Ixodid ticks of impala (*Aepyceros melampus*) in Swaziland: effect of age class, sex, body condition and management

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Five species of ixodid ticks, *Amblyomma hebraeum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi evertsi* and *R. muehlensi*, were commonly collected from impala (*Aepyceros melampus*) in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex in north-eastern Swaziland. The prevalence and apparent intensity of infestation of most tick species was greater on yearlings (13–24 months of age) and adults (> 24 months) than on lambs (≤ 12 months), and on adult males than on adult females. The packed cell volume and marrow dry weight were lower in impala infested with *A. hebraeum*, and in lambs and adults with moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus*. The age and sex patterns of tick infestation were probably determined by both body condition and host behaviour. The prevalence and apparent intensity of infestation of most tick species was greater in the unmanaged, densely populated area of the reserve than in the managed area from which impala had been culled. This trend was consistent in all months, and in all age classes.

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Introduction

In a preceding paper (Gallivan & Surgeoner 1995) we reported the differences in distribution, host-parasite associations and seasonal trends in infestation of some of the ticks of wild ungulates in Swaziland. These factors determine the 'macroscopic' patterns in tick infestations. However, there were often marked differences in the tick infestations between individuals within a host species, and between sub-populations of the host species within the reserves. This indicates that other factors are important in determining the 'microscopic' patterns in tick infestations. In the present paper we examine the relationships between tick infestations and age class, sex, body condition, and management. Age and sex differences in tick infestations have been reported from studies on cattle (Seifert 1971; Utech, Seifert & Wharton 1978; Sutherst, Wharton, Cook, Sutherland & Bourne 1979), and cattle on a low plane of nutrition are less resistant to tick infestations (O'Kelly & Seifert 1969; 1970; Sutherst, Kerr, Maywald & Stegeman 1983). It has been suggested that the high host population densities in many small reserves may be a factor in the increased tick burdens of wild ungulates (Horak 1980; Lightfoot & Norval 1981; Norval & Lightfoot 1982), but there are no published studies testing this hypothesis. As management differed between the reserves, and there were marked differences in ungulate density and habitat conditions, this study provided an opportunity to examine the effect of management.

Materials and Methods

This study was conducted in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex in the north-eastern Swaziland lowveld. The basic physiography of the reserves and the ungulate and ectoparasite collections are described in the preceding paper (Gallivan & Surgeoner 1995).

The north end of Mbuluzi Nature Reserve was intensively managed, and over 1000 impala had been culled from this area in the six years prior to this study. The managed area was dominated by an open moist broadleaved savanna of *Sclerocarya birrea, Acacia caffra, A. gerrardii* and *A. nilotica*. It was burned at least every second year and had a well developed grass sward of *Themeda triandra, Sporobolus pyramidalis* and *Cymbopogon* spp.

Mlawula, Simunye and the south end of Mbuluzi had not been intensively managed, and contained approximately 95% of the impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and warthog (*Phacochoerus aethiopicus*). This unmanaged area was dominated by an *A. nigrescens, S. birrea* savanna which was overgrazed and had been invaded by *Dicrostachys cinerea, A. nilotica* and *Ziziphus mucronata*. Remnants of the *T. triandra, Panicum maximum* grass sward occurred towards the north end, but annual grasses, or more commonly forbs, had replaced the perennial grasses throughout most of this area. Many of the *Acacia* spp. thickets had a well developed browse line.

Impala were collected monthly by shooting from October

1985 to August 1986, with monthly sample sizes from 7–24 animals. The impala were aged as lambs (≤ 12 months), yearling (13–24 months) or adult (≥ 24 months) on the basis of body size, dentition and reproductive status. In most months an attempt was made to collect animals of all age and sex classes from both the managed and umanaged areas. However, no lambs (≤ 12 months of age) were collected in November or December, the first month after birth, and no adult females were collected in December or January when the lambs were dependent on the dam. In October and November 1985 the relative load (light, moderate or heavy) of ticks on each impala was estimated, but samples of the ticks were only collected from some individuals. Samples of the visible ticks were collected from all of the impala from December 1985 to August 1986. The sampling procedures are described in the preceding paper (Gallivan & Surgeoner 1995).

Body condition measurements

Four indices of body condition; visual body condition (VBC), packed cell volume (PCV), marrow dry weight (MDW) and kidney fat index (KFI), were recorded for each animal. Visual body condition (VBC) was assessed as good, fair or poor using the criteria of Riney (1960). Two blood samples were collected from the severed carotid arteries into heparinized microcapillary tubes immediately after the animals were shot. The tubes were placed on ice and the packed cell volume (PCV) was determined within 4 h using a microhaematocrit centrifuge. All of the aninuls were necropsied within 2 h of shooting for the determination of disease and parasite status. At that time the kidney fat index (KFI) was measured as described by Riney (1955), and one metacarpus was collected for the measurement of marrow dry weight (MDW). The bone was frozen and later thawed, at which time a marrow sample of approximately 1 g was taken from the middle portion. The sample was weighed to the nearest 0,1 mg on a precision balance, dried to a constant weight in a 100°C forced air oven, then reweighed. The MDW, calculated as a percentage of wet weight, is strongly correlated with marrow fat content (Brooks, Hanks & Ludbrook 1977).

