" DIURNAL AND SEASONAL ACTIVITY OF UNFED ADULTS OF RHIPICEPHALUS APPENDICULATUS, Neumann 1901 IN RELATION TO SOME FACTORS IN THE MICRO-ENVIRONMENT"

By

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DECLARATION.

This thesis is my original work and has not been presented for a degree in any other University.

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This thesis has been submitted for examination with our approval as University supervisors.

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SUMMARY

A study was conducted on the activity response of unfed adults of Rhipicephalus appendiculatus to some of the environmental changes during the three main seasons here in East Africa.

Ticks of two different ages were subjected to various treatments in the laboratory to vary their physiological (hydration) states and thereafter exposed in the field. Observations were made on the activity responses in relation to changes in temperature and relative humidity within the micro-habitat at two different sites.

The results obtained showed that fully hydrated ticks were more active than the dehydrated ones.

Similarly, six months old ticks were more active than the two months old ones. The fully hydrated ticks became active immediately after release into the field plots, while the dehydrated ticks needed to replenish the water lost during the dehydration process before they showed any sign of activity. They, therefore, remained inactive for 1 - 2 days after release.

Although the dehydrated ticks were taking up water more rapidly during the wet season, the fully hydrated did not show any significant changes in their degree of water uptake. The ticks were generally losing more water during the day than they were able to replenish at night during the hot dry season, hence, progressive loss of water.

The vertical distribution of ticks in the habitat was very much related to season, with most ticks found in the upper part of the vegetation during the rainy season while most of them were found at the soil level during the hot dry season.

Temperaturs between 20^oC - 30^oC seemed to be the optimal range for activity of the fully hydrated tick, below or above which activity will be markedly reduced. Temperature, therefore, seemed to be the triggering factor for activity.

Ticks appeared to be indifferent to changes of darkness and light, but with the right hydration state, probably near full hydration, temperature and relative humidity of the microhabitat appear to be the cues for the daily pattern of tick activity which is also reflected in the seasonal pattern of activity.

There was no significant difference in activity between the sexes, and also between the two sites.

Probably due to the small number of ticks active, the seasons also did not differ significantly.

CHAPTER I

INTRODUCTION

1. CLASSIFICATION AND GENERAL FEATURES OF TICKS

Although some people regard ticks as insects, they are infact members of the phylum Arthropoda, in which insects are included. Ticks are in the class Arachnida, order Acarina, the super-family Ixodoidea, Banks. The class Arachnida includes ticks, mites, spiders, scorpions, harvestmen and related forms. It is one of the largest of the classes of Arthropoda and is exceeded only by the Hexapoda. The order Acarina (ticks and mites) are air-breathing arthropods with no apparent antennae. They possess, as adults, six pairs of appendages (chelicerae, sensory palps, representing the pedipalps, and four pairs of legs). Externally the acari show very little resemblance to other Arachnida. They lack a border between the gnothosoma and the idiosoma and they possess a discrete head structure, the capitulum. The underlying organization of their anatomy reveals, however, that they are properly placed within the Arachnida and that they have evolved a highly specialised type of structure correlated with their parasitic mode of life.

The super family Ixodoidea unites the representatives of three families:

1) Ixodidae (hard ticks)
2) Argasidae (soft ticks)
3) Nuttalliellidae (intermediate forms)

The ticks of the family Argasidae, with nearly 100 species described, have a leathery integument and the capitulum in nymphs and adults is either subterminal or distant from the front margin of the body. The mouth parts are thus not visible from above. Generally, argasid ticks inhabit xeric habitats where the relative humidity is generally low.

Members of the family Ixodidae, or hard ticks, differ morphologically from argasids in that they have a dorsal shield or scutum at all stages of their life histories, and the capitulum with its associated mouth parts is always anterior and visible from above. These ticks occur throughout the world where terrestrial vertebrates are found, attacking most land mammals whilst some of them parasitize birds and reptiles. Biologically there is much uniformity of pattern in this family of ticks and their success in the difficult environment which they select is probably due to their high rate of reproduction. The ability of most genera to withstand a comparatively wide range of temperature and humidity fluctuations, compared with other arthropods, is also very good. These advantages are, however, offset by their aimless wandering and dropping from hosts, either after engorgement or due to the unsuitability of the host, and also their indiscriminate egg-laying habits unlike other arthropods. This family, is represented by about 700 described species.

The third family of ticks, Nuttalliellidae, is represented by only one species described and appears to possess intermediate characters between the other two families of Argasidae and Ixodidae. An outline of the scutum is evident as in the Ixodidae but it is not structurally differentitated from the rest of the dorsum. The capitulum and mouthparts are anteriorlly placed as in Argasidae. The single species has been described from South West Africa (Namibia).

Other differences between the ixodids and argasids are that the latter are chiefly nest-borrowing blood suckers. They are, therefore, mostly multihost. As a result of the linear relationship between the amount of blood ingested and the number of eggs laid, the argasids lay relatively fewer eggs after each blood meal.

The Ixodidae on the other hand increase their survival under theharsh environment by increasing their feeding time and taking more blood, thus, producing more eggs, at a time. Some hard ticks have also evolved tendencies to change from three-host to one-host.(see page 5)

2. ECONOMIC IMPORTANCE OF TICKS

The role of ticks in the human economy merits special consideration for not only are they annoying pests, but in the temperate and tropical countries they surpass all other arthropods in the number and variety of diseases they transmit to man and his domestic stock. This together with blood-sucking Diptera are specific vectors of the chief groups of agents of transmissible infections of man and animals.

These include viruses, rickettsiae, bacteria, spirochetes, filariae, and the widespread protozoa. Ticks are known to transmit diseases like Rocky Mountain spotted fever, East Coast Fever, South African tick typhus, Colorado tick fever, red-water, tularemia, heart water, gallsickness, louping ill of sheep, Nairobi sheep disease, encephalomyelitis, corridor disease, and many others.

A single tick species may be capable of transmitting a number of diseases and similarly a single disease can be vectored by a number of tick species. The largest group of micro-organisms transmitted by ticks are Protozoa Diseases caused by these organisms are the most widespread and are the major killers of livestock in many countries to-day. In Kenya, for example, "51% of all cattle dying to-day do so from tick-borne diseases and 75% of these are due to East Coast Fever, a protozoan disease of cattle". (Ann.Rep.Vet.Dept.,1966).

The distinct ecological, morphological and physiological properties of ticks (Ixodoidea) as parasites of terrestrial vertebrates also determines the nature of their interrelationship with disease agents. In contrast to insects, ticks have no peritrophic membrane in the gut to act as a mechanical barrier to micro-organisms passing from the gut cells, and the exceptional pinocytotic ability of tick digestive cells assures passive transportation of agents into the cells. Long-feeding ticks constantly inject fresh saliva into the host body and discharge from the anus large amounts of faeces and semi-digested blood; argasidae also discharge coxal gland fluid, thus, providing exceptionally favourable conditions for inoculative and contaminative, e.g. spirochaetes, transmission of pathogens to susceptible animals. Moulting also changes properties in the body and ovary structure provides easy transstadial and transovarial transmission of the organisms.

3. TICK LIFE CYCLES

All ticks have very complex developmental cycles. In argasids the life cycle consists of the following stages:- egg, larva, 2-7 nymphal instars and adult. In ixodids, the nymphal stage is reduced to a single instar.

Ticks usually feed once in each active instar. Some species of argasids, however, (e.g. Ornithodoros moubata) have a non-feeding larval stage. The main differences between the three instars are both morphological and physiological.

Larvae - These are relatively smaller in size than either nymphs or adults. They have three pairs of legs, and are sexually immature.

Nymphs - These are relatively smaller than adults and bigger than larvae. They possess four pairs of legs, resemble morphologically the adult females but lack the "porose areas" which are found on the dorsal side of the basis capituli. They are also sexually immature.

Adults - These are bigger than the other two stages, with four pairs of legs. The male and female have distinct morphological and physiological features. Sexual maturity in some ixodids is attained after a blood meal, while in others, sexual maturity is attained immediately after moulting even before taking a blood meal, e.g. some of the members of the genus *Ixodes*.

Blood feeding in larval, nymphal and adult stages results in very complex developmental cycles involving regular alterations of free-living and parasitic existence together with changing hosts. Tick life cycles are divided into four groups on the basis of the number of host changes and moults. These are multi-host, 3-,2-, and 1-host.

Multi-host - This is mostly characteristic of most argasids. This is associated with irregular but numerous feeding nymphal instars and several adult gonotrophic cycles.

Three-host - This cycle is characteristic of most hard ticks. Ticks with this life cycle remain on the host only while feeding. The larva hatching from the egg climbs up the nearest vegetation and waits for a passing host to which if suitable, attaches and feed. After engorgement it drops to the ground and after getting a suitable place, it moults. The emerging nymph again climbs the vegetation and waits for a passing host. After it has fed and engorged, it drops to the ground and also moults. The adults also climb up the vegetation and wait for a host to pass. After feeding on its blood for some days the two sexes meet and copulate. The fertilized female after engorgement drops to the ground and lays a batch of eggs which hatch into larvae. The female soon dies after egg laying. The hatched larvae then repeat the cycles.

Two host - In a two-host cycle the larva after climbing the vegetation, finds a host and remains attached to it even after engorgement and moults to nymph. This detaches only after it has fed. The adults also look for a new host.

One-host - This is a cycle where all the moults occur on the first host and only fertilized and engorged female detaches to lay eggs on the ground.

Transition to 2 - and 1 - host development cycle is regarded as one of the most important parasitic adaptations of the relatively immobile field blood suckers to large nomadic animals.

For ixodids the potential for finding a host are very much reduced and thus mortality is very high and, therefore, acquiring the ability to moult on the same host reduces a number of necessary encounters and thus increases chances for tick survival. Climatic and seasonal factors in the host's life have not affected the feeding pattern so much as the duration and seasonal regulation of the tick's life cycles.

The complexity of life cycles of ticks made their control especially difficult. With this, and the economic importance of ticks as vectors of important diseases of man and livestock in mind, several scientists have mounted intensive research on various aspects of their behaviour, physiology and ecology.

Veterinarians and herdsmen tend to think of ticks primarily in association with cattle and other livestock hosts on which they are to be found but, in fact they are mainly dwellers of the soil and vegetation. Some species like *Ixodes ricinus* spend only about 2 - 3% of its life on the vegetation tips (Lees and Milne, 1951). *Rhipicephalus appendiculatus* spends between 18 - 22 days, in total, on the hosts while taking bloodmeals, (larvae 3 - 5 days, nymphs 5 - 7 days, females 7 - 10 days) (Nattall, 1913, quoted by Hoogstraal, 1956; Tukahirwa, 1976). The rest of the tick's life is spent on the ground.

4. OBJECTIVE OF THE STUDY

As the principal vector of *Theileria parva,* the protozoan which causes East Coast Fever in cattle, *Rhipicephalus appendiculatus* is the most important tick species in Kenya. Even in the absence of collections its presence may be suspected in areas where ECF is enzootic (Walker, 1974).

Seasonal occurrence of *R. appendiculatus* is now fairly well established and documented. As will be seen from the next chapter on literature review very little work has been done to study the population behaviour of this economically important tick species, with the aim of trying to control it's number and subsequently the control of the diseases it transmit to its host.
Survival of the tick and its response to changes within

the micro-habitat are very essential when one tries to understand the behaviour of the tick population.

Theiler (1959) referring to R. appendiculatus admitted, "What the factor is determining the seasonal tick activity we do not yet know". Twenty years later, we are still not in a position to explain the factors regulating activity of this tick species in East Africa.

It was, therefore, the purpose of this study to investigate the response of ticks in different physiological states (water content, sex and age) to changes in the micro-environment at different raasons of the year.

It was hoped that these results will help in elucidating the factors regulating seasonal and daily tick activity under natural field conditions.

For the purpose of this study, "Activity" was defined here to mean: that part or aspect of behaviour when the unfed tick leaves its resting site on the ground or in the vegetation and moves to the upper part of the vegetation in response to external stimuli from the microenvironment or its own internal stimuli, whether it is passive or in questing posture. All aspects of behaviour with respect to the host were deliberately omitted.

CHAPTER II

LITERATURE REVIEW

1. GENERAL DISTRIBUTION OF TICKS

Ticks are widely distributed in the world. The Argasidae are found as far north as 50^0, and the Ixodidae are even more widely distributed and occur in all natural and climatic zones from the equator almost to the poles. However, most species are found in tropical and subtropical regions.

In arid regions of the world, the Argasidae and, the Hyalomma and Rhipicephalus species of the Ixodidae, predominate. In more humid habitats,species of the genera Boophilus, Ixodes, Amblyomma, Haemaphysalis, Rhipicephalus and Dermacentor are commonly found.

The distribution of each tick species is determined mainly by such climatic factors as humidity, temperature, vegetation and the relationship between the tick species with the host species, especially if the tick is one with a restricted host preference, for example the distribution of the tick species Ceratoxides putus is associated with the host distribution. It is a feeder of the sea bird and occurs beyond the arctic circle, (Balashov, 1972).

2. TICK ACTIVITY

2.1. DISCUSSION OF "ACTIVITY"

The end of the post-moulting phase is shown when the tick acquires the ability to parasitize a host or when the tick develops "aggressiveness" (Balashov, 1972).

Host-finding behaviour of parasitic animals is generally passive in nature. Camin (1963) recognized three categories of parasitic Acarina:

a) Those acarines which are transferred only by direct contact between hosts, e.g. Analgesoidea (feather mites), Psoroptoidea (mange mites), and Myobiidae (the fur mites).

b) Nidicoles or nest-parasites, such as the members of the Argasidae and some of the ixodid species. Most of the acarines in this group are haemotophagous and are only found on the hosts when feeding. They feed less frequently than the first group, but generally take more blood at each feed. Members of this group have highly developed olfactory organs and crawl to the host in response to various stimuli from the host, like carbon dioxide.

c) This group includes those acarines which find a vantage point in the environment where they await contact with a passing host. Their host finding is largely dependent on the activities of the host. This group includes the ixodidae and the chiggers, and are only found on the host whilst feeding. They feed less frequently than the members of the second group. They also live much longer than the members of the other two groups, and are able to survive much longer periods of starvation.

Since they spend a far greater proportion of their time off the host compared to other acarines, they are highly subject to changes of the physical environment and they must be able to adjust if they are to survive until a host becomes available. Host to host contact, therefore, plays little or no part in the dissemination of such parasites.

Newly hatched or moulted ticks are unable to attack or attach to hosts for sometime. For R. appendiculatus this period varies from 7-21 days for all stages (Branagan, 1970; Hoogstraal, 1956; Tukahirwa, 1976). This lack of activity is due to the following factors (Balashov, 1972).

a) Delay whilst cuticle hardens including the mouth-parts which are necessary for penetration into the host's skin.

b) The hypertrophied gut cells of the previous phase are being gradually replaced by the flattened undifferentiated epithelium.

c) The malpighian tubules continue to gradually discharge the great quantity of guanine accumulated during the previous period of intensive morphogenesis.

d) The salivary gland alveoli have not yet reached the final size and are not filled with secretion.

e) Cell division continues in the gut and ovary epithelia.

When the time comes for the tick to look for a host it usually clings vertically to the tops of leaves or shoots of the vegetation, or applies itself on the upper or lower leaf surface. The tick assumes a passive posture with the fore legs folded under the body or all the four pairs of legs clasping the stalk. When the tick receives a stimulus from an approaching host it assumes a characteristic "questing" posture. The forelegs, richly provided with sense organs, are extended forward ; the other pairs of legs continue clasping the substrate (Fig 1). Their reaction to a particular stimulus or groups of stimuli varies not only according to nutritional state but also according to several other intrinsic factors such as developmental stage, water balance, and even previous activity.

Lees (1948) divided host finding behaviour of ticks into three phases:-

1) The passive phase - The tick moves to a vantage point in the environment where a host is likely to contact it.

2) The questing phase - The tick is alerted to the approach or the presence of a host, orients to it, and moves towards it and then climbs on to it.

3) The host-discrimination phase - The tick probes the host and either attaches and feeds, or else rejects it, drops to the ground and returns to phase one again.

MacLeod (1935) however, defined activity of *Ixodes ricinus* as tick infestation on the host. Activity has been used in this sense by almost every investigator studying seasonal incidence of ticks

Fig. 1. Resting position of R. appendiculatus adults on the vegetation.

Seasonal activity in a tick population can be monitored in two ways:

(a) By sampling the ticks on the hosts at regular intervals.

(b) By sampling the ticks on the vegetation regularly using the blanket method of MacLeod (1932) and Milne (1943). A woollen cloth is dragged over the habitat and some of these ticks which are up on the vegetation waiting for a host will cling to the blanket and they can be collected and counted. This method is especially useful in sampling the immature stages (MacLeod, 1932).

The diurnal cycle of tick activity is mainly the response of individual ticks in the population to diurnal environmental changes and is superimposed on any seasonal pattern.

2.2 SEASONAL ACTIVITY

In situations where there are marked seasonal differences there may be long periods when certain species of ticks are not to be found on their hosts. In tropical climates seasonal changes are far less marked although they do occur. In these circumstances the adults, in particular, of the various species of ticks are likely to be found on their hosts throughout the year.

Seasonal incidences of some species of ticks are given below with the factor suggested to control their activity patterns:-

1) *Ixodes ricinus*

This species is known to have two phases of activity, especially in Britain during the warm part of the year. The first phase in spring (March-May) being the major peak of activity and the lesser peak of activity in autumn (September - October) (MacLeod, 1932, 1939; Milne, 1945, 1947). During the hot part of summer there is a marked decline in activity. In northern Russia the tick is active in summer while in North Africa the tick is active in winter.

Several factors, both physical and biological, have been suggested as factors governing the tick's activity.

MacLeod (1932) did not find any correlation of tick activity with rainfall, but observed that ticks were more active at temperatures of 45^0 - 60^{0}F (7.0^0- 15.5 ^{0}C), than when 60^{0}F (15-5^{0}C) is exceeded. In 1935, he found that the most favourable temperature for tick activity was between 14-24^{0}C and the same was also found by Totze (1933). He therefore suggested temperature to be limiting in parasitization as opposed to that for survival. Although Totze (1933) had found ticks to be photopositive at this temperature range, MacLeod (1935) found them to be photonegative and also negatively geotrophic.

MacLeod (1939) advanced three theories to account for the observed periodicity of ticks on sheep:-

(a) The "two-brood theory - This theory postulated the presence of separate broods of ticks, active in spring and autumn. It was believed that the summer drop in tick activity was due to lack of ticks as the first brood became exhausted. No further infestation was possible until these had moulted to infest again in autumn.

(b) Totze's theory - This theory advocated that diapause occurred during the winter, thus forming a physiological rhythm in the metabolism of the tick.

(c) The temperature control theory - This theory put forward by MacLeod (1936) showed that there was correlation between tick activity and atmospheric temperature with the maximum activity between 45^0 - 60^0F (7.0- 15.5^{0}C). Since *Ixodes ricinus* does not diapause in England, (MacLeod, 1932, 1935) the diapause theory of Totze was, therefore, found to be invalid, but may only explain the winter inactivity of the ticks. In Russia, however, *Ixodes ricinus* does diapause. It was, therefore, suggested that physiological activity in the species is a simple function of temperature irrespective of the season. Contrary to MacLeod's findings Milne (1945) showed that most of the annual activity occurred at temperatures above 60^0F (15.5^{0}C) and started to wane in autumn when the temperature went below the 60^0F (15.5^{0}C) level. He then suggested that if macro-climatic temperature is too high and humidity too low for too long during day time and suitable conditions are occuring deep down in the vegetation mat the ticks might then tend to remain immobile in the vegetation mat, rather than undergoing the stress and expenditure of energy involved in frequent ascents and descents of the vegetation. On the other hand, where micro-climatic gradient is steep, ticks may find suitable conditions at a point not too far from the tips for them to remain active and ready to attack.

Lees and Milne (1951) said that tick activity is mainly a reflection of the "availability" of unfed ticks in the vegetation. The availability of such a population at any given season will depend primarily upon two factors. First, on the timing of the cycle of development. Secondly, on the behaviour and possible survival of unfed ticks from season to season.

In Russia the seasonal activity regulation is ensured by egg, larval and nymphal diapause (Balashov, 1972). In long day conditions (18-24 hours of light), engorged larvae moult into nymphs without delay, but in short day conditions (9-14 hours) diapause appears in all larvae and metamorphosis extends for about 200 days. Lees (1948) showed that for unfed tick Ixodes ricinus, light is of very little importance and is never attracted to it and may be repelled by directed illumination, especially for newly moulted ticks. As the tick ages it becomes indifferent to such changes.

Unless permanently sheltered by a humid environment the survival of the terrestrial arthropod will depend to a considerable extend on its ability to limit evaporation. This is true especially as the fasting tick must often spend a lengthy time awaiting a suitable host. A tick is capable of taking up water from a humid environment or humid air. Similarly, it is capable of losing its water through evaporation to dry environment (Lees, 1946).

