonal adaptations of insects.* New York: Oxford University Press, pp.411

THERON, G.K. & VAN ROOYEN, M.W., 1980. Vegetation of the lower Kuiseb River. *Madoqua.* 11, 327-345.

TILSON, R., 1980. Klipspringer (Oreotragus oreotragus) social structure and predator avoidance in a desert canyon. *Madoqua.* 11, 303-314.

TILSON, R.L., 1977. Palewinged starlings and klipspringers in the Kuiseb Canyon, Nambi Desert Park. *Ostrich.* 48, 110-111.

VAN WYK, A.J., OPPERMAN, D.P.J. & KOK, O.B., 1985. Availability of water in the Lower Kuiseb and its use by large vertebrates. In: Huntley, B.J. (eds.) *The Kuiseb environment: the development of a monitoring baseline* (pp. 113-118). Pretoria: FRD/CSIR.

WALKER, J.B., 1991. A review of the Ixodid ticks (Acari, Ixodidae) occuring in southern Africa. *Onderstepoort J. vet. Res.* 58, 81-105.

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Juliane Zeidler

Juliane Zeidler Frankfurt am Main, the 01. February 1995