Statistical analysis

The prevalence data for the ticks were analysed using contingency tables with χ^2 and Mantel-Haenszel statistics (Fleiss 1981) with age class, sex, month and area (managed or unmanaged) as the independent variables. The relationships between body condition and tick prevalence were analysed using linear models (PROC GLM, SAS Institute Inc. 1985) with tick prevalence, month, and area as the independent variables. The body condition indices and the variance in the indices differed between age classes, and the seasonal patterns in the body condition indices and the variance in indices also differed between age classes, as well as between the sexes in the adults (Gallivan, Culverwell & Girdwood 1995). Unequal and changing variance increases the probability of Type II errors in analysis of variance procedures, therefore, the relationships between body condition and tick prevalence were examined separately in each age class, and in adult males and females. Type IV sums of squares (SAS Institute Inc. 1985) were used in the linear models as the impala collections were not balanced across the independent variables, and all of the results are based on the most parsimonious model obtained using backward elimination (Kleinbaum & Kupper 1978). The MDW was arcsin transformed prior to analysis, and the KFI was log-transformed as the variance in monthly samples was correlated with the mean. All of the data were plotted prior to analysis to check for outliers and influential points.

Results

The ixodid ticks commonly collected from impala were *Amblyomma hebraeum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi evertsi* and *R. muehlensi*. The prevalence from December to August is presented in Table 1, and the seasonal patterns are described in Gallivan & Surgeoner (1995).

Age class and sex

Seventy per cent of the samples with *A. hebraeum* adults (n = 23) were from adult male impala, and all of the samples with more than three *A. hebraeum* adults, and those with maturing females (Gallivan & Surgeoner 1995), were from adult males in October or during and after the rut (April to August). *A. hebraeum* nymphs were collected more frequently from impala males than females (43 *vs* 26%; χ^2 = 4,80; p = 0,029), but there was no difference in the frequency of collections between age classes.

The prevalence of *B. decoloratus* adults did not differ significantly between age classes, nor between the sexes in lambs and yearlings. *B. decoloratus* adults were more prevalent on adult male impala than adult females (69 *vs* 48%; χ^2 = 3,78; p = 0,052), even after exclusion of the collections in December and January, in which there were no adult females. Maturing females were more prevalent on yearlings and adults than on lambs (52 *vs* 9%; χ^2_2 = 12,77; p = 0,002), but there was no difference in prevalence between the sexes. Nymphs were collected more frequently from lambs and yearlings than from adults (42 *vs* 17%; χ^2_2 = 11,84; p = 0,003), and there was a similar trend for larvae. There was no difference in the frequency of collections of nymphs between the sexes.

R. appendiculatus adults were collected less frequently from impala lambs than from yearlings and adults (50 *vs* 83%; χ^2_2 = 15,82; p < 0,001), and the sample sizes from lambs were always small (< 10). The prevalence did not differ significantly between the sexes. No maturing females were collected from lambs, but 45% of the samples with *R.*

Table 1 Prevalence of adult ixodid ticks on impala (n = 155) in the Mlawula-Mbuluzi-Simunye Nature reserve and Protected Area complex from December 1985 to August 1986

Species	Prevalence (%)
Amblyomma hebraeum	12,9
Boophilus decoloratus	60,0
Rhipicephalus appendiculatus	61,9
Rhipicephalus evertsi evertsi	49,0
Rhipicephalus muehlensi	93,6

appendiculatus from yearlings (n = 11) contained maturing females, as did 26% of samples from adults (n = 45). On yearlings the prevalence of maturing females did not differ between the sexes, but maturing females were more prevalent on adult males than adult females (56 *vs* 7 %; χ^2 = 12,08; p = 0,001). The frequency of collection of nymphs did not differ between age classes, or the sexes.

R. e. evertsi adults were more prevalent on yearling and adult impala than on lambs (58 *vs* 27%; χ^2_2 = 12,70; p = 0,002), but the prevalence did not differ between the sexes. The frequency of collections of nymphs did not differ between the age classes or the sexes.

R. muehlensi adults were more prevalent on impala males than females (96 *vs* 77 %; χ^2 = 3,88; p = 0,049) in the managed area, but there was no difference in prevalence between the sexes in the unmanaged area. The prevalence of maturing females and the frequency of collection of nymphs and larvae did not differ between the age classes and sexes.