As a result of this knowledge several people have tried to relate tick activity to the water regulation. Balashov (1972) pointed out that behaviour of active unfed ticks is determined by many external factors of the environment and their physiological states. Tick climbing on the vegetation is ensured by their negative geotaxis but in unfavourable conditions of temperature and humidity, which reduce their normal water content, a positive geotaxis develops and the ticks return to the ground litter. Direct reactions to the humidity gradient in air layers above the soil are also important.

MacLeod (1935) had recognized the effect of prolonged low humidities on the ticks. He pointed out that changes in the moisture equilibrium of the air, within the narrow limits permissible for Ixodes ricinus, would not be expected to produce immediate responses, but rather to take effect through their prolonged application altering the water content of the body. Earlier, Buxton (1932) had pointed out that tracheate species of arthropods appear to be more resistant to drying than the non-tracheate species. It is possible that this may be the reason why nymphs and adults do survive better than larvae and under arid conditions they are able to conserve moisture probably by closing the spiracles.

The equilibrium humidity for Ixodes ricinus is about 92% R.H. and Lees (1946) showed that if the humidity is near by the relative humidity and not saturation deficit, but below that then the exchanges of water may be correlated with saturation deficit. After desiccation, some ticks that were exposed to humidities slightly below the equilibrium were able to take up water very slowly while others continued lo sing it to the atmosphere. Those that were exposed to higher humidities took up water at about the same rate as they lost it, reaching their original weights after 2 - 3 days. Those ticks which were exposed to saturated atmosphere took up water very rapidly with the rate of increase diminishing as the original weight is approached. Sometimes, however, uptake can be exaggerated and rather more water is gained than has been lost during desiccation. He also indicated that as the tick ages the ability to take up water and also to withstand desiccation declines. This event of loss/uptake can be repeated one. In prolonged contact with water ticks swell up. At times complete immersion kills.

By relating water balance to tick activity, Lees (1948) showed that when their water balance is normal they avoided higher humidities but this response disappears after the tick is desiccated and the tick is active in dry air until it comes to rest in humid air. On taking up water the water balance is restored and the first response reappears. He then concluded that with the April - June macro-atmospheric condition below 90% R.H. for about 18-19 hours a day it is logical to think that water gain would not compensate for water loss at the vegetation tips. The tick will then be able to take up water only from the upper mat of the vegetation.

2) Hyalomma asiaticum

The main adult seasonal incidence, mostly on camels, is observed in March - May, although all stages are found on hosts and in their principle biotopes throughout the year, (Balashov, 1972).

During the low activity of June-August, most adults are greatly emaciated. Summer heat and increased saturation deficiency near the soil surface undoubtedly lead to the death of most ticks that have been unable to find hosts. Spring engorged nymphs moult during summer into adults which remain in burrows until the following spring. A few may become active and attack domestic animals in the fall of the same year. Late summer engorged nymphs probably moult into adults during the same season. However, if they engorge in the fall, low temperatures may delay moulting until the next spring. Thus, seasonal incidence of H. asiaticum is under direct influence of climate and the presence of active unfed ticks depends on vertebrate host accessibility and on adult and immature survival for many months. Before sunrise ticks were inactive, remaining motionless on soil surface or hiding cover. As air and soil surface temperatures increased at sunrise the ticks began to move. Maximum activity was observed when soil temperature rose to between 30-40^{0}C and relative humidity was between 20-50% R.H. As the temperature began to increase ticks again began hiding in various shelters. By 1800 hours when the soil temperature began to drop to 35^0 - 40^{0}C and 20% R.H. the ticks again began to be active. At night fall they were again motionless even when the air and soil surface temperatures were again high.

3) Dermacentor variabilis

The American dog tick has one major peak of activity during summer (June), with the activity spreading from March - August (Smith and Cole, 1941; Sonenshine et al, 1966). Smith and Cole (1941) found no relationship between tick activity with the air temperature but found that the length of daylight was the significant factor. Sonenshine et al (1966) showed a significant relationship between daily adult questing and daily solar radiation received, but no significant relationship was seen between activity and air temperature. Long term weather trends were also found to influence the activity of the tick populations.

More recently, McEnroe and McEnroe (1973) showed that questing behaviour of the tick is regulated by its water balance. A loss of 4-5% of the saturated equilibrium weight reverses the questing behaviour. Darkness had no immediate effect on questing behaviour

4) Ambyomma americanum

The adults of the lone star ticks show a single peak of activity from late May to early June (Semtner and Hair, 1973).

Adults after moulting do not become active during the first year until after 2-3 years (Semtner et al, 1973). The young ticks were, however, able to respond to human breath. As temperature decreased during the evening the ticks returned to the soil litter. They therefore suggested that temperature and relative humidity gradient have a marked effect on the early seasonal behaviour of adult ticks. High temperature in combination with low humidities during day-time hours were suggested by Robertson, et al (1975) to cause a gradual decline in total numbers of active ticks from early to late summer. This is in response to an upper temperature limit. A. americanum body water loss of 10-15% of the original weight is enough to elicit a response to the high humidities in a humidity gradient chamber. Thus, activity patterns of A. americanum may be governed by body water content. Ticks kept in cages started an upward migration when the average daily temperatures were over 25°C. The percentage of ticks ascending the vegetation increased from zero in mid-April to ninty (0-90) during late May and June. In early July a gradual movement of ticks back to the ground and into the leaf litter at the base of the cages was observed. By late July a second movement up the vegetation was noticed, but much more reduced (Semtner, et al, 1973). The authors concluded, therefore, that the vertical migration of adult lone star ticks appears to be regulated by a combination of factors, including relative humidity, temperature and photoperiod. Increasing temperatures are very important in the initiation of early seasonal activity. The daily pattern showed two peaks of activity with fewest ticks found on the ground in the evening and the most during the morning with movement of ticks to the ground during hotter part of the day. Since it was shown that the critical equilibrium humidity (CEH) for A. americanum is 85% R.H. (Sauer and Hair, 1971) all habitats of A. americanum have relative humidities too low during much of the day to prevent water loss. The high temperatures encountered in the meadows are responsible for higher metabolic activity and excessive water loss and that in many cases the water loss is in excess of the amount that adults are able to reabsorb during the period when the relative humidity in these habitats is above the critical equilibrium of the tick.

5) *Amblyomma variegatum*

This is essentially an African species, occurring in East, Central, Western, and Southern Africa and also in southern Sudan, (Hoogstraal, 1956; Theiler, 1962). It has been imported to the West Indies and the Cape Verde Islands. It is noted to have a very close association with *Rhipicephalus appendiculatus* in that they both show very distinct seasonal activity patterns wherever they are found together (Wilson, 1953; Yeoman, 1964, 1968; Yeoman and Walker, 1967).

In Central Africa with only one rainy season the species shows one peak of activity, (Wilson, 1946, 1950; MacLeod, 1970; MacLeod et al, 1977), while here in East Africa where there are two rainy seasons they show two distinct peaks of activity (Wilson, 1953; Smith, 1969). The peaks always fall in the rainy seasons of April-May and November.

The tick species occurs at altitudes from sea level to at least 8,500 ft. (2,800m) (Lewis, 1932; Wiley, 1953,1958).

A. variegatum is more resistant to desiccation than its associate *R. appendiculatus*, hence, a wider distribution in Africa covering more drier parts. The factors governing these marked seasonal incidences have not been elucidated.

3) PHOTOPERIODISM

The natural rhythm of daylight and darkness provides a link between the organism and its environment and through this link environmental information is communicated to the living system. The daily photoperiod supplies the temporal signals needed for the sychronization of internal functions and some of the information required for coping with the exigencies of the outside world. The ability to detect photoperiodic stimuli and to respond to them in adaptive ways, has enabled organisms to exploit environmental and ecological niches that would otherwise remain inaccessible. The responses of organisms to photoperiod have been found to play essential roles in phenomena as diverse as geographic distribution and programming of developmental patterns.

On biological rhythms in terrestrial arthropods Danilevsky et al, (1970) summarised by saying that they involve all cyclic processes in living organisms and the frequency spectrum can be very wide, ranging from milliseconds to years. Physiological rhythms are characterized by rapid oscillation and thus ensure synchrony of all the internal processes in an organism, e.g. the enzyme-substrate systems.

The possession of internal oscillator enables organisms to prepare in time for the changes in ecological conditions during each day (daily rhythms), month (lunar rhythms) or year (seasonal rhythms). The adaptive implication and the mode of displaying the three types of rhythms varies considerably.

It can thus be seen that ticks, like other arthropods, display a large variety of rhythms. Seasonal activity is a phenomenon shown by almost all the tick species except, perhaps, the one host species which do not show marked seasonality in their rate of infestation.

Diapause has been demonstrated in a number of species, such as *Ixodes ricinus* and *Ixodes persulcatus* as delayed metamorphosis of engorged larvae and nymphs, or as interrupted oogenesis in such species as *Demacentor pictus* and *Dermacentor variabilis* has been shown (Smith and Cole, 1941).

Although it is clear that adaptation to lunar and seasonal periodicity evolve by way of time measuring within a daily cycle(Danilevsky,et al 1970), little attention has been given to daily tick activity rhythms. Most studies have been of the drop off of engorged ticks. Balashov, (1954) studied the diurnal rhythm of detachment of engorged females of *Ixodes persulcatus*. Kitaoka (1962) also studied diurnal and nocturnal changes in feeding activity during the blood sucking process of *Haemaphysalis bispinosa*. Hitchcock (1955) studied the rhythm of drop off in *Boophilus microplus*. While working on *R. appendiculatus*, Kitaoka (1962) observed no apparent diurnal rhythm of dropping.

Some activity rhythms are controlled by external (exogenous) and others by internal (endogenous) factors.

Exogenous rhythms - these are caused by external changes and the organism is only a high-sensitive indicator of a daily variation of the micro-climate.

Endogenous rhythms - In these rhythms extrinsic conditions only synchronize the phase of oscillations which arise inside the organism. Any rhythm may be rightfully called endogenous if it displays at least one of the following properties:

a) Initiation by a single short stimulus.

b) Phase of the rhythm must be in advance of external synchronizing signals.

c) The rhythm persists for some time in the absence of rhythmic light or temperature fluctuations, but may change to free-running oscillations gradually or suddenly. Distinction between exogenous and endogenous rhythms in nature is often impossible since the daily rhythm can be conditioned by endogenous signal or internal oscillators which can be suppressed by exogenous responses to favourable environmental conditions. In conditions which are constant in respect to light and temperature, and in the absence of any other entraining signals, endogenous rhythms always persist. The phase of a circadian rhythm is synchronized by daily periodic changes of the environmental factors. The main entraining signal is photoperiod, or the periodic repetition of light and darkness in a daily cycle. Thermoperiod entrains circadian rhythms of many arthropods as does photoperiod. (Danilevsky,et al 1970)

4. RHIPICEPHALUS APPENDICULATUS.

4.1 DESCRIPTION

Ticks of this species are very commonly referred to as the "brown ear ticks". This name was given to this species due to the fact that the individuals are brown in colour and the predilection site for the adults is around the ear pinna. This name could just as appropriately be applied to a number of other species of this genus which also feed on the ears of their hosts and are just equally brown in colour, particularly Rhipicephalus hurti, Rhipicephalus jeanelli and Rhipicephalus pravus. It should not, therefore, be assumed that all "brown ear ticks" are Rhipicephalus appendiculatus. Apart from the morphological differences these species can to a cetain extent be separted according to their localities. R. hurti and R.jeanelli are commonly found at higher altitudes than R. appendiculatus while R. pravus is a semi-arid species where conditions are again inimical to R. appendiculatus (Walker, 1974).

The overall length of the adults is from 1.8 mm to 4.4 mm. Usually brownish or reddish-brown but may be very dark; legs always reddish-brown. For detail identification of adult stages reference is made to Hoogstraal (1956).

4.2 LIFE CYCLE AND HOST SPECIFICITY

The life cycle of R. appendiculatus is of a three-host type. As described above (Section 3 of chapter 1) each stage (larva, nymph, and adult) require independent hosts for their feeding and development.

Theiler, (1959) puts R. appendiculatus among the group host-specific for herbivores which also includes R. compositus, R. avertsi, R. kochi, R. mühlensi, R. supertritus and R. tricuspis. This has been confirmed by Yeoman and Walker (1967) and Walker (1974), who give extensive host records. The most important host is nevertheless domestic cattle.

It has not been collected from either birds or reptiles.

4.3 DISTRIBUTION

The distribution of this species in Africa extends from southern Sudan and somewhere in Ethiopia, moves southwards to cover such countries like Kenya, Uganda, Ruanda, Burundi, Zaire, Tanzania, Malawi, Zambia, Rhodesia, Congo, Mozambique, Angola, Boswana, Namibia (South West Africa), Lesotho, Swaziland, and the coastal area of South Africa. (Hoogstraal, 1956; Theiler, 1949, 1962).

The species distribution in Kenya is shown in Fig. 2. It is restricted to Western, Nyanza, Rift Valley, and Central Provices, with the exception of the northern arid districts of the Rift Valley, Eastern, North-Eastern and Coast provinces. The tick is present along southern coastal areas. It is, however, absent from the semi-arid districts of Kitui and parts of Machakos in Eastern Province and it is also scatchy in the Kajiado district in southern Rift Valley province (Lewis, 1934; Wiley, 1958; Theiler, 1962; Walker, 1974).

The distribution is very much influenced by the microclimate of its habitat. The tick occurs from sea level to 7,000 feet (2,300 m). Above this altitude it diminishes in numbers. The tick is only numerous in areas with an annual rainfall of more than approximately 600 mm. It does not occur in areas with high rainfall coupled with high altitudes of

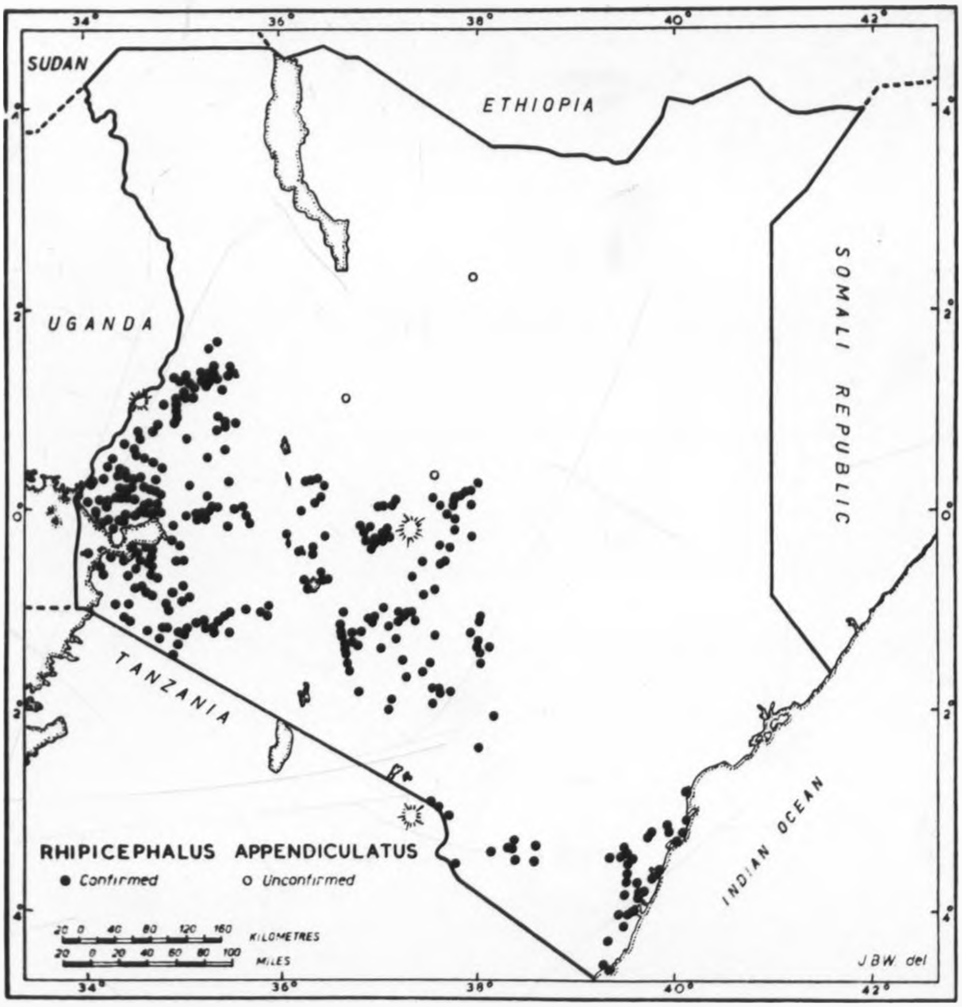

Fig. 2. The distribution of R. appendiculatus tick in Kenya. (Walker, 1974)

well over 2,700 meters. The species is generally absent from forests and extensive open grasslands , (Theiler, 1962; Lewis, 1939; Theiler, 1949; Wiley, 1953, 1958; Hoogstraal, 1956; Yeoman and Walker, 1967; Walker, 1974). In South Africa, however, it can exist in areas with an annual rainfall of only about 15-20 inches (400-500mm), where it is linked to a climate with a winter and diapause may also be involved (Theiler, 1959).

It has been suggested that the factor limiting survival of R. appendiculatus is humidity with a good vegetation cover, (Lewis, 1939; Wilson, 1950; Theiler, 1959; Yeoman, 1967; and Branagan, 1970). Theiler (1949) had suggested that since the tick survives in the river valleys and in more isolated areas tends to point to overgrazing as the limiting factor affecting the survival of R. appendiculatus.

As early as 1932 Lewis pointed out that there existed some small pockets which were infected with East Coast fever These small pockets were also known to the indigenous herdsmen especially among the Masai tribe and it was assumed that some factor or factors exists in the restricted areas which are not present outside the areas and which created a suitable environment for the development and propagation of tick life and the maintenance of the causal organism of the disease (East Coast Fever).

Yeoman (1966) described a Lake shore climate (L. Victoria) suited for the tick and the hinterland climate which is unsuitable for R. appendiculatus, with a gradient between the two. As one proceeds inland from the lake the rainfall and humidity decreases and temperature range increases. These in the absence of any other factors, would determine the steepness of the fadeout gradient of

R. appendiculatus and set an absolute limit on its zone of infestation, but with the knowledge of the conditions under which this tick survives in other parts in its area of distribution, these would hardly be accepted as the factors responsible for the rather sudden transition from enzooticity to epizooticity. He then postulated that if it is not the geoclimatic then could it be variation in climate from year to year. While the potential distribution of R. appendiculatus would be dictated by climatic factors, it is primarily determined by the physiognomic nature of the grass and the grazing cover.

4.4 SEASONAL ACTIVITY

Although adults of R. appendiculatus are active all the year round, their numbers markedly increase during the rainy seasons. In countries with only one rainy season per year activity remains high throughout the rainy season. This pattern of seasonal occurence has been shown in such countries in Central Africa like, Malawi, Zambia, and Rhodesia (Wilson, 1946, 1950; Jooste, 1966; MacLeod, 1970; MacLeod et al, 1977).

A similar picture has been observed in Tanzania (Yeoman, 1964, 1966, 1968; McCulloch et al, 1968). The main period of activity in these countries is between November to March each year with low numbers during the other part of the year which is generally hot and dry.

In South Africa the adults of R. appendiculatus are active mostly between summer and autumn (Theiler, 1959).

In Kenya and Uganda the adult population of this tick species shows two marked peaks of activity, with both coinciding with the two rainy seasons of March - May (long rains) and October-November (short rains) (Wilson, 1953). Earlier, Lewis (1939) stated that R. appendiculatus adults increased in numbers between April and August in Kenya, while Smith (1969) summarized the picture in the Bugisu district of Uganda by stating that adults rose during periods of increased rainfall and fell during the dry season. He also noted in one of his stations that following an unusual early start of the main rains tick numbers started to increase immediately. He, however, cautioned that factors other than rainfall must be considered when attempting to interpret the overall level of activity at any particular site. The distribution of rainfall throughout the year must also be taken into account. He was, however, not able to show any correlation between temperature, humidity and tick infestation variation in numbers. He concluded that generally the most important factors affecting tick numbers and the variation in populations and species are:

a) Rainfall distribution,

b) Vegetation cover (tied with stocking rate),

c) Total annual rainfall,

d) Types of husbandry, crops and density of human populations.

CHAPTER III

MATERIALS AND METHODS

1. STORAGE AND HANDLING OF TICKS

Only adult ticks of the species *Rhipicephalus appendiculatus* were used for this study.

All the ticks were received from the tick colony of the East African Veterinary Research Organization, Muguga. This tick colony has been maintained since 1952 using the methods described by Bailey (1960) and modified by Branagan (1970).