Several impala were heavily infested with *R. muehlensi* and/or *R. appendiculatus*. To determine the factors influencing the occurrence of moderate to heavy loads of these ticks, the impala were separated into two groups, those with, and those without, moderate to heavy loads of these species. Moderate to heavy loads were defined as samples with ≥ 20 adult *R. muehlensi* and/or *R. appendiculatus*. The use of ≥ 20 ticks as the defining sample size was based on the frequency distribution of sample sizes, and a comparison of the size of the collected samples with field notes on the intensity of infestation. The use of higher (≥ 30 ticks) or lower (≥ 15 ticks) cutoffs did not change the patterns.

Moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were present throughout the year. There was an increased prevalence from March to June (χ^2_K = 19,51; p = 0,012) associated with the occurrence of *R. appendiculatus*, but *R. muehlensi* also contributed to the loads in this period. Moderate to heavy loads were more prevalent on yearlings and adults than on lambs (49 *vs* 18%; χ^2_2 = 13,39; p = 0,001). The prevalence did not differ significantly between the sexes on lambs and yearlings (Table 2), but moderate to heavy loads were more prevalent on adult males than adult females (59 *vs* 36%; χ^2 = 4,65; p = 0,031). The seasonal patterns also differed between the age and sex classes (Figure 1). There was no seasonal trend in lambs, but most of the yearlings had moderate to heavy loads from February to May. The prevalence was highest on adult females in March and April, but declined in May after the lambs were weaned. On adult males the prevalence increased to 100% in April and May, then declined. From June to August moderate to heavy loads were collected from males that retained territories, or were in very poor condition.

Table 2 Prevalence of the moderate to heavy loads (≥ 20 ticks per sample) of the ear ticks, *Rhipicephalus muehlensi* and *Rhipicephalus appendiculatus*, by sex and area in the three age classes of impala

	Age class		
	Lambs	Yearlings	Adults
Sex			
Male	23,8(21)[a]	52,6(19)	58,7(46)
Female	12,5(24)	66,7(3)	35,7(42)
χ^2; p	0,98; 0,322	0,21; 0,650	4,65; 0,031
	χ^2_{MH}[b] = 4,49; p = 0,034		
Area			
Managed	10,5(19)	37,5 (8)	22,2 (27)[c]
Unmanaged	23,1(26)	64,3(14)	59,0(61)
χ^2; p	1,18; 0,277	1,47; 0,225	10,16; <0,001
	χ^2_{MH} = 12,06; p < 0,001		

[a] number of impala; [b] Mantel-Haenszel χ^2; [c] the distribution of sexes did not differ between the areas (p = 0,33)

Ticks and body condition

Impala in poor body condition (MDW < 80%; PCV < 30%) were heavily infested with ticks in October. There was a marked improvement in body condition following the spring rains in late October and early November, and six of the eight impala examined in November had few ticks, while the two in poorest condition, both from the unmanaged area, had much heavier infestations.

A. hebraeum was the only tick species for which prevalence was associated with body condition from December to August. Impala infested with adult *A. hebraeum* had a lower PCV (p = 0,028) and MDW (p < 0,001) than those that were not infested. Four of the five adult males in poor VBC were infested with *A. hebraeum* while only 10 of the 41 in fair or good VBC were infested (χ^2_2 = 7,88; p = 0,019). Adult males infested with *A. hebraeum* (n = 14) also had a lower PCV (36,9 ± 8,6% (x ± s); p = 0,003) and MDW (67,4 ± 32,5%; p = 0,050) than those which were not infested (PCV = 42,3 ± 4,6%; MDW = 86,3 ± 9,1%; n = 32).

Moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were associated with a lower PCV in lambs and adult males (Figure 2), and a lower MDW in lambs, adult males and adult females. Lambs in poor condition with moderate to heavy loads were collected from January to April (Figure 3), and adult males in poor condition with moderate to heavy loads were collected in December and February and after the rut from June to August. Adult females with moderate to heavy loads had a lower MDW in February and March, but there was no effect of loads from April to August.

In adults the relationship between moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* and body condition was confounded by the presence of *A. hebraeum*, which was associated with moderate to heavy loads (κ = 0,25; p < 0,001) and body condition. Five of six adult males with PCV ≤ 36 were infested with both *A. hebraeum* and moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus*, as were all of the adult males (n = 5) and adult females (n = 2) with MDW < 50%.

Management

The prevalence of *A. hebraeum* adults was higher in the unmanaged area than the managed area (18 *vs* 4%; χ^2 = 6,24; p = 0,012), and all of the maturing females were collected in the unmanaged area. Nymphs were also collected more frequently in the unmanaged area (49 *vs* 11%; χ^2 = 21,50; p < 0,001), and there was a similar trend for larvae.

Neither the prevalence nor the sample sizes of *R. appendiculatus* adults and maturing females differed significantly

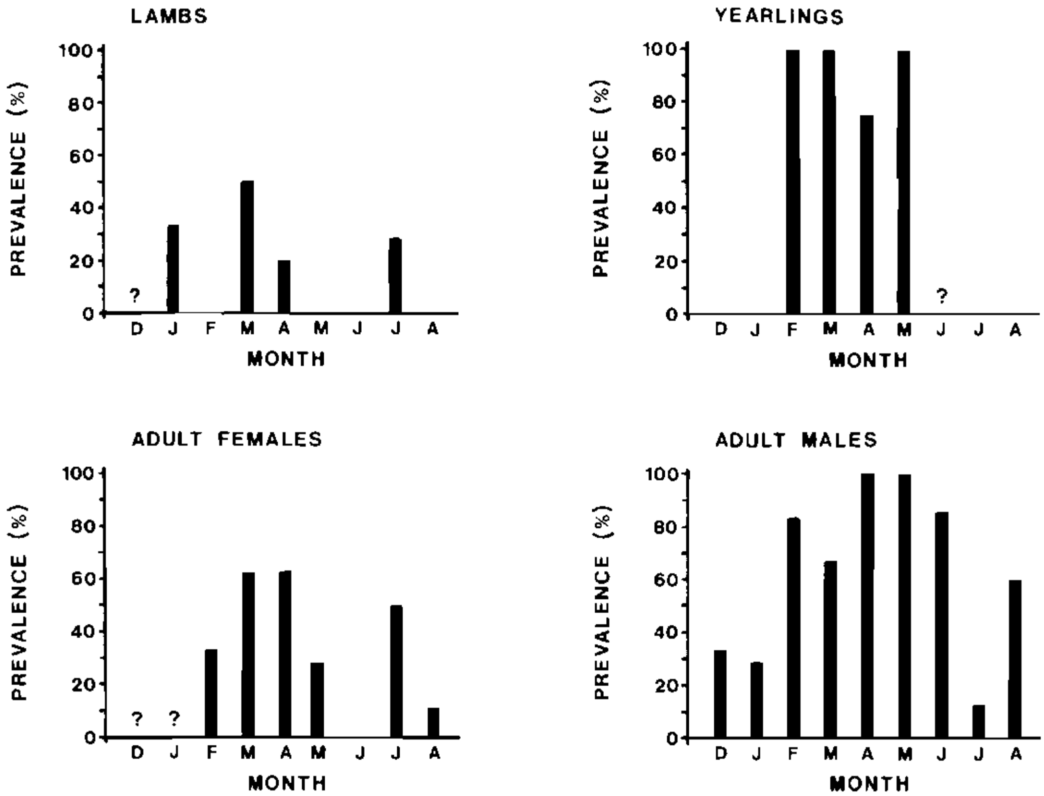

Figure 1 Prevalence of moderate to heavy loads (≥ 20 ticks per sample) of *Rhipicephalus muehlensi* and/or *R. appendiculatus* in the age and sex classes of impala by month from December 1985 to August 1986. '?' indicates that no impala in that age and sex class were examined.

between areas. Nymphs were collected more frequently in the managed area (44 *vs* 26%; $\chi^2 = 5{,}63$; $p = 0{,}018$), and the mean sample size, excluding samples without nymphs, was larger ($t = 3{,}79$; $p < 0{,}001$) in the managed area ($x = 32{,}4$) than the unmanaged area ($x = 8{,}7$).

R. e. evertsi nymphs were collected more frequently in the unmanaged area (37 *vs* 17%; $\chi^2 = 6{,}72$; $p = 0{,}010$), but the prevalence of adults did not differ between areas.

R. muehlensi adults were more prevalent in the unmanaged area (98 *vs* 85%; $\chi^2 = 9{,}60$; $p = 0{,}002$), and the mean sample size, excluding samples with no *R. muehlensi* adults, was significantly larger ($t = 7{,}50$; $p < 0{,}001$) in the unmanaged area ($x = 21{,}3$) than the managed area ($x = 6{,}2$). Maturing females were more prevalent in the unmanaged area (54 *vs* 18%; $\chi^2 = 16{,}20$; $p < 0{,}001$), and nymphs were collected more frequently in the unmanaged area (53 *vs* 33%; $\chi2 = 5{,}73$; $p = 0{,}017$).

Moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were more prevalent in the unmanaged area than the managed area (51 *vs* 20%; $\chi^2 = 13{,}31$; $p < 0{,}001$). This difference was consistent in all months (Figure 4), and in all age and sex classes (Table 2). It was particularly evident for lambs in January when large samples were collected from lambs in the unmanaged area, while lambs from the managed area had few, or no, ticks (Figure 5). Lambs from the unmanaged area were infested not only with the *R. muehlensi*, but also with *B. decoloratus* and *R. e. evertsi*.

Lambs in the unmanaged area had a lower PCV ($p = 0{,}008$), and the effect was additive with the effect of moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus*. Yearlings in the unmanaged area had a lower PCV ($p = 0{,}029$) and MDW ($p = 0{,}050$), but MDW appeared to increase ($p = 0{,}051$) when they were infested with moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* as loads were most common in the summer when they were in the best condition. There was no relationship between area and body condition in the adults.