The ticks were fed on rabbits as larvae and nymphs and placed in an incubator to moult at a temperature of 28°C and 80% R.H. After moulting they were stored at approximately 23°C and 85% R.H. until they were needed for experiments. The ticks were kept in glass tubes which were closed with a perforated stopper with a layer of muslin gauze to allow ventilation. They were then sorted on a white enamel tray and handled with soft forceps.

2. TREATMENT OF TICKS BEFORE EXPOSURE

In studying the response of adult *Rhipicephalus appendiculatus* ticks to environmental changes it was necessary to subject the m to various treatments in order to compare the response of various groups of ticks to the changes in the same environment. The other naturally occuring variables like sex, and age were already accounted for. In this respect the two sexes were treated separately. One month and six months old ticks were also treated separately. Three levels of water content were compared, 100% (full hydration), 85% (loss of 15% of initial hydration weight) and 65% (loss of 35% of initial hydration weight). The treated ticks were released in two different sites in the field, a tree shaded and an open site .

The field observations were carried out during the three main seasons of the year here at Muguga. These seasons are the hot dry season, the rainy season, and the cold dry season. These seasons are distinctively shown in Table 1, which summarizes the weather data for Muguga over the last 18-26 years. The hot dry seasons fall between the months of December to March. The rainy seasons fall mainly between the months of April to May (long rains) and November (Short rains). The cool dry seasons fall within the months of June and August.

3. HYDRATION AND DEHYDRATION

In order to obtain ticks of various levels of hydration, and probably of different states of hunger by depletion of their food reserves, it was necessary to keep the ticks at various controlled relative humidities and subject them to dehydration by keeping at low relative humidities using saturated salt solutions described by Winston and Bates (1960) and shown in Table 2:

Potassium sulfate (K_2SO_4) gives a relative humidity of more than 96% R.H. at temperatures below 35^{0}C. Potassium chloride (KCl) gives a relative humidity between 83% R.H. and

TABLE 1

MUGUGA MEAN MONTHLY METEOROLOGICAL SUMMARIES

DATA TABULATED AS AT THE END OF 1976

REG. No. 91.36/121 LONG. 36° - 30'E LAT. 1° - 13'S ALT. 2,096 METRES

	January	February	March	April	May	June	July	August	September	October	November	December	Mean
Mean Rainfall (20 Years) mm.	61.4	42.1	68.0	227.8	171.5	42.8	22.3	21.6	28.1	53.3	121.8	78.1	938.8 *
Mean Minimum Temperature °C (24 Years)	11.1	11.6	12.3	12.6	11.7	9.8	8.9	9.0	9.5	11.1	11.7	11.3	10.9
Mean Maximum Temperature °C (24 Years)	22.6	23.4	23.3	21.6	19.9	19.0	18.2	18.8	21.0	22.0	20.7	21.4	21.0
Mean Air Temperature °C (24 Years)	16.9	17.5	17.8	17.1	15.8	14.4	13.5	13.9	15.2	16.6	16.3	16.3	15.9
Mean Wind Speed KMH at 2 metres (24 Years)	13.3	13.4	14.2	12.0	9.1	7.8	7.6	8.6	10.3	12.9	13.9	13.6	11.4
Mean Sunshine Hours (24 Years)	9.4	9.5	9.0	7.5	6.4	5.9	4.9	5.2	7.0	8.1	7.5	8.0	7.4
Mean Radiation gm/cal/cm (ly/day) (18 Years)	590	586	569	488	412	394	342	379	486	534	511	555	457 **
Mean Penman (Eo) Estimate of Evaporation mm. (20 Years)	184	178	193	150	120	105	97	111	144	174	154	167	1776 ***
Mean Dew-Point °C (24 Years)	10.7	10.6	11.4	12.9	12.9	11.4	10.6	10.4	10.3	10.7	12.0	11.6	11.3
Mean Saturation Deficit (Mean of 0900 & 1500 Hours) m.b. (24 Years)	6.2	7.1	6.7	4.6	3.1	2.9	2.7	3.3	4.6	6.0	4.4	4.9	4.7
Mean Class "A" PAN open water evaporation mm. (19 Years)	202	198	210	150 1..	110	97	89	104	140	178	149	172	1799 ***

* Mean Annual Total.

** 1 mm of water = 59.0gm/cal/cm^2

*** Total Average Mean.

(COURTESY OF THE DIRECTOR - EAAFRO - MUGUGA)

TABLE 2 Relative humidity values over saturated salt solutions at various temperatures for the three chemicals used during the study (Winston and Bates, 1960)

Compound	TEMPERATURE					
	10 °C	15 °C	20 °C	25 °C	30 °C	35 °C
Potassium Chloride (KCl)	88.0	86.5	85.0	85.0	84.5	83.0
Potassium Sulfate (K_2SO_4)	98.5	99.0	98.0	97.5	96.5	96.0
Zinc Chloride ($ZnCl_2$)	10.0	10.0	10.0	10.0	10.0	10.0

88% R.H. at temperatures below 35°C. Zinc chloride ($ZnCl_2$) gives a constant 10% R.H. at all temperatures even above 35°C.

The critical equilibrium humidity (CEH) for *R. appendiculatus* adults is about 85% R.H. at 23° C. (Mongi, personal communication).

Before the ticks were put under any treatment they were removed from the storage room, sexed and put into clean vials separately. The required number of vials containing ticks were then placed in a desiccator over KCl solution for a week at a constant temperature of 23°C. Each vial contained a total of twenty five adult ticks, being the standard number in each sample. After one week all the ticks which will be dehydrated later, were transferred to another desiccator containing potassium sulfate(K_2SO_4)at a humidity of over 96% R.H. for a total of three days. All the ticks were then removed from the glass vials and their hydrated weights taken. A Sartorius Analytical Balance (model 2472) with a measure of accuracy of 0.00001 gramme was used. An aluminium foil piece 4 x 4 cm in size, was first weighed, then the 25 ticks in the sample were wrapped in it and the ticks' weight was calculated. After their weights had been taken, they were transferred to a nylon bag and the bag was then sealed with a hot iron and the combined weight of the ticks with the nylon bag was again taken. The nylon bags (Fig 3) were produced from the nylon mesh ("Nybolt", grade 70 GG with mesh size 236μ) and prepared by taking a piece of a numbered nylon cloth 6 x 3 cm, folding and sealing along each side with a hot soldering iron. After sealing, the bags containing ticks were put into a

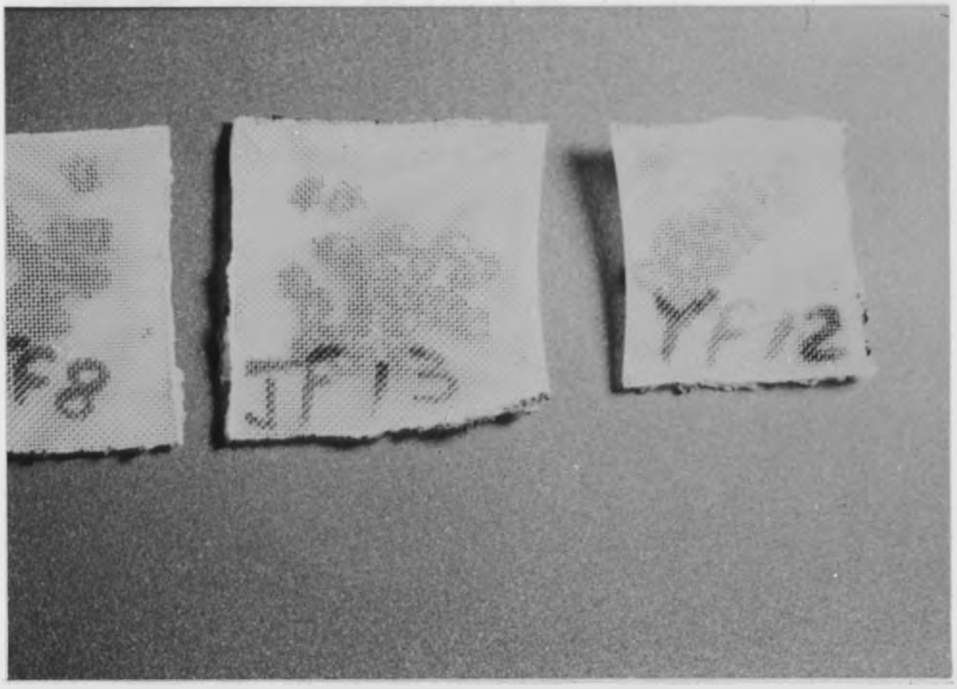

Fig. 3. The nylon mesh bags containing ticks used for weighing the ticks.

desiccator over $ZnCl_2$ to give 10% R.H. and held at a constant 27^0C in an incubator (Hotpack, model 352700).

The bags containing ticks were then weighed daily until the required percentage weight losses of the ticks had accumulated.

Preliminary tests showed that it took approximately three days for a loss of 15% in weight and nine days for a loss of 35%. The treatments were staggered so that ticks of approximately 100%. 85%, and 65% hydration would all be ready for exposure in the field on the same day. The exact degree of dehydration or hydration was determined by the final weighing of each bag on the last day.

4. MARKING AND RELEASING TICKS IN THE FIELD

After the final weighing the ticks were transferred to a plastic bag and dusted with "Day Glo" fluorescent powder by shaking gently. Two colours were available. The marked ticks were then immediately released in the field in 0.25 m^2 plots, each surrounded by a wooden frame with 15 cm above ground and 5 cm in the soil (Fig. 4). A thick layer of "tanglefoot" was applied all around the top of the frame. This had been shown to stop the ticks from escaping by acting as a repellant. The grass inside the plots was trimmed so that no bridges were left for the ticks over the tanglefoot.

After release of the ticks on the soil, they were allowed to settle for half an hour before any observations were made. Into another plot, representative groups of ticks, still

Fig. 4. The field plots, surrounded by the wooden frames, where marked ticks were released.

in their original bags, were placed inside the vegetation. These were weighed twice daily in their bags, at 0830 hours and 1830 hours. Each sample consisted of two bags of 25 ticks each. This was intended to give information on changes in water content of the treated ticks held on the soil surface.

5. MEASUREMENT OF TEMPERATURE AND HUMIDITY

Temperature at two levels of the vegetation (a) 5 mm below the soil surface and (b) at the level of the grass tips, were measured with a Yellow Springs Instrument Co. Telethermometer(mod 44)using the probes (serial No. 401). The probes were left in position in a neighbouring plot with no ticks. Temperatures were read at two hour intervals, i.e. during each observation. The upper probe was shielded from direct sun light and rain.

Humidity was measured using cobalt thiocyanate impregnated paper (Solomon, 1957). Pieces of the paper 3 x 3 cm were placed beside the thermister probes. One piece was buried at the 5 mm level and the other was suspended at the level of the grass tips. They were exposed in the atmosphere for two hours after which they were transferred with a pair of forceps into a vial of liquid paraffin to prevent any further colour change. They were removed into the laboratory for assessment against the permanent glass colour standards provided in the Lovibond 1000 comparator discs calibrated to relative humidity in steps of 5% from 60%-100% and 10% from 0% - 60%.

6. FIELD OBSERVATIONS ON TICK ACTIVITY

During each season the following comparisons were made at an open and tree-shaded site:

a) Old males v. Young males

b) Old females v. Young females

c) Young males v. Young females ,

using ticks of three levels of hydration (100%, 85%, and 65%).

Each series of observations was made to compare ticks of two types, distinctively shown as described above. The first observations were made 30 minutes after the ticks were released in order to establish their immediate distribution. Temperature and humidity readings at the two levels of the vegetation were taken during each observation. Humidity papers were replaced as the old ones were collected for assessment in the laboratory.

At the end of each experiment the grass was searched in each plot thoroughly and as many as possible of the released ticks were recovered. Their positions in the vegetation were recorded to give data on their vertical distribution.

7. LABORATORY EXPERIMENTS ON TICK ACTIVITY

A known number of ticks was exposed to various treatments in the laboratory.

During the continuous darkness regime the ticks were kept in darkness in an incubator, housed in a darkened room. They were observed with the help of an ultra-violet lamp since the ticks were marked with a fluorescent powder. Six months old ticks were used throughout these experiments.

A glass aquarium tank measuring 30 x 20 x 20 cm was used, with a layer of dry sand on the floor 5 cm in depth (Fig. 5). Twenty five oven-dried sections of stem of the grass Hyparrhenia rufa, each 20 cm in length, were stuck into the sand in rows of 5 x 5. The stems were cut so as to leave a short piece of the base of a leaf blade projecting out near the tip. Small pieces of filter paper were spread on the sand surface between the grass stems. Glass tubes, 8 x 2.5 cm were placed at the corners of the aquarium and filled with the appropriate saturated salt solution to give the required relative humidity (Winston and Bates, 1960). The tubes were covered with a perforated plastic stopper and a piece of muslin gauze. Ticks were prevented from climbing the walls of the aquarium tank and the glass tubes, by applying a thick narrow line of "tanglefoot" all around the aquarium and the glass tubes. The tank was covered with sheet of glass and sealed with adhesive tape.

8. CONTINUOUS OR ALTERNATING DARKNESS AND LIGHT

Prior to exposure of ticks to either continuous darkness or light, they were kept in a desiccator at 85% R.H. for a period of three days and left on the bench, to give them the natural day/night rhythm of approximately 12 hours light and 12 hours of darkness. They were then transferred into the aquarium on the bench and left undisturbed for another hour, still unreleased. At the start of the natural darkness, at around 1830 hours, the stopper of the tube was removed very slowly to minimize the disturbance and the aquarium was transferred with the ticks to the incubator. The light was switched off immediately for the ticks to start the night phase of the regime.

Fig. 5. An aquarium inside the climate chamber used in the laboratory experiments.

The type of incubator used for these experiments was with a glass window for making the required observations with the minimum disturbance of the samples inside. These were fitted with fluorescent light bulbs giving an illumination of about 7,000 lux. The incandescent lamps were not used in order to prevent any further temperature increase inside the chamber. The first observation was made ten minutes after release and thereafter at intervals of two hours. Similarly, extra observations were made every time a change of light or darkness occurred.

9. TEMPERATURE AND HUMIDITY CHANGES IN THE CHAMBER

For these experiments the aquaria were kept open and the required temperature and humdity were set on the machine and checked with dry and wet bulb thermometer.

The required temperature and humidity were set twelve hours earlier and allowed to stabilize before the ticks were introduced and released.

Temperature changes were effected without opening the chamber, and the tick response was observed through the glass window. All the ticks were released in the aquarium on the sand surface and some eventually came up and started climbing the stems. The number of ticks found on top of any grass stem was recorded during each observation. The first observation was made ten minutes after release and after every change of temperature and humidity, with the rest of the observations at two hour interval.

For the reduction of humidity, the control was first brought to zero, so as to let in dry air for some time until the humidity reading reached the required level before the knob was brought to the point of the required humidity.

Each experiment lasted three days.

CHAPTER IV

RESULTS

1.1 RESPONSES OF TICKS TO FACTORS IN THE ENVIRONMENT AND THE EFFECTS OF THE HYDRATION STATUS

When treated ticks were released into the field plots, they showed immediate differences in their response to the environment according to their hydration states.

During the hot dry season (Fig. 6., Table 3) the fully hydrated ticks started to climb up the vegetation immediately, but the 65% hydrated groups showed no activity until the following day when the males started to appear on the vegetation in appreciable numbers. The 85% hydrated groups behaved in a similar manner with the fully hydrated groups, with considerable activity on the first day. On the second day, however, the two most active groups showed a reduction in activity, while the 65% hydrated male groups showed an increase. On the third day activity increased in all groups except the 65% hydrated females, and by the fourth day there was no difference between them.

In the wet season (Fig. 7, Table 4) there was again no immediate activity by the 65% hydrated groups on the first day, while the 100% hydrated groups were again active straight after release, and the 85% hydrated group showed an intermediate response with little or no activity on the first day by either males or females. By the second day, however, there were approximately

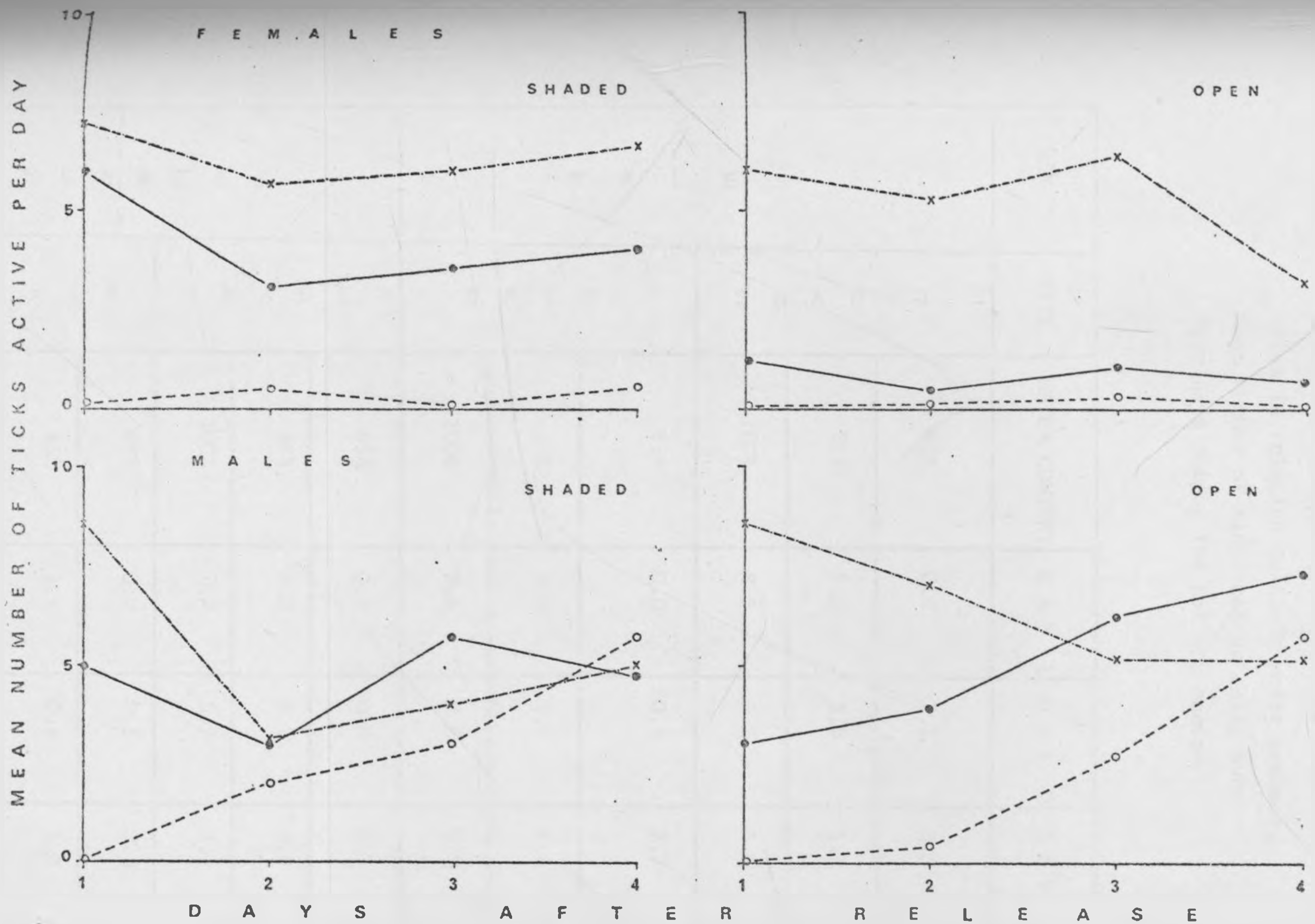

Fig. 6. Mean number of male and female R.appendiculatus active per day during the hot dry season for four days of exposure, in relation to their hydration state. Open and shaded sites compared for each sex.

Key: ----o---- 65% hydration; ——•—— 85% hydration; -·-·-x-·-·- 100% hydration.