Discussion

Lambs had the lowest prevalence and apparent intensity of infestation of the adults of most of the tick species, and adult males had the highest. A number of factors have been proposed to explain age and sex patterns of tick infestation, but the two most likely factors in impala were nutritional status and behaviour.

Impala infested with *A. hebraeum* and with moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were in poorer condition, and warthog, blue wildebeest and kudu in poor condition were also heavily infested with these tick species (Gallivan, unpubl. obs.). Tick infestation can cause anaemia and reduced weight gain (O'Kelly & Seifert 1969; 1970; Lewis 1981; Taylor & Plumb 1981; Norval, Sutherst, Kurki, Gibson & Kerr 1988; Norval Sutherst, Jorgensen, Gibson & Kerr 1989), but the only segment of the population in which tick infestation may have been the primary cause of poor condition was lambs in January. None of the heavily infested lambs had other obvious parasites or diseases (Gallivan, unpubl. obs.).

In other segments of the population, the tick infestation was probably secondary to the poor body condition. Animals in poor condition or on a poor quality diet have an impaired immune response and have less energy available for tick

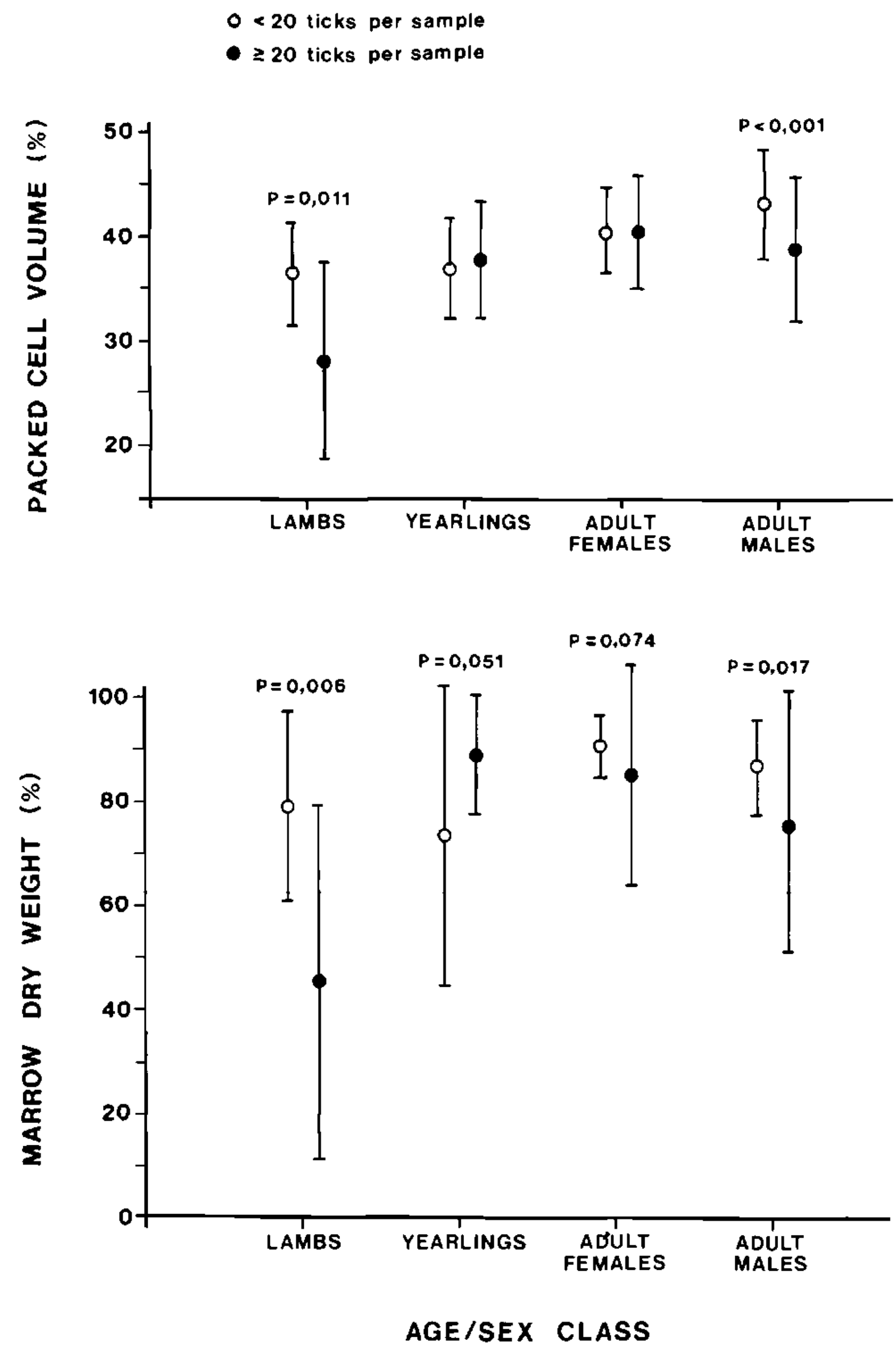

Figure 2 The effect of moderate to heavy loads (≥ 20 ticks per sample) of *Rhipicephalus muehlensi* and/or *R. appendiculatus* on packed cell volume and marrow dry weight in the age and sex classes of impala. The vertical bars are ± 1 standard deviation. The *p*-values are derived from 2-factor models with area and load as the independent variables for the lambs and yearlings, and month and load as the independent variables for the adults.

avoidance or grooming. Thus, resistance to tick infestation is reduced on a low plane of nutrition (O'Kelly & Seifert 1969, 1970; Sutherst *et al.* 1983), and the anaemia and weight loss caused by ticks are accentuated (O'Kelly & Seifert 1969; 1970). Diet quality is reduced in the winter (van Rooyen 1992) and many impala lambs, yearlings and adult males were in poor condition prior to the spring rains, particularly in the unmanaged area (Gallivan, Culverwell & Girdwood 1995). This would explain the heavy infestations of ticks on some of the impala in October.

Reproductive demands also influenced body condition in the adults. There was a marked decline in the condition of adult males after the rut, and many of the males infested with *A. hebraeum* and moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were in very poor condition. These individuals often had other injuries which would have limited

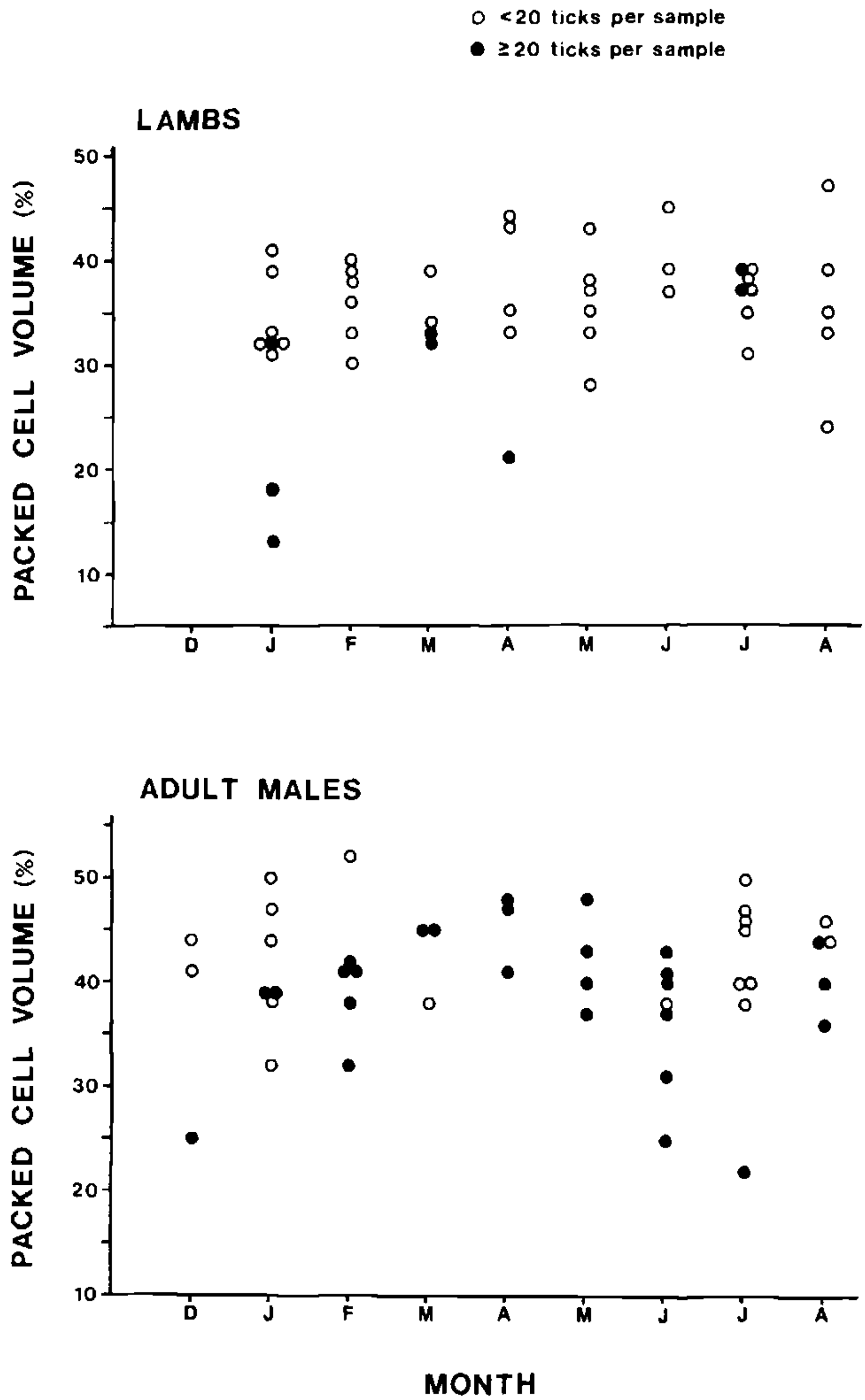

Figure 3 The relationship between moderate to heavy loads (≥ 20 ticks per sample) of *Rhipicephalus muehlensi* and/or *R. appendiculatus* and packed cell volume in impala lambs and adult males by month from December 1985 to August 1986.