TABLE 3 Daily activity of R. appendiculatus males and females at the two different sites in relation to their water content. Mean number of ticks active daily over four days during the hot dry season

SEX	SITE	WATER CONTENT	D A Y 1	D A Y 2	D A Y 3	D A Y
MALES	SHADED	65%	0.0	2.1	3.0	5.7
		85%	5.0	3.0	5.7	4.7
		100%	8.6	3.3	4.1	5.0
	OPEN	65%	0.0	0.4	2.7	5.7
		85%	3.0	3.9	6.3	7.3
		100%	8.6	7.0	5.3	5.3
FEMALES	SHADED	65%	0.2	0.6	0.1	0.7
		85%	6.0	3.1	3.6	4.0
		100%	7.2	5.7	6.1	6.7
	OPEN	65%	0.0	0.1	0.3	0.0
		85%	1.4	0.4	1.1	0.7
		100%	6.0	5.4	6.4	3.3

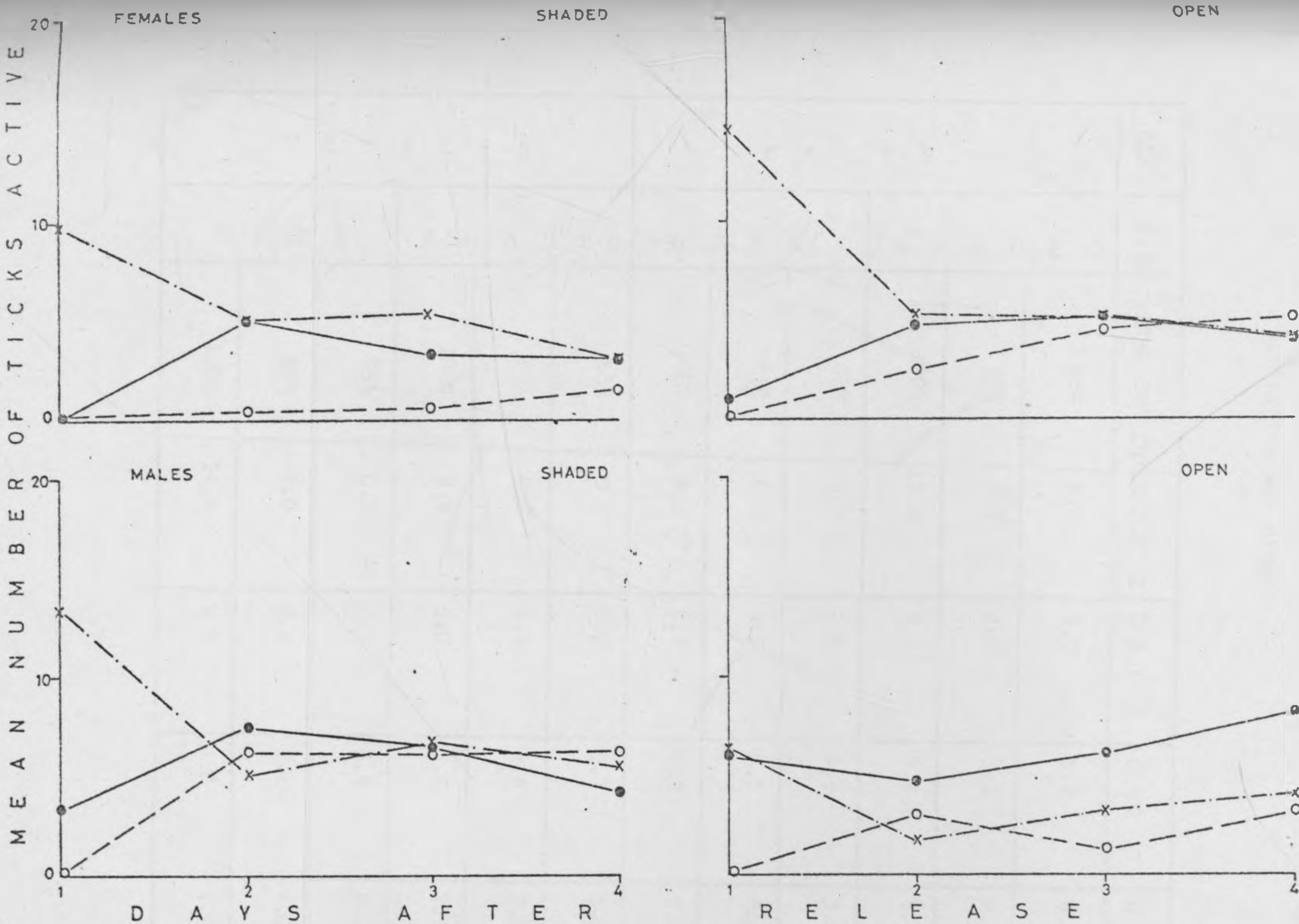

Fig.7. Mean number of male and female R.appendiculatus active per day during the rainy season for four days of exposure, in relation to their hydration state. Open and shaded sites compared for each sex.

Key: ----o---- 65% hydration; ——●—— 85% hydration; —·—x—·— 100% hydration.

TABLE 4 Daily activity of *R. appendiculatus* males and females at the two different sites in relation to their water content. Mean number of ticks active daily over four days during the wet season

SEX	SITE	WATER CONTENT	DAY 1	DAY 2	DAY 3	DAY 4
MALES	SHADED	65%	0.0.	5.9	5.8	6.0
		85%	3.4	7.7	6.3	4.3
		100%	13.4	4.9	6.4	5.3
	OPEN	65%	0.0	2.9	1.4	3.0
		85%	6.0	4.7	6.1	8.3
		100%	6.2	1.7	3.3	4.0
FEMALES	SHADED	65%	0.0	0.6	0.7	1.5
		85%	0.0	5.1	3.4	3.0
		100%	9.8	5.0	5.3	3.0
	OPEN	65%	0.0	2.6	4.4	5.0
		85%	1.0	4.7	5.1	4.0
		100%	14.4	5.3	4.9	4.0

equal numbers of active ticks in all the groups as the number of active ticks in the fully hydrated group had decreased and those active in the dehydrated groups, on the other hand, had increased.

During the cool dry season there was a similar picture (Fig. 8, Table 5). The 65% hydrated groups showed no immediate activity on release. The females in this group, in fact, showed no activity throughout the period of observation, while the males did not appear in any appreciable numbers until the third and fourth days. The 85% hydrated groups also showed very little change in the number of active ticks, except on one occassion when they increased on the third day. The 100% hydrated groups were again immediately active on the first day and decreased steadily in activity to almost the same level with the other groups by the fourth day.

1.2 DAILY ACTIVITY PATTERNS IN RELATION TO TEMPERATURE AND RELATIVE HUMIDITY

In general the ticks were active during the hours of daylight, with very few active at night. There was a regular daily increase of active numbers in the morning reaching a peak at a certain time of day followed by a steady decrease again towards evening.

For each season, all the data on the number of active ticks were pooled and expressed as a frequency distribution against time of day with the observations of temperature and relative humidity also displayed in a similar form against each time of day, (Figs. 9 , 10, 11). For each parameter the median

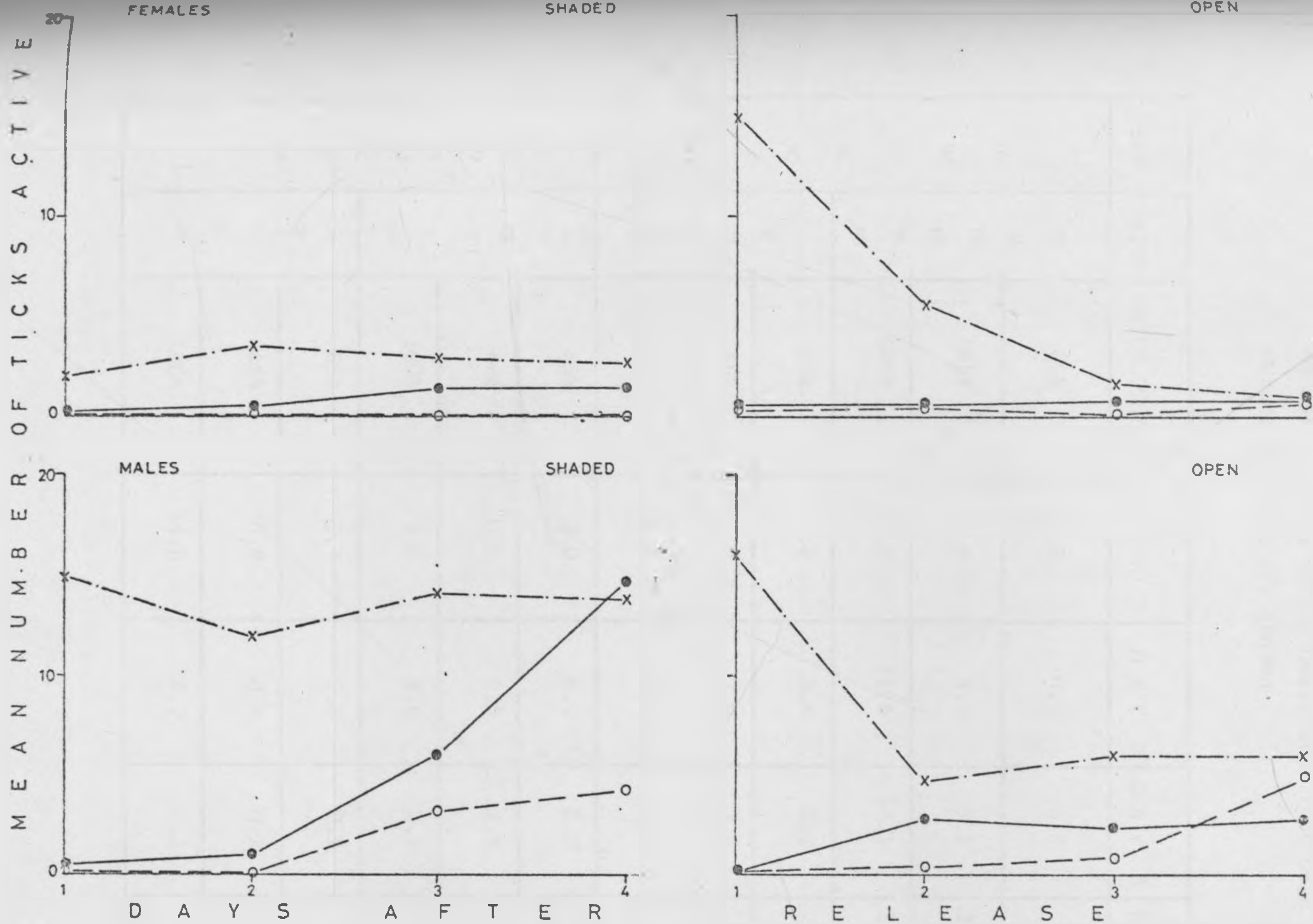

Fig. 8. Mean number of male and female R.appendiculatus active per day during the cool dry season for four days of exposure, in relation to their hydration states. Open and shaded sites compared for each sex.

Key: ----o---- 65% hydration; ——•—— 85% hydration; —·—x—·— 100% hydration.

TABLE 5 Daily activity of R. appendiculatus males and females at the two different sites in relation to their water content. Mean number of ticks active daily over four days during the cool dry season

SEX	SITE	WATER CONTENT	DAY 1	DAY 2	DAY 3	DAY 4
MALES	SHADED	65%	0.0	0.0	3.4	4.3
		85%	0.4	1.1	6.1	14.7
		100%	14.8	11.8	14.1	13.7
	OPEN	65%	0.2	0.4	0.9	5.0
		85%	0.2	2.9	2.4	2.7
		100%	16.2	4.7	6.0	6.0
FEMALES	SHADED	65%	0.0	0.0	0.0	0.0
		85%	0.2	0.4	1.6	1.7
		100%	4.0	5.6	2.9	2.7
	OPEN	65%	0.4	0.6	0.3	0.7
		85%	0.6	0.6	0.7	0.7
		100%	14.8	5.7	2.1	1.7

value at each time of day was determined and plotted.

During the hot dry season (Fig. 9) the open site showed a rising activity from 0830 hours to 1230 hours followed by a marked drop at 1430 hours. Although there was an increase again at 1630 hours this was followed by a final drop at 1830 hours. The midday drop in activity coincided with the maximum temperature (above 30^{o}C) and the minimum relative humidity (as low as 30% R.H.).

The shaded site was different in that it showed a steady increase in activity reaching a peak at 1030 hours and remained at a high level through the hottest part of the day until 1430 hours, then decreased steadily to a low level again at 1830 hours. The temperature at this site never exceeded 25^{o}C.

During the wet season (Fig.10), there were very steady changes of activity on both sites. The open site showed most activity between 1230 hours and 1430 hours. The temperature increased steadily up to a maximum of 30^{o}C. The shaded site showed a prolonged peak from 1230 hours to 1630 hours. Temperatures here were lower, reaching a maximum of 25^{o}C at 1430 hours. On most mornings relative humidity remained high. Most tick activity coincided with a drop from 95% R.H. to 70% R.H. between 1230 hours and 1630 hours in the shaded site.

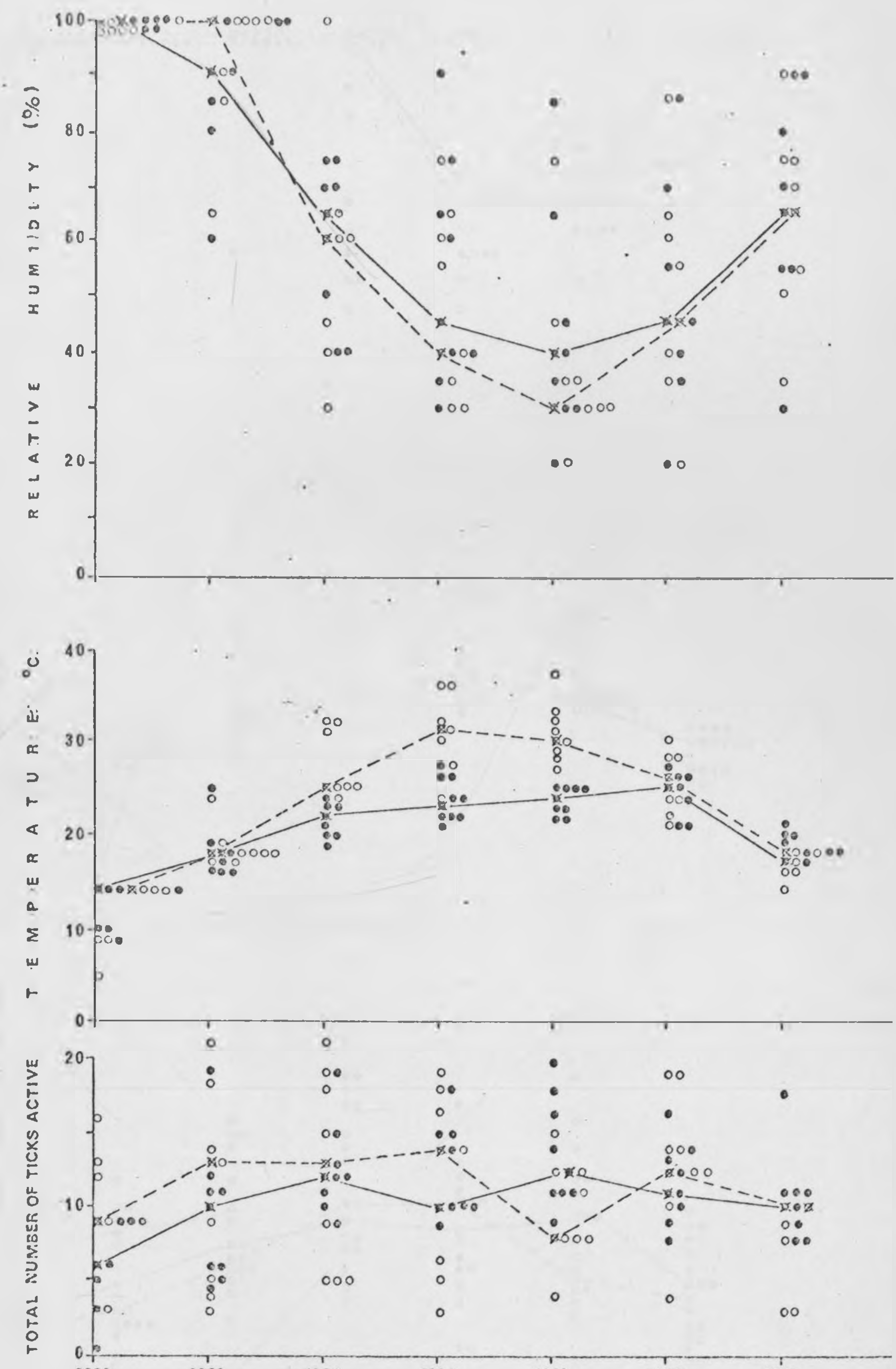

Fig.9. Daily distribution of activity of R.appendiculatus adults in relation to daily distribution of air temperature and relative humidity in the field during the hot dry season.
Key: X=Median number of observations at each time of day.
----X---- Open site; ——X—— Shaded site.

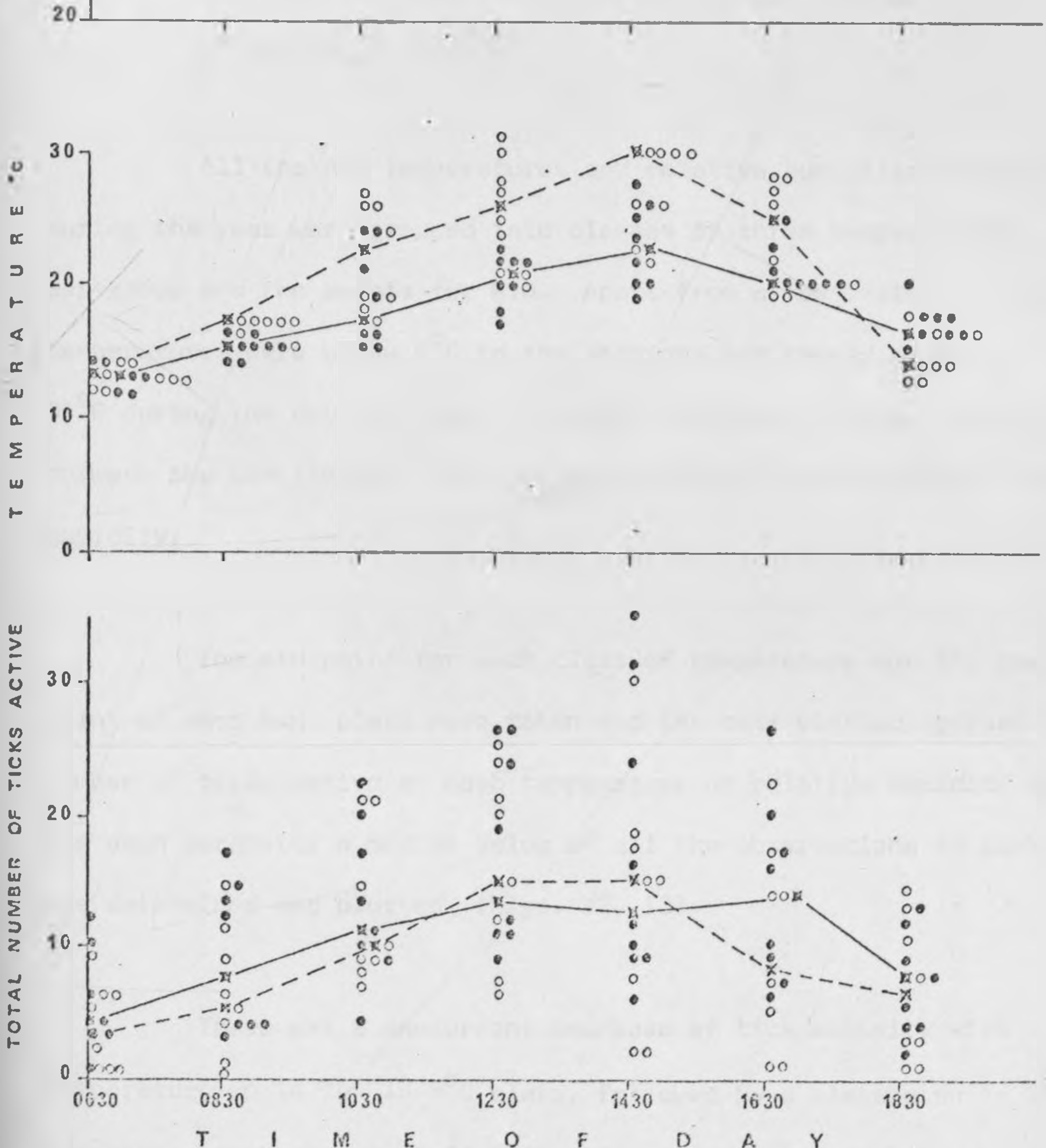

Fig.10. Daily distribution of activity of R.appendiculatus adults in relation to daily distribution of air temperature and relative humidity in the field during the rainy season.
Key: X = Median number of observations at each time of day. ----X---- Open site; ——X—— Shaded site.

In the cool dry season (Fig. 11) both sites showed intermediate patterns of activity. The open site had an activity peak between 1030 hours and 1230 hours and a steady drop there after. Temperatures were lower and rarely exceeded 25°C. The R.H. pattern was similar to that of the hot dry season. On the shaded site there was high activity from 1030 hours to 1630 hours when temperatures were fairly uniform and R.H. ranged from 50% - 80%.

1.3 DISTRIBUTION OF ACTIVITY IN RELATION TO TEMPERATURE AND RELATIVE HUMIDITY

All the air temperatures and relative humidities recorded during the year were grouped into classes of three temperatures per group and ten points for R.H. Apart from a few instances when temperatures were below 9°C in the mornings and rarely exceeded 35°C during the day, the most frequent temperatures recorded were between the two limits. 20% R.H. was also the lowest recorded relative humidity.

The mid-point for each class of temperature and the lower point of each R.H. class were taken and the data plotted against the number of ticks active at each temperature or relative humidity class. For each parameter a median value of all the observations in each class was determined and plotted (Figs. 12, 13).

There was a concurrent increase of tick activity with temperature up to the 19.5°C class, followed by a plateau up to 28.5°C and then a decrease at 31.5°C (Fig. 12).

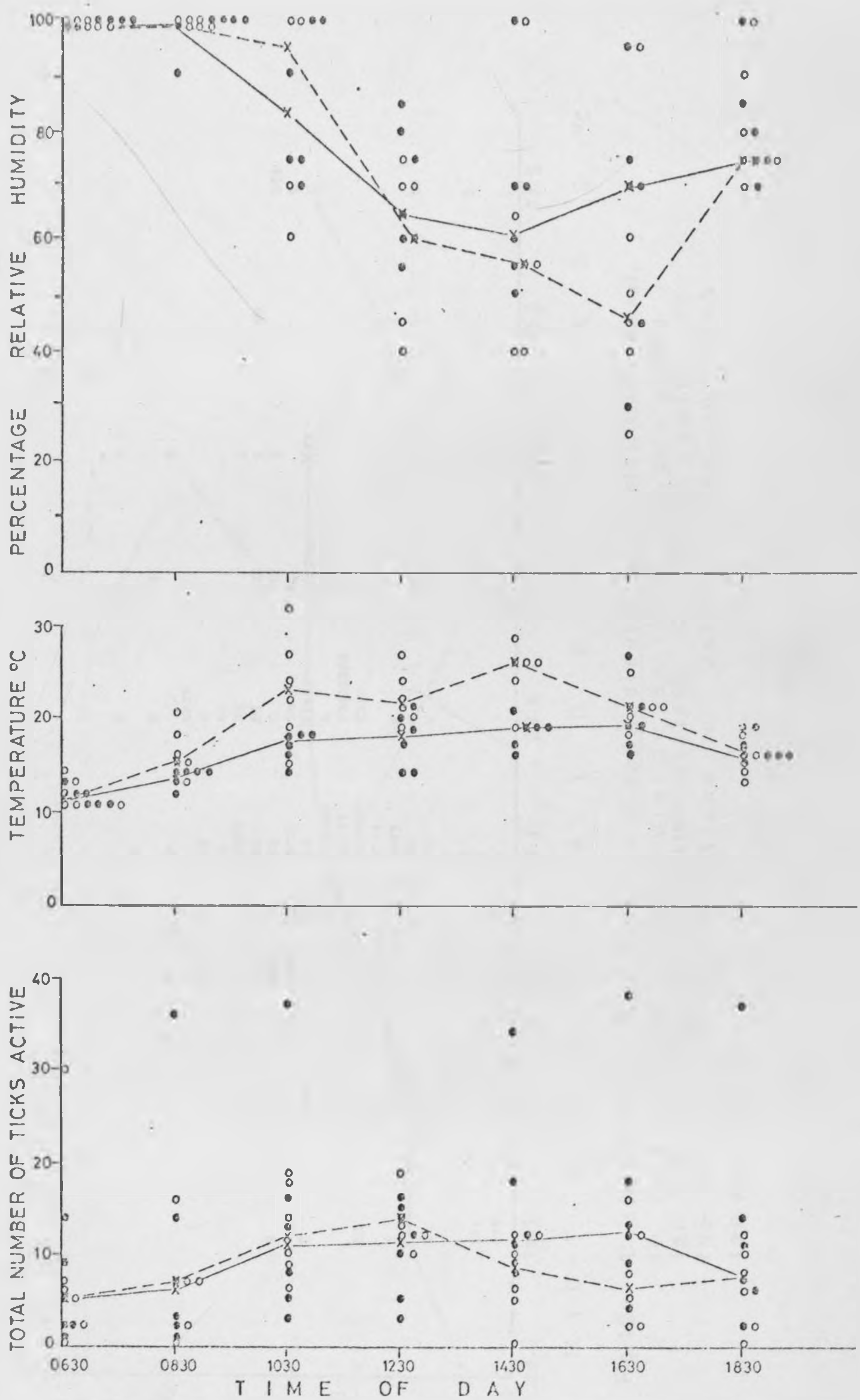

Fig.11. Daily distribution of activity of _R.appendiculatus_ adults in relation to daily distribution of field air temperature and relative humidity during the cool dry season.
Key: X = Median number of observations at each time of day.
------o------ Open site; ——•—— Shaded site.

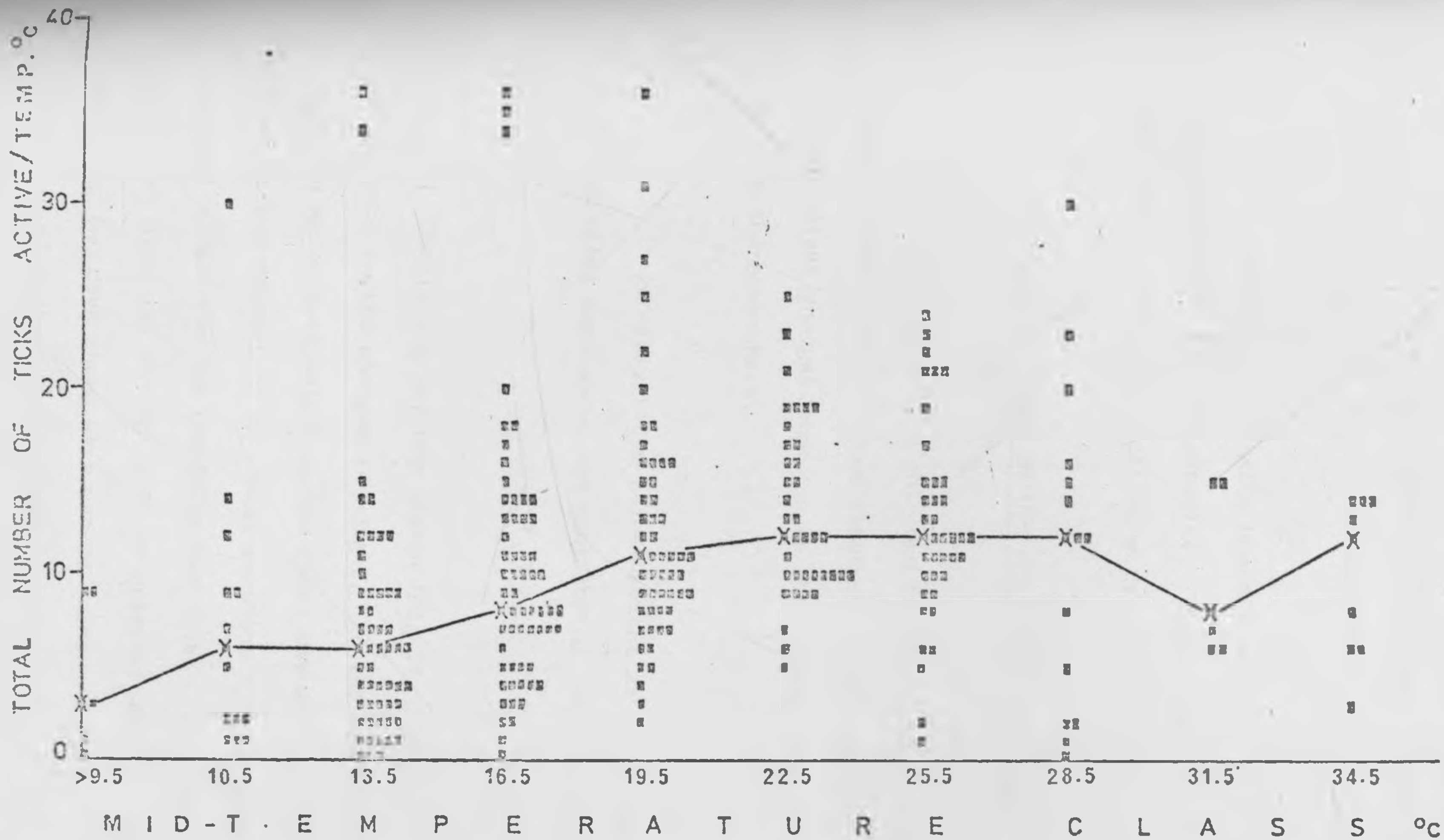

Fig. 12. Distribution of activity of R. appendiculatus adults, (150x16 groups), in relation to temperature in the field. (All data pooled for 2ages x 2sexes x 3hydration states). X = Median point for the number of observations of active ticks in each temperature class.

There were more positive activity observations, although in small numbers of ticks, at temperature between 13.5°C and 25.5°C.

Changes in relative humidities (Fig. 13) did not produce graded responses in tick activity. There seemed to be a general preference for high humidities with little activity below 90% R.H.

1.4 WEIGHT CHANGES IN TREATED TICKS AFTER RELEASE IN THE FIELD

Although any weight loss by the ticks would obviously include small losses of food reserves, it was assumed here that much of the weight changes were due to the losses and gains of water to or from the atmosphere.

In general, ticks gained weight at night and, unless the humidities were above the equilibrium, they lost weight during the day.

During the hot dry season (Fig.14, Table 6) all the groups showed very marked changes in weight. In the shaded site, fully hydrated males lost weight on the first day with some up-take at night and maintained an almost constant loss of about 1% of the original weight for the remaining two days. The other groups gained weight on the first day up to 5% of original weight. During the remaining two days there were marked gains and losses, leaving a net gain of 3-5% of the original weight.

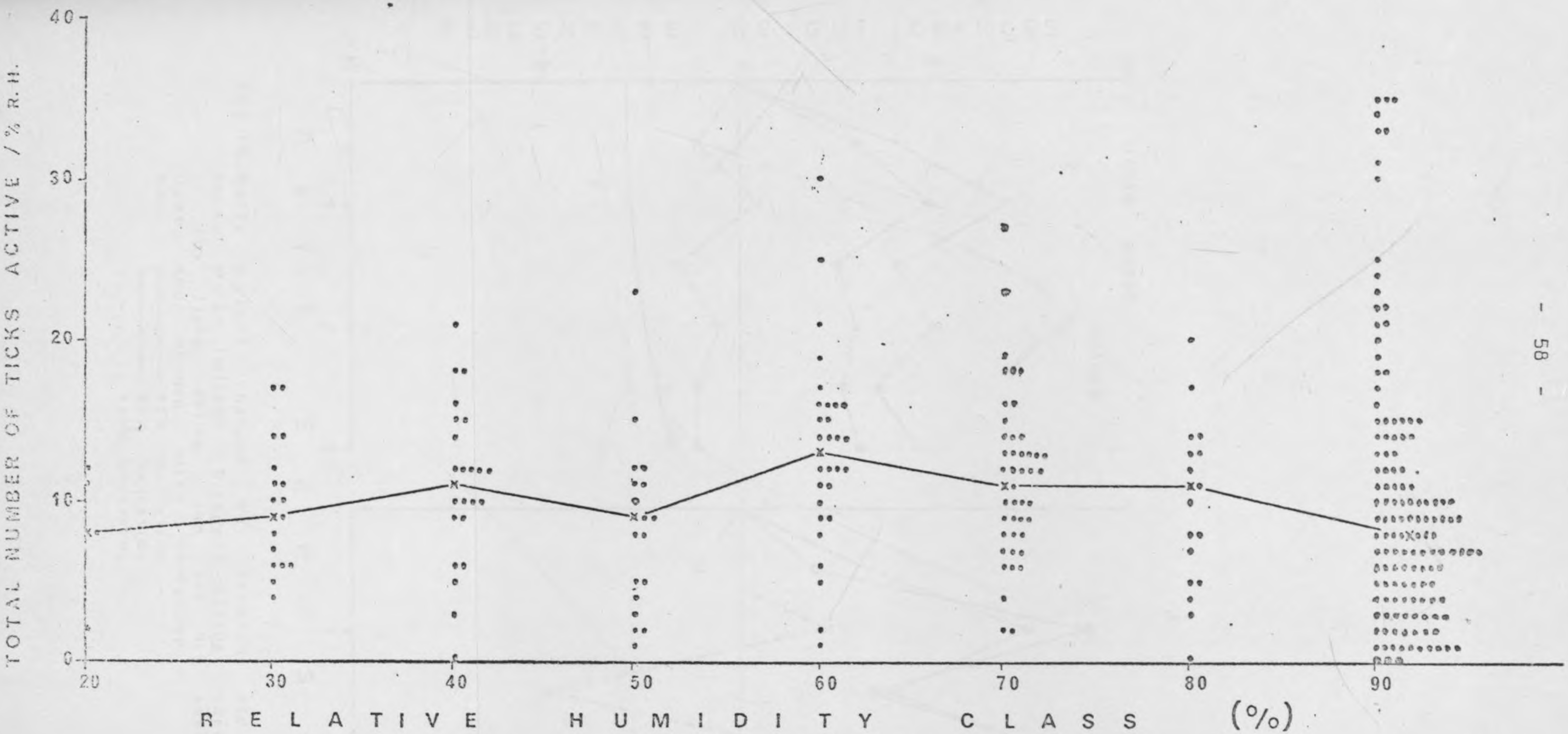

Fig.13. Distribution of activity of R.appendiculatus adults, (150x16 groups), in relation to relative humidity in the field. (Data pooled for 2 ages x 2 sexes x 3 hydration states). X = Median point for the number of active ticks in each relative humidity class.

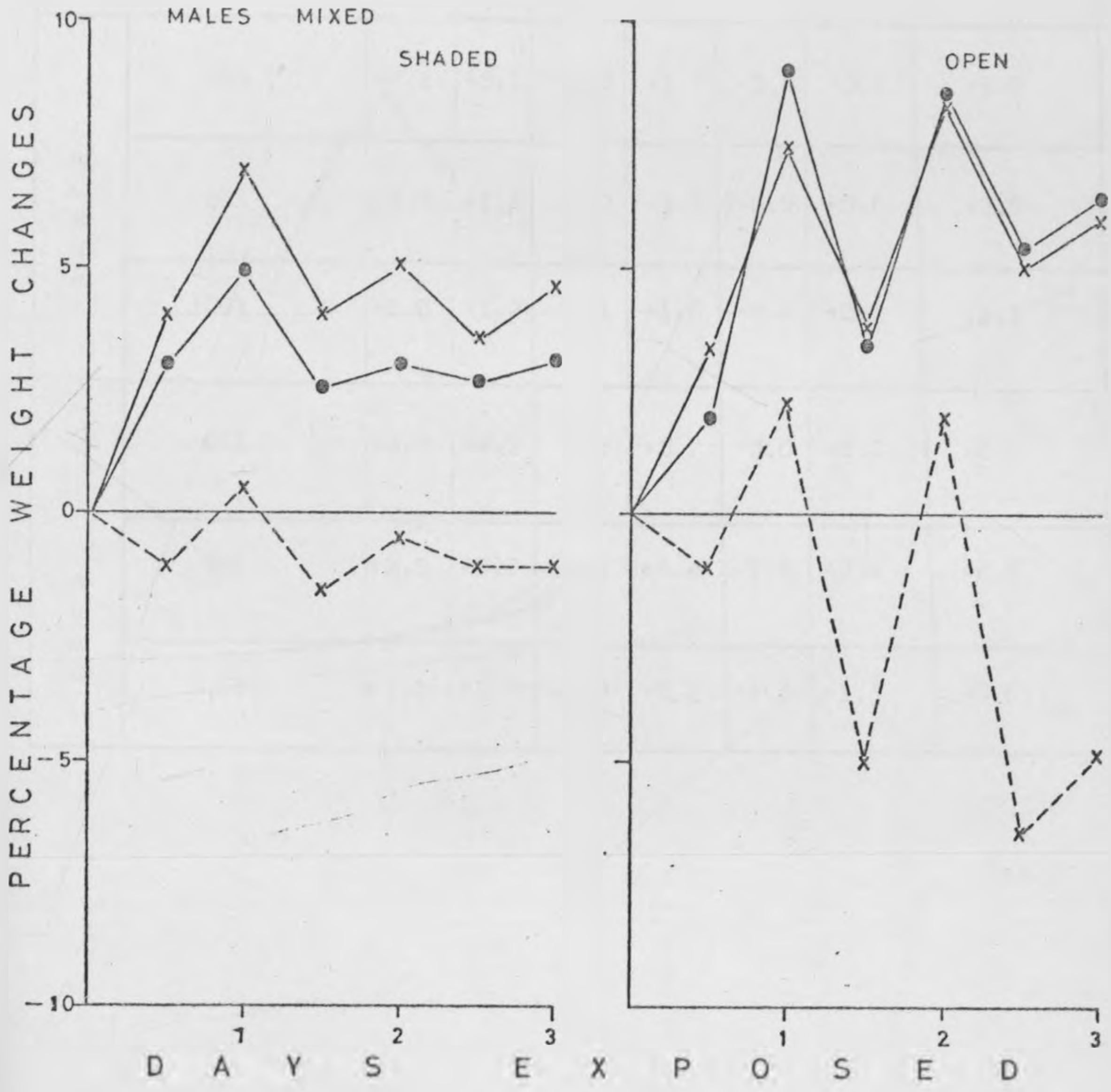

Fig.14. Daily weight changes by treated old and young males (mixed) R.appendiculatus exposed in the field during the hot dry season. Open and shaded sites compared.

Key: ——x—— 65% hydration
——●—— 85% hydration
----x---- 100% hydration

TABLE 6. Weight changes of treated R. appendiculatus adult males (both ages combined) when exposed to the field during the Hot Dry Season. Weights expressed as mean percentage gains or losses of original weight

SITE	WATER CONTENT	DAY 1		DAY 2		DAY 3		TOTAL
		1830 hrs	0830 hrs	1830 hrs	0830 hrs	1830 hrs	0830 hrs	TOTAL
SHADED	65%	+4.1	+3.1	-3.0	+1.1	-1.0	+0.7	+5.0
	85%	+3.5	+1.4	-2.2	+1.1	-0.9	+0.6	+3.5
	100%	+1.0	+1.7	-2.1	+1.0	-0.7	+0.1	+1.1
OPEN	65%	+3.2	+4.2	-3.3	+3.7	-3.0	+2.2	+7.0
	85%	+2.3	+6.7	-5.4	+4.4	-2.6	+2.1	+7.5
	100%	-1.1	+3.6	-7.7	+3.2	-4.4	+1.5	-5.0

The open site showed some very big gains and losses by all the groups. The fully hydrated at each end of day were operating between 2% gains and more than 5% losses. The hydrated groups gained weights of almost 10% on the first day. For the remaining two days the changes were much less violent and they were having approximately 4% gains, after the day's losses, by the end of day, and about 8% gains by the following morning after the night's up-take.

A comparison between young males and females (Fig. 15, Table 7) showed that in the shaded site, the fully hydrated males tried to maintain their weights with losses and gains of less than 1% throughout. The dehydrated groups had night up-take and day losses, just to finish on the third day with 5% above their initial weights. In the open site, the fully hydrated and the 65% hydrated groups, after the day's losses, dropped in weight to the initial level, but with up-takes at night, gained up to about 3%. The 85% hydrated group also alternated between 3%, after the day's losses, and 6% after the night gains, to reach a final 6% gain on the third day.

All the females in the 65% hydration group unfortunately died before exposure. The other groups, however, gained between 2 - 4%, for the fully hydrated and the 85% hydrated respectively, by the third day. In the open site the two groups made small gains. of between 3% and about 7%.