their ability to groom (Gallivan, unpubl. obs.). Each maturing *A. hebraeum* female may reduce the live weight gain of cattle by 10 g and each maturing female *R. appendiculatus* reduce gain by 4 g (Norval *et al.* 1988; 1989). Thus, the inability to remove these ticks would contribute to a further deterioration in body condition, which would then reduce the resistance to further infestations.

Moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were common on lactating females from February to April, and three of the four adult females infested with *A. hebraeun* were collected in February and March. The prevalence of moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* declined in May after the lambs were weaned. The decline in prevalence of loads on the females may be due to the reduction in energy demands at the end of lactation, and the subsequent improvement in condition (Gallivan, Culverwell & Girdwood 1995).

Energy balance does not explain the high prevalence of moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* on yearlings and adult males from March to May when they were in good to excellent condition, nor the low prevalence of ticks on lambs which have a high energy demand for growth. Seasonal patterns in tick populations could explain the loads of *R. muehlensi* and/or *R. appendiculatus* on adult males and yearlings, but this should be reflected in all segments of the population. Seasonal patterns also don't explain the increased prevalence of *B. decoloratus* adults on adult males, or the occurrence of *A. hebraeum* on adult males in excellent condition during the rut. Behaviour may explain the patterns in adult males and lambs.

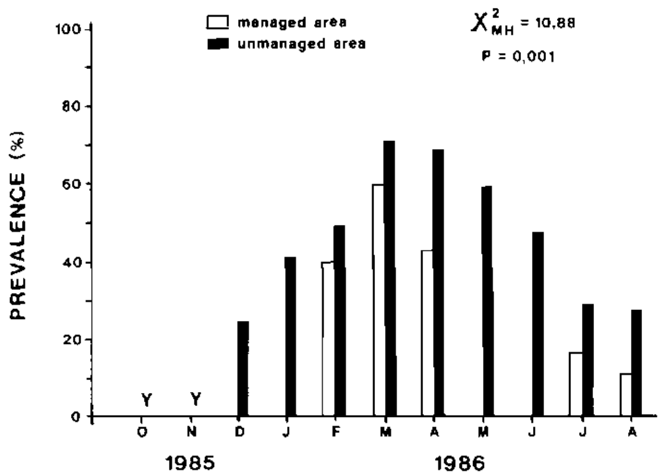

Figure 4 Prevalence of moderate to heavy loads (≥ 20 ticks per sample) of *Rhipicephalus muehlensi* and/or *R. appendiculatus* in the managed and unmanaged areas by month from October 1985 to August 1986. 'Y' indicates that loads were present, but the prevalence was not determined.

Throughout much of the year impala males remain in bachelor herds where they engage in social grooming (Jarman & Jarman 1973; Hart & Hart 1992). However, males become less tolerant of each other several weeks prior to the rut, and territorial males are intolerant of other males (Murray 1982). Territorial males do not engage in social grooming, which may be important for reducing tick burdens on the head and neck (Hart & Hart 1992), and auto-groom less frequently than other segments of the population (Hart, Hart, Mooring & Olubayo 1992). Territorial males also spend more time standing and resting in shaded areas than other segments of the population (Jarman & Jarman 1973). These areas may be foci for detaching *R. appendiculatus*, and *R. muehlensi* nymphs were abundant in the winter (Gallivan & Surgeoner 1995). Impala are predominately browsers during the winter (Smithers 1983), and rest in the shade in the hot, dry period in the spring (Jarman & Jarman 1973). *R. appendiculatus* adults remain active for longer periods in woodlands than open grasslands (Minshull & Norval 1982), and *R. muehlensi* appears to prefer bush habitats (Gallivan & Surgeoner 1995). Thus, males will be exposed to greater tick challenge at a time when the reduction in social and auto-grooming will reduce tick removal. Even though there was a decline in body condition of all males after the rut in May, from June to August moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were only found on males which retained territories, or were in very poor condition.