A comparison between old and young females during this season (Fig.16, Table 8) indicated that there was a general downward trend, especially by the old females, with all the groups on both

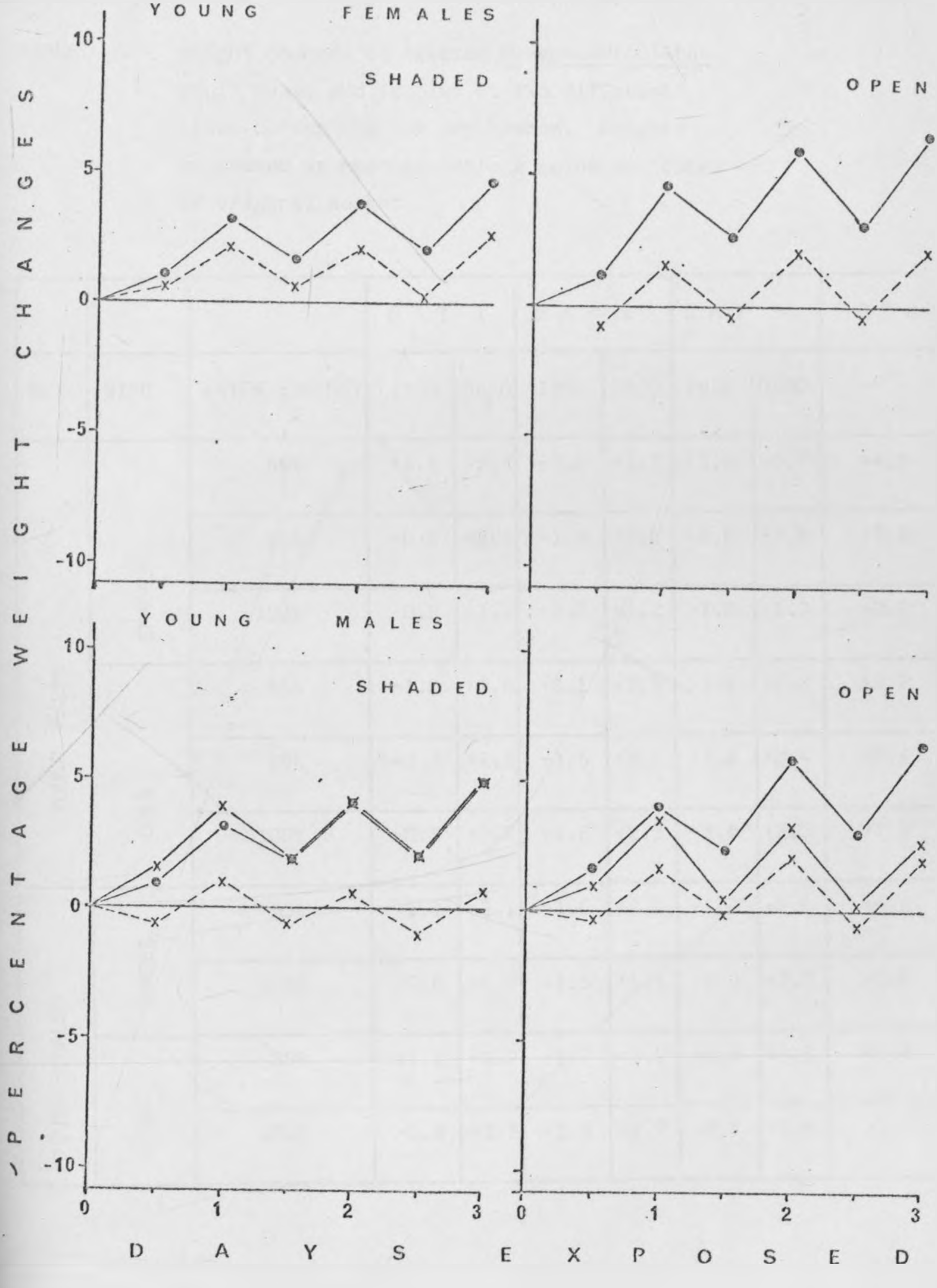

Fig.15. Daily weight changes of treated young male and female R.appendiculatus exposed in the field during the hot dry season. Open and shaded sites compared.

Key: ———x——— 65% hydration
———o——— 85% hydration
- - - -x- - - - 100% hydration

TABLE 7. Weight changes of treated R. appendiculatus adult males and females at two different sites during the hot dry season. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
SEX	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
YOUNG MALES	SHADED	65%	+1.5	+2.4	-2.0	+2.1	-1.8	+2.7	+4.9
		85%	+0.9	+2.3	-1.4	+2.2	-2.0	+2.9	+4.9
		100%	-0.6	+1.7	-1.7	+1.2	-1.6	+1.7	+0.7
	OPEN	65%	+1.0	+2.6	-3.1	+2.9	-3.2	+2.5	+2.7
		85%	+1.8	+2.1	-1.5	+3.5	-2.9	+3.4	+6.4
		100%	-0.3	+2.0	-1.8	+2.3	-2.8	+2.5	+1.9
YOUNG FEMALES	SHADED	85%	+1.1	+2.1	-1.6	+2.1	-1.7	+2.6	+4.6
		100%	+0.6	+1.5	-1.5	+1.5	-1.8	+2.3	+2.6
	OPEN	85%	+1.2	+3.2	-1.7	+3.2	-2.8	+3.5	+6.6
		100%	-0.8	+2.3	-2.1	+2.7	-2.7	+2.9	+2.3

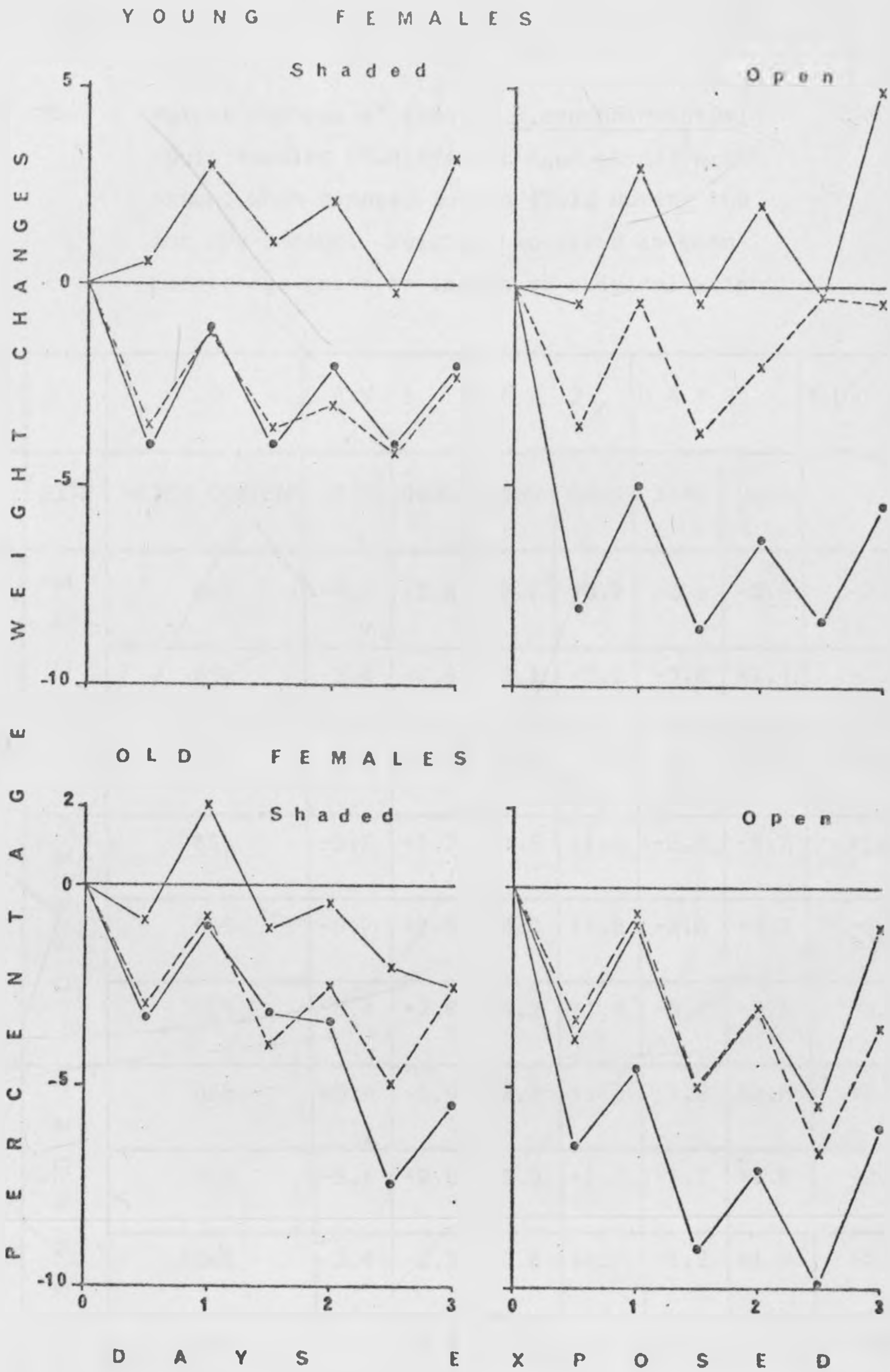

Fig. 16. Daily weight changes of treated old and young female *R. appendiculatus* exposed in the field during the hot dry season. Open and shaded sites compared.
Key: ——x—— 65% hydration
——•—— 85% hydration
----x---- 100% hydration

TABLE 8. Weight changes of treated R.appendiculatus adult females of different ages at different sites, when exposed to the field during the hot dry season. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
AGE	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
OLD FEMALES	SHADED	65%	-0.7	+2.6	-3.1	+0.7	-1.3	-0.5	-2.3
		85%	-3.4	+2.4	-2.1	-0.2	-3.8	+1.4	-5.7
		100%	-3.3	+2.2	-2.8	+1.2	-2.3	+2.6	-2.4
	OPEN	65%	-3.7	+3.2	-4.5	+1.9	-2.5	+6.7	+1.1
		85%	-6.7	+2.3	-4.6	+1.8	-2.6	+3.7	-6.1
		100%	-3.4	+2.6	-4.2	+1.8	-3.4	+3.5	-3.1
YOUNG FEMALES	SHADED	65%	+0.4	+2.6	-2.2	+1.0	-1.9	+3.3	+3.2
		85%	-3.8	+2.8	-2.9	+1.8	-1.7	+1.6	-2.2
		100%	-3.4	+2.3	-2.6	+0.7	-1.2	+1.8	-2.4
	OPEN	65%	-0.5	+3.6	-3.5	+2.4	-2.2	+5.0	+4.8
		85%	-8.3	+3.5	-4.1	+2.6	-2.4	+3.2	-5.5
		100%	-3.4	+3.0	-3.2	+1.9	-1.9	+3.2	-0.4

sites losing as much as 7-10% by the third day. As a rule, there was always uptake at night and loss during the day, but here, losses were higher than gains. The young females of 85% hydration and 100% hydration groups, had losses of almost 5% in the shaded site and between 5 - 8% in the open site. The 65% hydration groups on both sites, however, had very small gains.

During this season out of a total of 114 recordings of relative humidities at the grass top height, (all times of day lumped together,(Table 9) 79 recordings had humidities below 85% R.H., 30 had humidities above 85% R.H., and only 5 recordings had humidities of 85% R.H.

In the wet season (Fig.17, Table 10) the dehydrated males in both groups (65% and 85%), gained between 5-15% weight by taking up more at night than they lost during the day. Even the fully hydrated groups took up an extra 2 - 4% with the exception of the old males in the open site. Although the 85% hydration groups were able to regain up to 10% original weights in three out of four occasions, the 65% hydration groups were only able to recover up to 15%. The old and young females comparision (Fig.18, Table 11) showed a rapid uptake on the first day by the dehydrated groups. The old females in the shaded site gained between 5-10% and almost 15% in the open site. The young females were able, however, to regain between 10 - 17% of their original weights. Apart from the old females in the open site taking up an extra 5%, all the other groups of the fully hydrated ticks first lost some weight and by the third day had gained less than 2%.

TABLE 9. Seasonal variation in the frequency of R.H. readings at grass height level. All times lumped together for the whole year

SEASON	< 85% R.H.	85% R.H.	>85% R.H.	TOTAL NUMBER OF OBSERVATIONS
HOT DRY SEASON	79	5	30	114
RAINY SEASON	40	3	82	125
COOL DRY SEASON	44	2	40	86
TOTAL	163	10	152	325

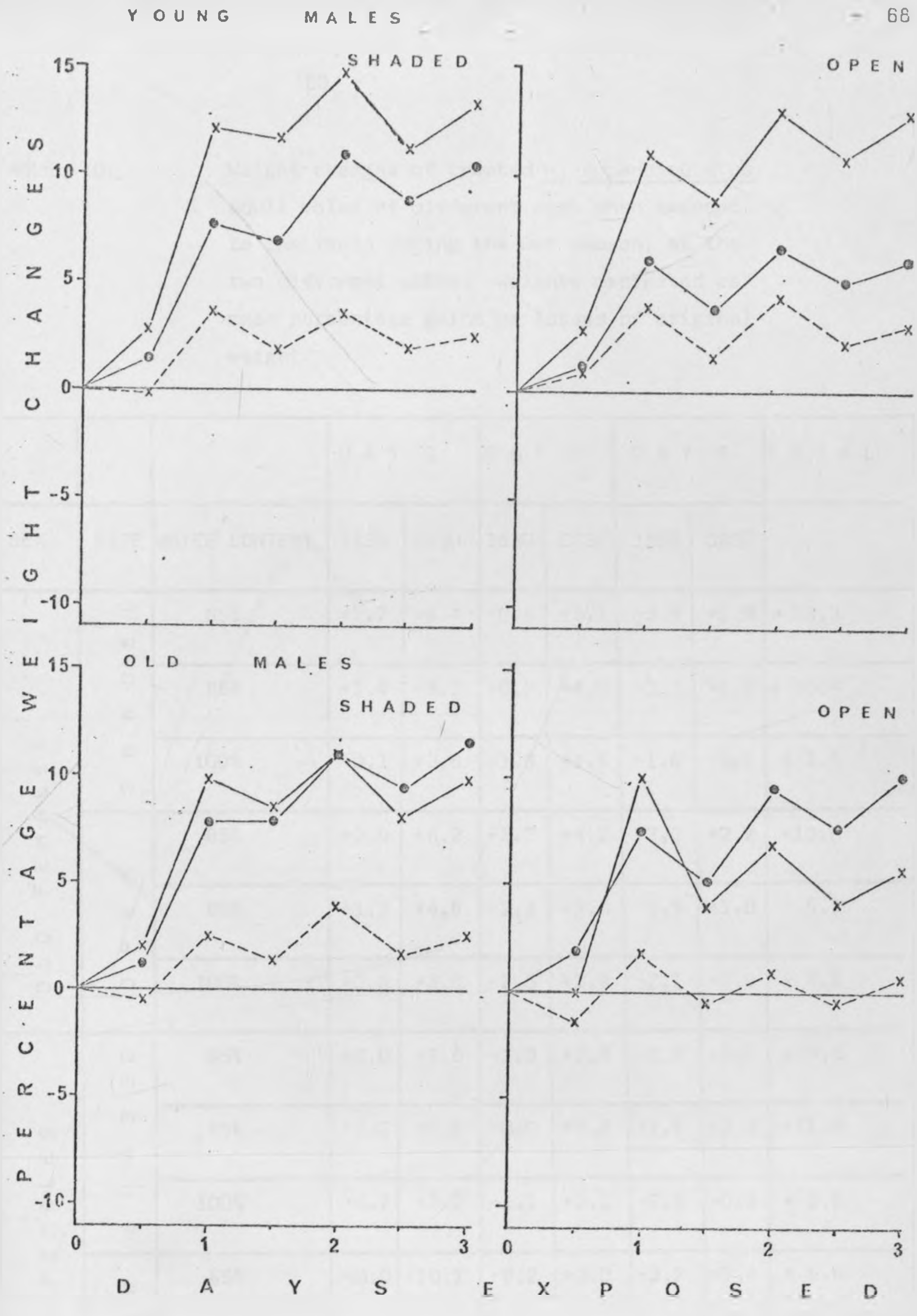

Fig. 17. Daily weight changes of treated old and young male *R. appendiculatus* exposed in the field during the rainy season. Open and shaded sites compared.

Key: ——x—— 65% hydration
——•—— 85% hydration
- - -x- - - 100% hydration

TABLE 10. Weight changes of treated R. appendiculatus adult males of different ages when exposed to the field during the wet season, at the two different sites. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
SEX	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
OLD FEMALES	SHADED	65%	+2.7	+9.4	-0.5	+3.1	-3.4	+2.0	+ 13.3
		85%	+1.4	+6.2	-0.7	+4.0	-2.1	+1.6	+ 10.4
		100%	-0.1	+3.6	-1.6	+1.5	-1.6	+0.7	+ 2.5
	OPEN	65%	+2.8	+8.2	-2.2	+4.2	-2.2	+2.2	+13.0
		85%	+1.2	+4.9	-2.3	+2.8	-1.5	+1.0	+ 6.1
		100%	+0.9	+3.0	-2.3	+2.8	-2.1	+0.9	+ 3.2
YOUNG FEMALES	SHADED	65%	+2.0	+7.8	-1.3	+2.5	-2.9	+1.7	+ 9.8
		85%	+1.2	+6.6	+0.0	+3.2	-1.6	+2.1	+11.5
		100%	-0.7	+3.2	-1.1	+2.5	-2.3	+0.9	+ 2.5
	OPEN	65%	+0.0	+10.1	-6.2	+3.0	-2.7	+1.4	+ 5.6
		85%	+1.9	+ 5.5	-2.2	+4.3	-1.9	+2.5	+ 10.1
		100%	-1.4	+ 3.1	-2.2	+1.4	-1.4	+1.1	+ 0.6

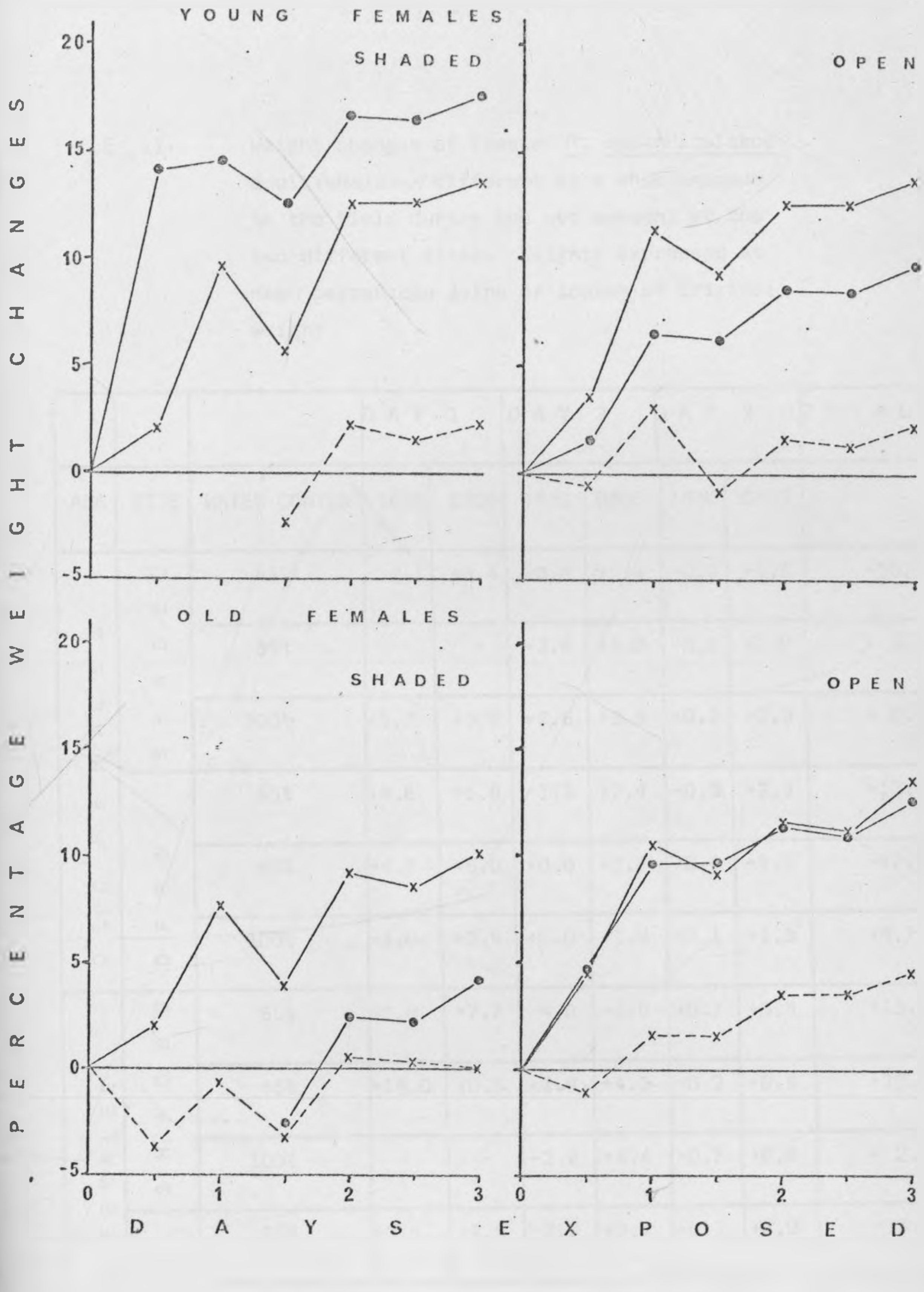

Fig.13. Daily weight changes of treated old and young female R. appendiculatus exposed during the rainy season in the field. Open and shaded sites compared.

Key: ——x—— 65% hydration

——o—— 85% hydration

----x---- 100% hydration

TABLE 11. Weight changes of treated R. appendiculatus adultfemales of different ages when exposed to the field during the wet season, at the two different sites. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
AGE	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	
OLD FEMALES	SHADED	65%	+2.1	+5.4	-3.6	+5.4	-0.8	+1.6	+10.1
		85%	-	-	-2.6	+5.0	-0.2	+2.0	+ 4.2
		100%	-3.7	+3.0	-2.6	+3.9	-0.2	-0.3	+ 0.1
	OPEN	65%	+4.6	+5.9	-1.3	+2.4	-0.3	+2.3	+13.6
		85%	+4.7	+5.0	+0.0	+1.7	-0.4	+1.5	+12.5
		100%	-1.0	+2.6	+0.0	+1.9	-0.1	+1.3	+4.7
YOUNG FEMALES	SHADED	65%	+2.0	+7.7	-4.0	+6.9	+0.1	+0.8	+13.5
		85%	+14.0	+0.5	-1.9	+4.2	-0.2	+0.8	+17.4
		100%	-	-	-2.2	+4.4	-0.7	+0.8	+ 2.3
	OPEN	65%	+3.5	+7.9	-2.0	+3.1	+0.1	+2.0	+13.7
		85%	+1.6	+4.9	-0.2	+2.3	-0.2	+1.4	+ 9.8
		100%	-0.6	+3.6	-2.1	+0.7	-0.4	+0.9	+ 2.1

Males and females of the same age, when compared (Fig. 19, Table 12) showed rapid weight gains in the dehydrated groups with final gains of 10% in the shaded site, for both sexes, and between 10-15% in the open site, with an exception of the 85% hydration group which took up less than 5%. The fully hydrated groups died before exposure during the preliminary laboratory treatments.

Out of a total of 125 humidity recordings from the vegetation tips during this season (Table 9), 82 had humidities above 85% R.H., 40 had humidities below 85% R.H. and only 3 recordings had humidities of 85% R.H.

During the cool dry season (Fig. 20, Table 13) there was a general uptake of water by males in the dehydrated groups, sometimes even during the day, with final gains of 8 - 12%. None of the groups, however, managed to recover fully the weight lost during dehydration. As the young fully hydrated groups in the shaded and open sites were gaining some weight, the old fully hydrated were losing. As a result, those in the open site were dead by the second day after losing almost 15%.

The old and young females (Fig. 21, Table 14) of the fully hydrated groups maintained their original weights with alternating gains and losses of about 2%. Although the 65% hydration groups in the shaded site had some further losses those in the open site had gains, but generally less than 5%. The 85% groups had gains, but none had more than 5%.

Eight-six recording of humidity at grass-top height were taken, 40 had humidities above 85% R.H., 44 had humidities below 85% R.H., and only 2 observations had humidities of 85% R.H. (Table 9).

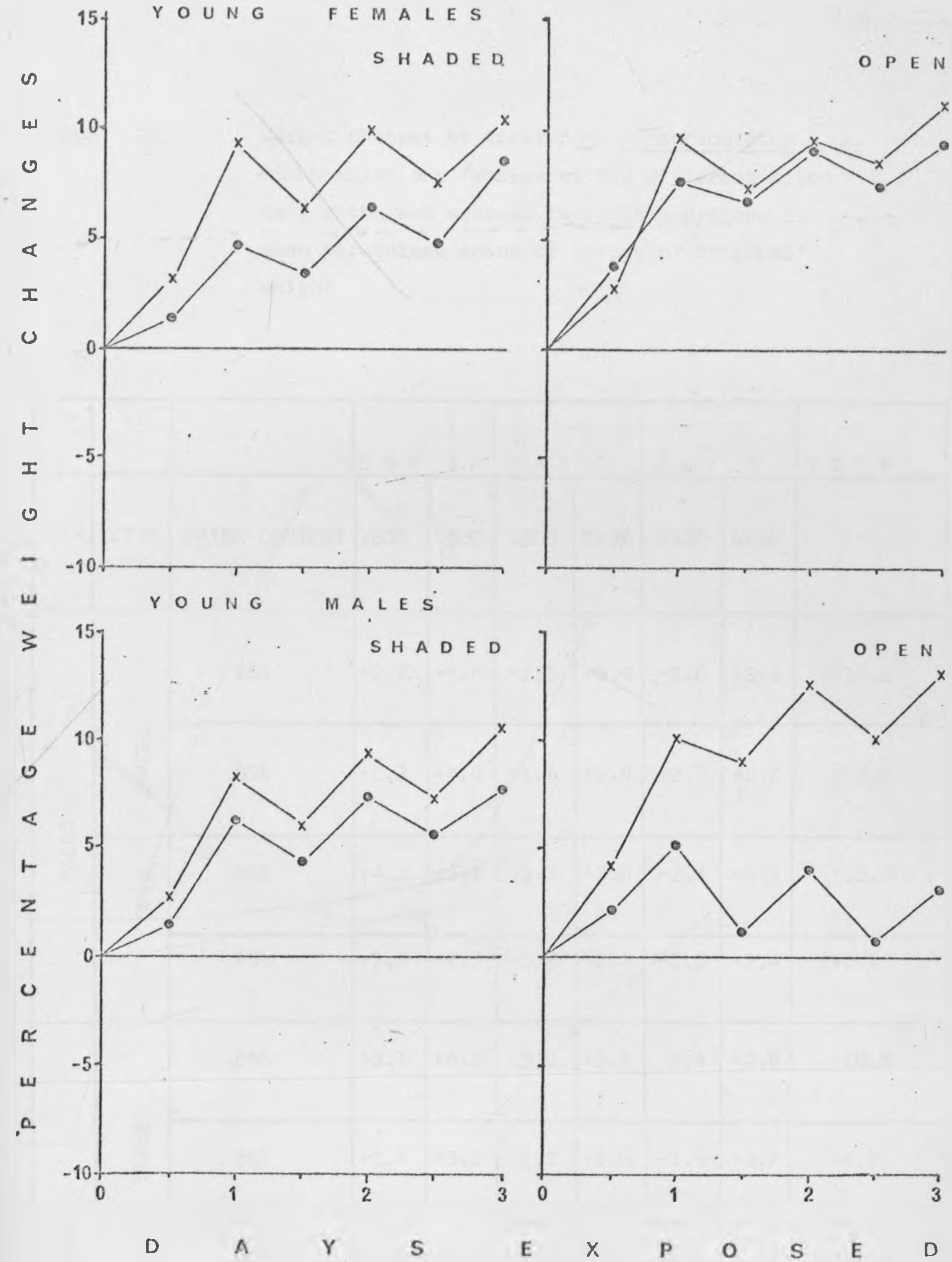

Fig.19. Daily weight changes of treated young males and female *R.appendiculatus* exposed in the field during the rainy season. Open and shaded sites compared.

Key: ——x—— 65% hydration
——•—— 85% hydration
----x---- 100% hydration

TABLE 12. Weight changes of treated *R. appendiculatus* young adult males and females at two different sites during the wet season. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
SEX	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
MALES	SHADED	65%	+2.7	+5.6	-2.3	+3.4	-2.0	+3.1	+10.5
		85%	+1.7	+4.6	-1.9	+2.9	-2.7	+2.2	+ 7.8
	OPEN	65%	+4.3	+5.9	-1.2	+3.6	-2.4	+3.1	+13.3
		85%	+2.3	+2.8	-3.9	+2.8	-3.2	+2.4	+3.2
FEMALES	SHADED	65%	+3.1	+6.3	-3.0	+3.6	-2.4	+2.9	+10.5
		85%	+1.4	+3.2	-1.2	+3.0	-1.5	+3.7	+8.6
	OPEN	65%	+2.9	+6.8	-2.4	+2.5	-1.2	+2.7	+11.3
		85%	+3.9	+3.9	-1.0	+2.3	-1.6	+1.9	+ 9.4

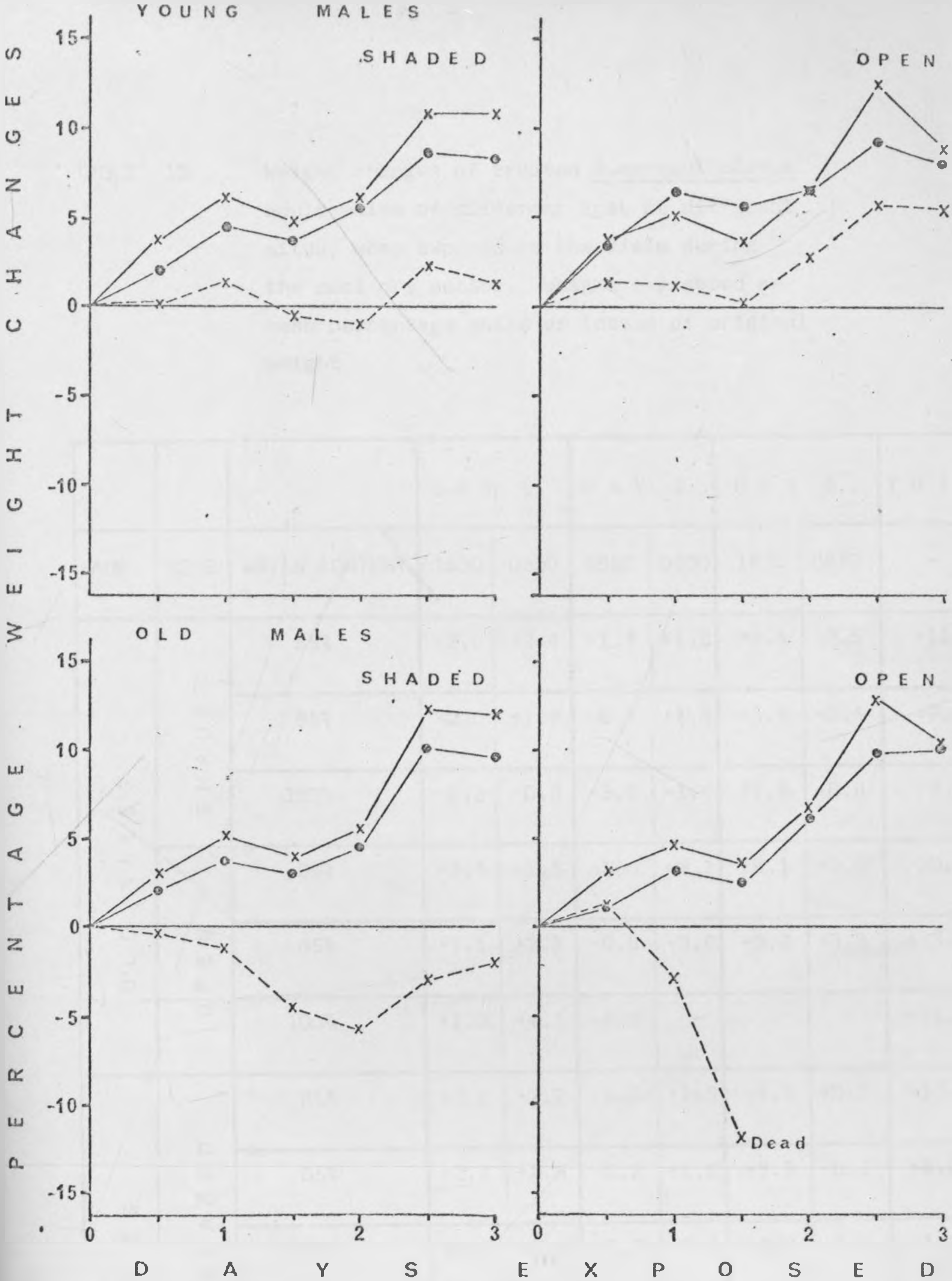

Fig.20. Daily weight changes of treated old and young male R. appendiculatus exposed in the field during the cool dry season. Open and shaded sites compared.

Key: ——x—— 65% hydration
——o—— 85% hydration
- - - -x- - - - 100% hydration

TABLE 13. Weight changes of treated R.appendiculatus adult males of different ages at different sites, when exposed to the field during the cool dry season. Weight expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
AGE	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
OLD MALES	SHADED	65%	+3.0	+2.4	-1.4	+1.6	+6.8	-0.5	+11.9
		85%	+2.0	+1.9	-0.7	+1.5	+5.5	-0.4	+9.8
		100%	-0.3	-0.9	-3.2	-1.4	+2.9	+0.9	-2.0
	OPEN	65%	+3.4	+1.3	-1.0	+3.1	+6.1	-2.5	+10.4
		85%	+1.1	+2.3	-0.9	+3.6	+3.8	+0.3	+10.2
		100%	+1.2	-4.1	-8.9	-	-	-	-11.8
YOUNG MALES	SHADED	65%	+3.9	+2.2	-1.2	+1.3	+4.5	+0.0	+10.7
		85%	+2.1	+2.5	-0.7	+1.6	+3.3	-0.2	+8.6
		100%	+0.2	+1.2	-1.8	-0.5	+3.3	-1.1	+1.3
	OPEN	65%	+3.8	+1.3	-1.3	+2.7	+6.2	-3.7	+9.0
		85%	+3.6	+2.9	-1.0	+0.8	+2.9	-1.1	+8.1
		100%	+1.3	-0.2	-0.8	+2.6	+2.9	-0.3	+5.5

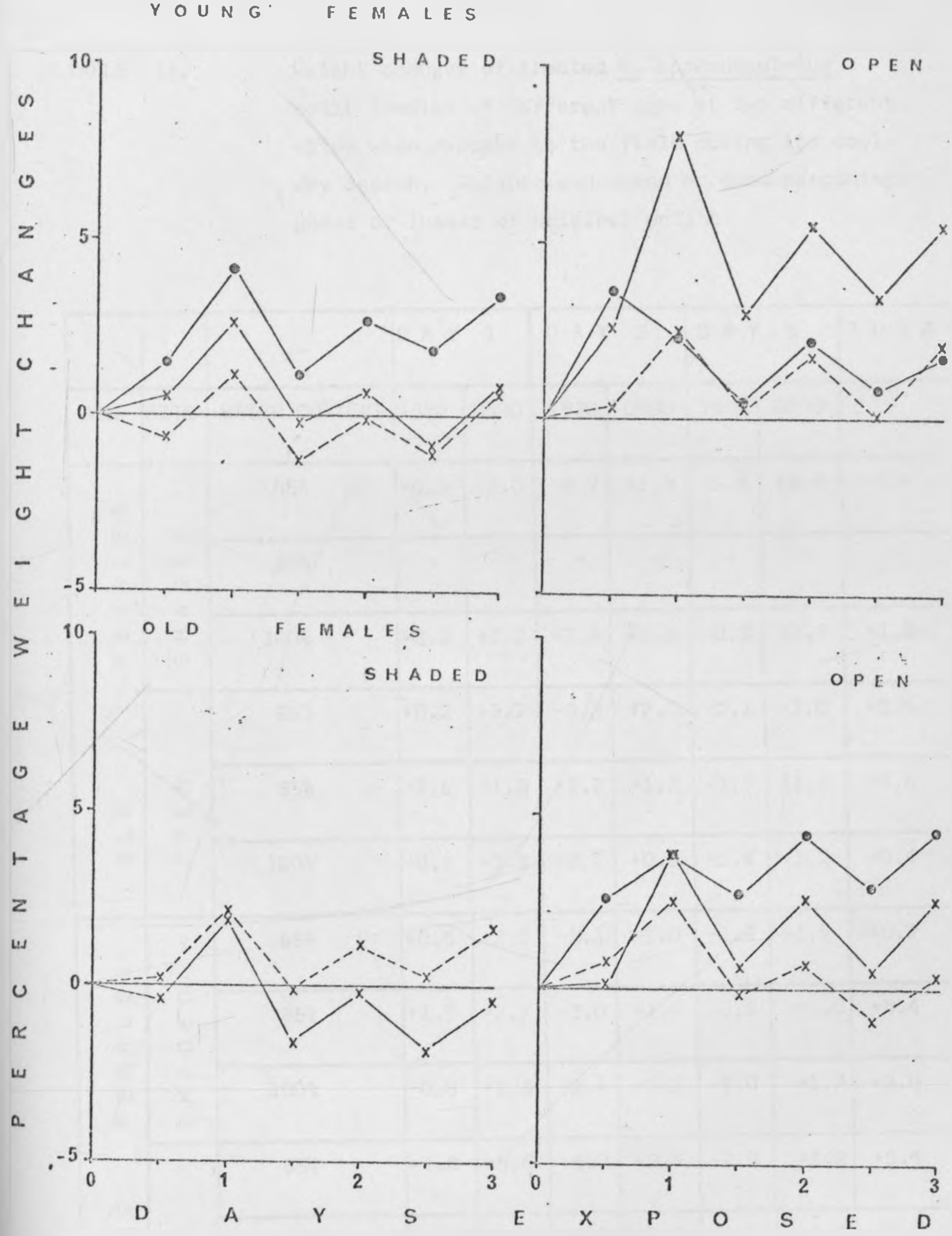

Fig.21. Daily weight changes of treated old and young female *R. appendiculatus* exposed in the field during the cool dry season. Open and shaded sites compared.

Key: ——x—— 65% hydration
——•—— 85% hydration
----x---- 100% hydration

TABLE 14. Weight changes of treated R. appendiculatus adult females of different ages at two different sites when exposed to the field during the cool dry season. Weights expressed as mean percentage gains or losses of original weight

			DAY 1		DAY 2		DAY 3		TOTAL
AGE	SITE	WATER CONTENT	1830	0830	1830	0830	1830	0830	-
OLD FEMALES	SHADED	65%	-0.3	+2.0	-3.2	+1.3	-1.6	+2.4	-0.4
		85%	-	-	-	-	-	-	-
		100%	+0.1	+2.2	-2.4	+1.3	-0.9	+1.3	+1.6
	OPEN	65%	+0.2	+3.7	-3.3	+2.0	-2.1	+2.0	+2.5
		85%	+2.6	+1.3	-1.2	+1.7	-1.5	+1.6	+4.5
		100%	+0.7	+1.8	-2.7	+0.8	-1.4	+1.2	+0.4
YOUNG FEMALES	SHADED	65%	+0.5	+2.2	-3.1	+1.0	-1.4	+1.5	+0.7
		85%	+1.5	+2.7	-3.0	+1.4	-0.8	+1.6	+3.4
		100%	-0.6	+1.8	-2.4	+1.1	-1.0	+1.7	+0.6
	OPEN	65%	+2.6	+5.6	-5.2	+2.5	-2.0	+1.9	+5.4
		85%	+3.6	-1.2	-1.9	+1.8	-1.5	+1.0	+1.8
		100%	+0.3	+2.2	-2.2	+1.5	-1.7	+1.9	+2.0

1.5 TICK ACTIVITY IN RELATION TO AGE, SEX, SITE, WATER CONTENT AND SEASON.

The whole year's data from the old males' and females' observations were pooled and an anlysis of variance was carried out. It can be seen (Table 15) that, there was no significant difference between seasons, whereas water content of the ticks and age showed highly significant differences ($P < 0.001$) There was also some difference($P < 0.05$) between sites. There was also a just significant ($P=0.05$) interaction of season and hydration state, but the interaction of season and site was not significant at all. The interaction of season and age was also not significant. Similarly, the interactions of water content and ages or sites were also not significant.

An analysis of variance on the pooled data from the young males and females (Table 16) showed no significant difference between sexes. Apart from the water content showing high significant difference ($P < 0.001$), season and site showed no difference. Similarly, only the interaction of season and water content which showed high significance ($P < 0.001$) while the rest did not have any significant interation effect. Using the simple sign test (Sokal and Rohlf, 1969) a test was carried out on the difference within the three hydration states. It was found that the 100% hydration group was more active than the 85% hydration group by a factor of 11, ($P < 0.01$) and the 85% hydration group was also 5 times more active than the 65% hydration group ($P<0.01$).

Similarly, it was shown that old ticks were 8 times more active than the young ones ($P < 0.001$).

TABLE 15. Analysis of variance on the effect of four factors (season, water content, site and age) on the activity of *R.appendiculatus* adult ticks in the field

Source of variation	df	SS	MS	F	
Season	2	455.72	227.86	0.34	NS
Water Content	2	14,612.05	7,306.03	11.04	***
Site	1	2,898.02	2,898.02	4.38	*
Age	1	14,440.03	14,440.03	21.81	***
Season X Water Content	4	8,531.62	2,132.91	3.22	*
Season X Site	2	2,798.73	1,399.37	2.11	NS
Season X Age	2	172.72	86.36	0.13	NS
Water content X Site	2	590.74	295.37	0.45	NS
Water Content X Age	2	3,804.06	1,902.03	2.87	NS
Site X Age	1	1,236.70	1,236.70	1.87	NS
Error MS = Residual MS	16	10,591.25	661.95		

*** = $P < 0.001$

** = $P < 0.01$

* = $P < 0.05$

NS = Not significant

TABLE 16 Analysis of variance on the effect of four factors (season, water content, site and sex) on the activity of R. appendiculatus adult ticks in the field

Source of variation	df	SS	MS	F	
Season	1	1,380.17	1,380.17	3.19	NS
Water Content	2	12,247.00	6,123.50	14.15	***
Site	1	48.17	48.17	0.11	NS
Sexe	1	192.67	192.67	0.45	NS
Season X Water Content	2	9,032.33	4,516.17	10.43	***
Season X Site	1	580.16	580.16	1.34	NS
Season X Sexe	1	112.66	112.66	0.26	NS
Water Content X Site	2	21.33	10.67	0.02	NS
Water Content X Sexe	2	221.58	110.79	0.26	NS
Site X Sexe	1	80.66	80.66	0.19	NS
Error MS =					
Residual MS	9	3895.77	432.86		

*** = $P < 0.001$

** = $P < 0.01$

* = $P < 0.05$

NS = Not significant

1.6 VERTICAL DISTRIBUTION OF TICKS IN THE HABITAT

At the end of each experiment the plots were searched carefully to recover as many of the released ticks as possible.