Habitat selection outside of the rut may also play a role in the increased prevalence and apparent intensity of infestation of ticks on males. Impala males frequent shrubland and dense herbaceous vegetation more than females (Anderson 1972;

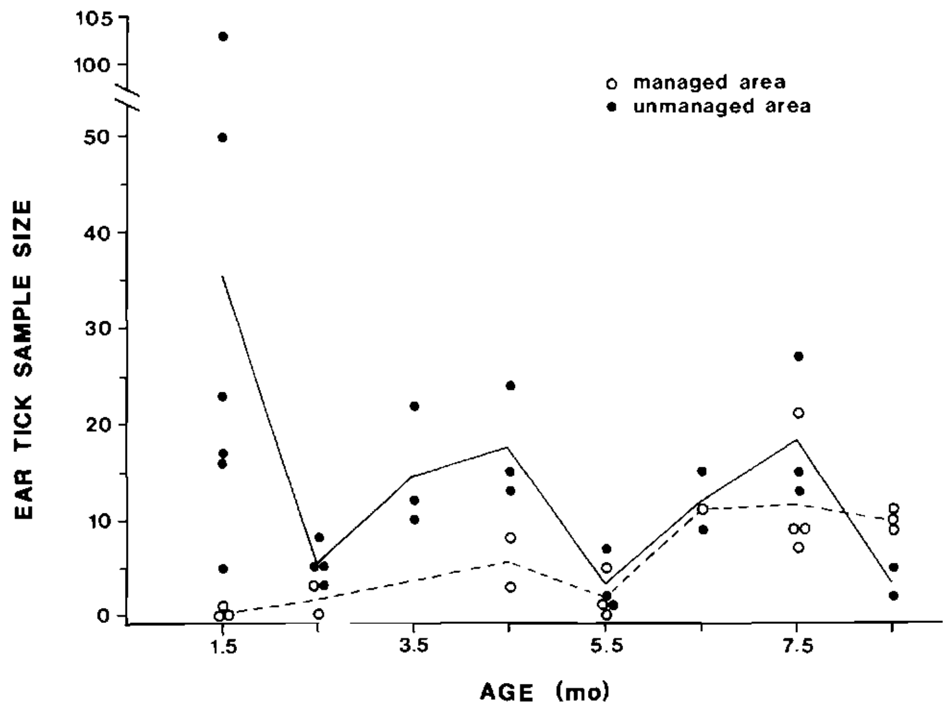

Figure 5 *Rhipicephalus muehlensi* and/or *R. appendiculatus* sample size from impala lambs from 1,5 to 8,5 months of age in the managed and unmanaged area. This age class corresponds to collections from January to August 1986.

Murray 1981), and many tick species are more common in protected habitats (Londt & Whitehead 1972).

Impala lambs are groomed by the female while they are nursing during the first two weeks of life, and engage in reciprocal allogrooming much more frequently than adults for at least the first three months (Mooring & Hart 1992). If the purpose of grooming is for tick removal, this would reduce the intensity of infestation of adult ticks on lambs. However, the larger samples of *R. appendiculatus* and *R. muehlensi* from lambs in the unmanaged area (Figure 5) which were in poorer condition indicate that nutritional balance was also important.

With the exception of *B. decoloratus* nymphs which were collected more frequently from lambs, the prevalence of immature stages did not differ between the age classes. The small size of the immature stages may preclude their effective removal during grooming, and they do not appear to affect growth (Norval *et al.* 1988, 1989).

Management

A. hebraeum adults and nymphs, *R. e. evertsi* nymphs, *R. muehlensi* adults and nymphs, and moderate to heavy loads of *R. muehlensi* and/or *R. appendiculatus* were more prevalent in the unmanaged area than the managed area, indicating that management practices significantly influenced tick prevalence and intensity of infestation. Possible reasons for the high tick burdens include increased host density, habitat changes, and poor body condition of the hosts, but these factors are not independent. Increased host density increases the probability that ticks will find a suitable host, and may also lead to overgrazing. In savannas overgrazing is often accompanied by bush encroachment (Cumming 1982) which provides cover, and may actually improve the microclimate for the free-living stages of some tick species. Overgrazing can also cause a reduction in the available biomass of plant material and a shift towards less nutritious invader species in the plant community. This can cause nutritional stress which reduces host resistance.

Tick infestation has been suggested as a cause of mortality in several ungulate species (Lewis 1981; Lightfoot & Norval 1981; Melton & Melton 1982). The only segment of the impala population in which tick infestations appeared to be a primary problem was in lambs from the unmanaged area in January, but there was no evidence that ticks were an important cause of mortality. However, tick infestations were probably a major factor in the high mortality of waterbuck (*Kobus ellipsiprymnus*) calves and zebra foals in Mbuluzi Nature Reserve (Culverwell, unpubl. obs.).

R. appendiculatus nymphs were more common in the managed area, but the prevalence and sample sizes of *R. appendiculatus* adults did not differ between the areas. The lower prevalence and smaller sample sizes of nymphs in the overgrazed, unmanaged area may be due to lower survival of the eggs and larvae which are sensitive to desiccation (Londt & Whitehead 1972; Branagan 1973). The difference in larval survival was probably offset by the fires in the managed grassland in August or September which would have reduced the survival of the nymphs (Spickett, Horak, Van Niekerk & Braack 1992). This would suggest that although impala from the unmanaged area had higher burdens of some tick species, the effects of management are complex, and may vary between tick species.

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