In the hot dry season 72.5% of the ticks were recovered (Table 17) with approximately one third (32.5%) of these on the upper part of the vegetation while the remaining two-thirds (67.5%) were at soil level.

In the wet season 67.1% of the ticks were recovered, and of these 85% were on the upper part of the vegetation and only 15% at soil level.

In the cool dry season 75.4% were recovered; 59% were on the upper part of the vegetation and 41% were at soil level.

A t-test was done on the mean numbers on and off the vegetation at each season. There were significantly more ticks on the ground in the hot dry season and more ticks on the vegetation in the wet season while in the cool dry season there was no significant difference between the ground and the grass levels (Table 17).

The majority of the ticks found near the ground were either at the base of grass stems or on the soil surface, mostly under the litter. Some ticks, especially among the dehydrated groups during the dry season, were found on the soil surface openly exposed at the site of release. They were found lying completely motionless with all their legs folded beneath them. They could only be activated with great difficulty(by breathing on them or

TABLE 17. Vertical distribution of marked *R. appendiculatus* adults recaptured on the vegetation during the three seasons of the year. Two habitat levels were compared (vegetation and soil levels), with the two means tested

	HOT DRY SEASON				RAINY SEASON				COOL DRY SEASON			
	No. RELEASED	No. RECAPTURED TOTAL	VEG.	SOIL	No. RELEASED	No. RECAPTURED TOTAL	VEG.	SOIL	No. RELEASED	No. RECAPTURED TOTAL	VEG.	SOIL
	792	584	188	396	752	504	427	77	512	386	229	157
% RECAPTURED	-	72.5	32.5	67.5	-	67.1	84.7	15.3	-	75.4	59.3	40.7
No. of OBSERVATIONS	-	18	-	-	-	18	-	-	-	12	-	-
MEAN PER OBSERVATION	-	32.4	10.4	22.0	-	27.3	23.6	3.7	-	32.2	19.1	13.1
t =			3.70	***			7.57	***			1.15	NS

*** = P < 0.001

NS = Not significant

by disturbing them). This slow response to disturbance and the camouflaged appearance could make unmarked ticks extremely difficult to detect on the soil. This foreseen problem was, however, overcome by marking the experimental ticks, which made it easier to detect even a motionless tick on the soil surface.

Ticks recovered from the upper part of the vegetation also showed very clear preferences in their choice of resting sites on the grass. During the active (rainy) season ticks were found on the flower heads of the common grasses, *Pennisetum purpureum*, *Panicum maximum* and *Themeda triandra* and were frequently in passive postures. In other plots where the dominant grass species was *Cynodon dactylon*, especially under the trees in the shaded site, ticks were found under the leaf sheaths or at the bases of the leaf blades. It seems also that ticks prefer dry grass stems to green ones. Even on the green stems, ticks prefer the dry leaf sheaths or leaves to the green fresh shoots. Few ticks were seen resting on the middle part of the grass stems.

Ticks in the upper part of the vegetation were more easily activated than those found on the soil surface. During the hot part of the day, especially at the open site, many ticks were seen resting on the lower surfaces of the leaves. They could easily be activated, where-upon they moved to the upper surfaces. Some climbed to the tip of the nearest grass stem or blade where a few quested for a while. They soon climbed down the vegetation again and disappeared into the turf.

All the ticks were released at the centre of each plot and most of them were recovered within a radius of 10 cm. from the point of release. This indicates that there was very little horizontal movement. R. appendiculatus, unlike Ixodes ricinus rests head downwards with the first pair of legs folded and the others holding the stalk (Fig. 1).

2. LABORATORY EXPERIMENTS

2.1 SPONTANEOUS ACTIVITY UNDER CONTINUOUS LIGHT OR DARKNESS

Batches of 25 ticks were released in the observation chamber. Some never came out of the containers. Of those which emerged, some sought shelter under the pieces of filter paper and only a few climbed the stems. After reaching the tips, they made a number of questing movements, then either settled up there or climbed down again to the sand surface. Browning (1976) observed the same situation.

When the ticks were exposed to continuous illumination at 18^{o}C, 23^{o}C, and 28^{o}C under 85% R.H. for 72 hours some ticks climbed to the tips of the stems during the first ten minutes after release. Most, however, remained in the tubes throughout the period of observation (Fig. 22, Table 18a) with only minor changes. One or two individuals moved up or down after four hours of exposure. Under these conditions, no rhythm of activity was demonstrated.

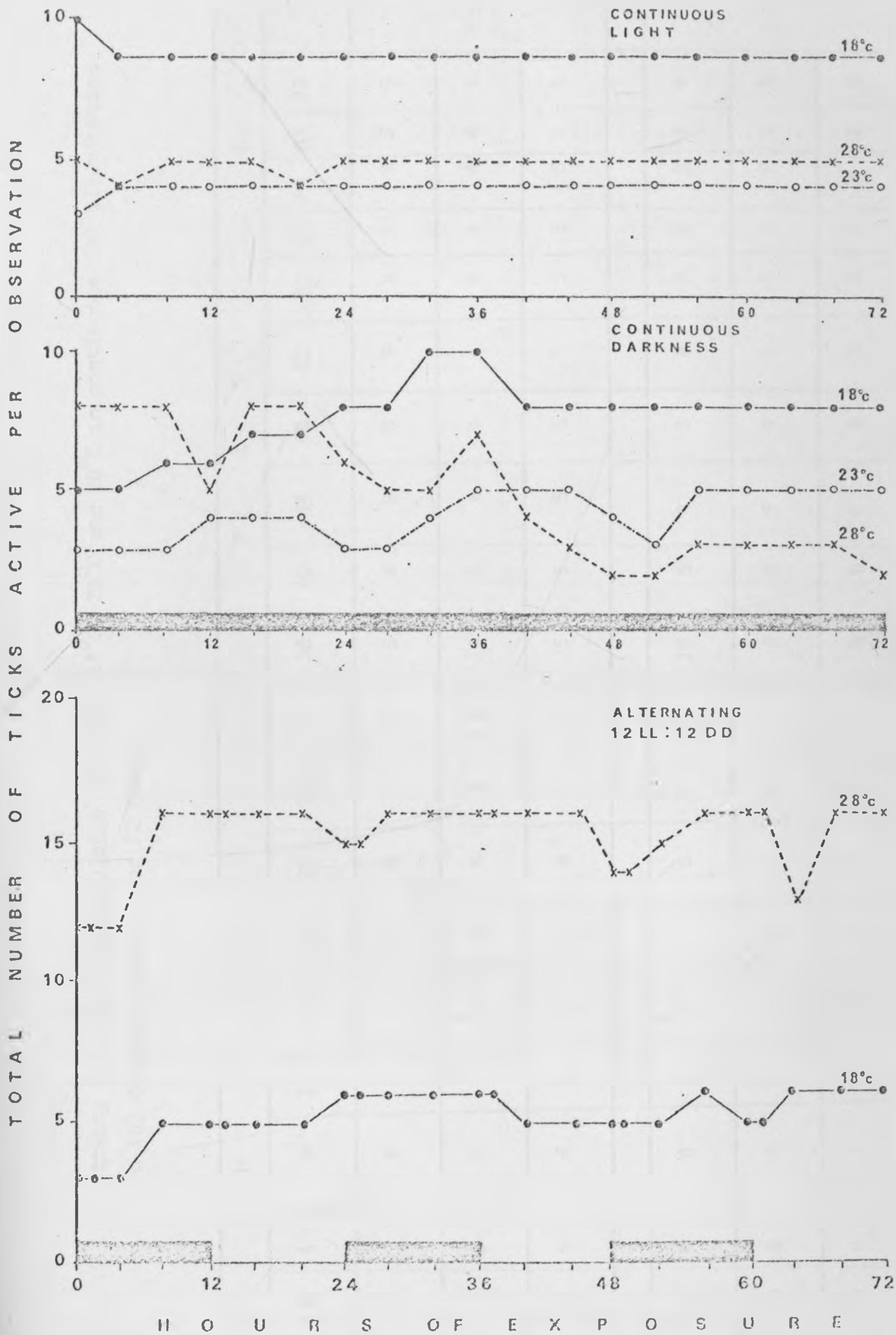

Fig.22. Activity of 25 R.appendiculatus males at different constant temperatures under continuous or alternating light and darkness regimes.

TABLE 18. Activity of 25 R. *appendiculatus* adults at 18°C, 23°C and 28°C in continuous (a) illumination and (b) darkness, exposed for 72 hours

	HOURS EXPOSED																			
	0	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	
18°C	10	10	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	
23°C	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	(a)
28°C	5	5	4	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	
18°C	5	5	6	6	7	7	8	8	10	10	8	8	8	8	8	8	8	8	8	
23°C	3	3	3	4	4	4	3	3	4	5	5	5	4	5	5	5	5	5	5	(b)
28°C	6	6	7	8	8	8	7	7	5	6	6	6	6	3	3	3	3	2	2	

A similar batch of ticks was also subjected to continuous darkness for 72 hours under the same conditions. Some activity was observed (Fig. 22, Table 18b) but again it was not rhythmic. At 18°C there was an increase in activity from 5 ticks to 10 ticks over the first 36 hours of exposure. This was followed by a slight decrease and that level was maintained throughout the remaining 36 hours. At 23°C the observed small changes in activity (3-5 ticks) were also not rhythmic. At 28°C after some initial climbing there was a steady decrease in numbers which was also arhythmic. It was later observed that although the stems had been oven dried, due to the high temperature (28°C) and relative humidity (85% R.H.) they started becoming mouldy, which could have been the cause for this steady reduction.

2.2 ACTIVITY UNDER VARYING CONDITIONS OF ALTERNATING LIGHT, TEMPERATURE AND RELATIVE HUMIDITY

Ticks were exposed to an alternating regime of 12 hours darkness and 12 hours light to look for any entrained rhythm. It was observed (Fig. 22, Table 19) that at 18°C tick activity increased slightly (from 3-6 ticks) during the first 24 hours but the number of ticks on the stems was almost constant for the rest of the period.

There was a similar increase in activity at 28°C during the first 24 hours of darkness and a few other changes later. None of these changes, however, occurred in a way that suggested that they might be related to the changes of light and darkness.

TABLE 19. The effect of alternating 12 hours light /12 darkness on the activity of the tick *R. appendiculatus* at 18°C and 28°C, n = 25

	REGIME																		
	L:D	D			L			D			L			D			L		
HOURS EXPOSURED	-	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72
18°C	3:3	3	5	5:5	5	5	6:6	6	6	6:6	5	5	5:5	5	6	5:5	6	6	6
28°C	12:12	12	16	16:16	16	15	15:15	16	16	16:16	16	16	14:14	15	16	16:16	13	16	16

It was observed, however, on a number of occassions, that some of the ticks resting on the stems started questing as soon as the lights were switched off, but none quested when the the lights were turned on.

Ticks were exposed to alternating temperatures while the humidity was kept constant and under constant illumination. It was observed (Fig. 23, Table 20) that under both increasing and decreasing temperatures there was an intial increase of tick activity. Although these changes were small for statistical analysis they definitely occured as a result of temperature changes.

Humidity (Fig. 24, Table 21) provided a direct response on tick activity on the increasing regime only, with maximum activity at 85% R.H. On the decreasing regime there was high activity only at 100% R.H. followed by a steady decrease of activity, as humidity decreased, which was not directly related to the humidity changes.

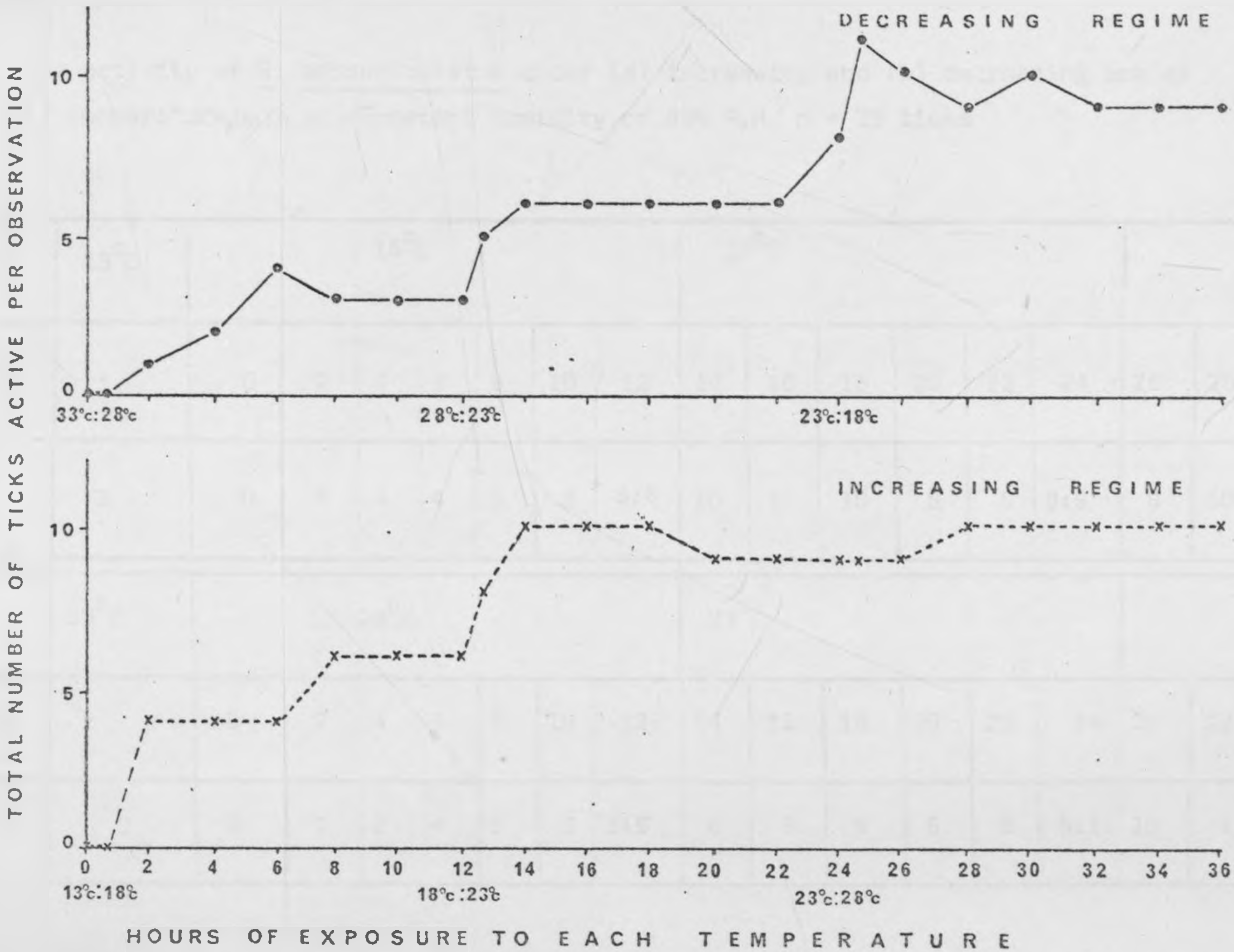

Fig.23. Activity of 25 *R.appendiculatus* males under increasing and decreasing temperature regimes.

TABLE 20. The activity of *R. appendiculatus* under (a) increasing and (b) decreasing scales of temperature, both at a constant humidity of 85% R.H. n = 25 ticks

	13°C	18°C							23°C						28°C						
HOURS OF EXPOSURE	-	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	(A)
NUMBER OF TICKS	0	0	4	4	4	6	6	6:8	10	10	10	9	9	9:9	9	10	10	10	10	10	
	33°C	28°C							23°C						18°C						
HOURS OF EXPOSURE	-	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	(B)
NUMBER OF TICKS	0	0	1	2	4	3	3	3:5	6	6	6	6	6	6:11	10	9	10	9	9	9	

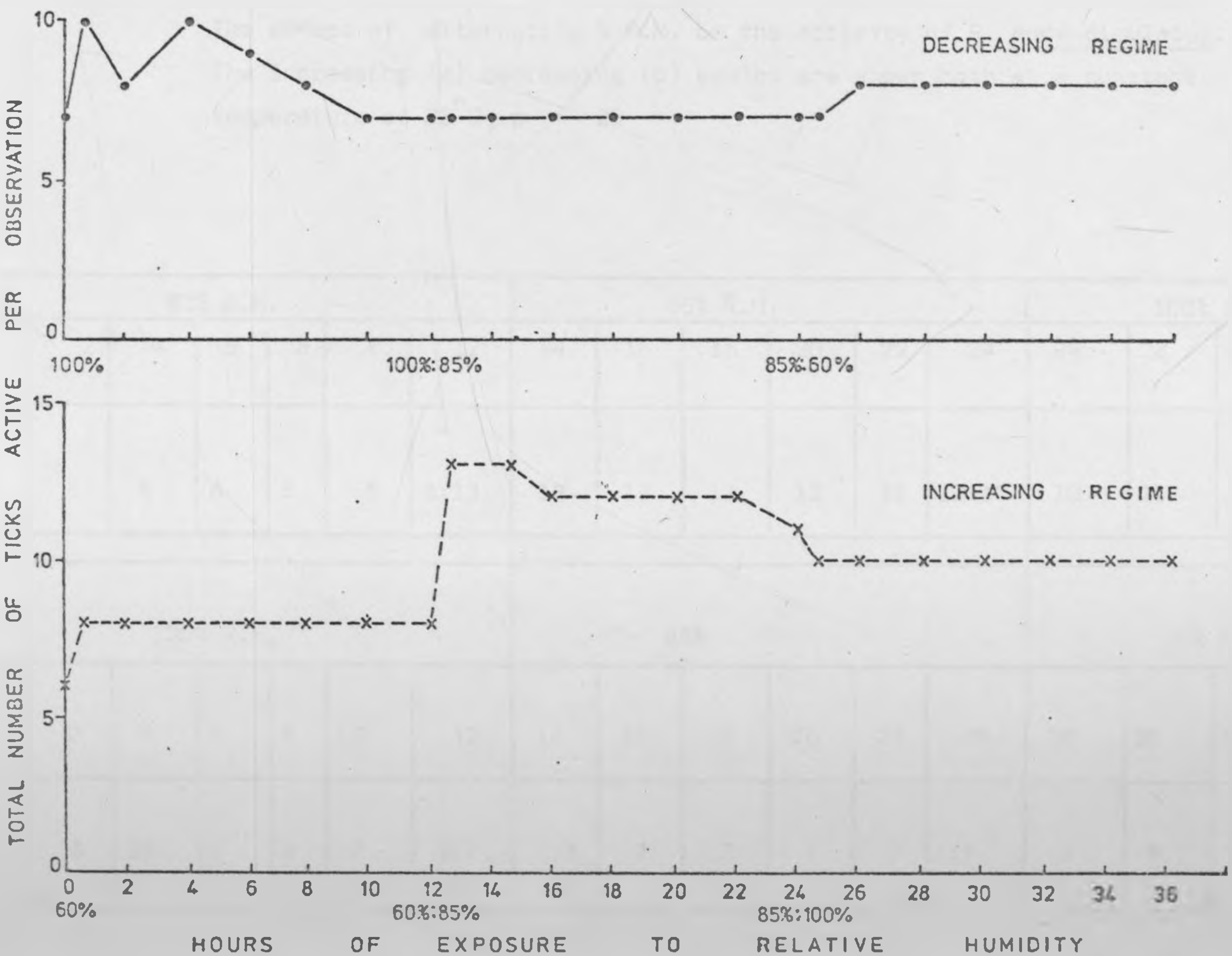

Fig. 24. Activity of 25 R.appendiculatus males under increasing and decreasing relative humidity rogimes.

TABLE 21.

The effect of alternating % R.H. on the activity of
The increasing (a) decreasing (b) scales are shown bo
temperature of 23°C; n = 25

	60%	60% R.H.							85% R.H.					
HOURS OF EXPOSURE	-	0	2	4	6	8	10	12	14	16	18	20	22	
NUMBER OF TICKS	6	8	8	8	8	8	8	8:13	13	12	12	12	12	12
	100%	100% R.H.							85%					
HOURS OF EXPOSURE	-	0	2	4	6	8	10	12	14	16	18	20	22	
NUMBER OF TICKS	7	10	8	10	9	8	7	7:7	7	7	7	7	7	7:

CHAPTER V

DISCUSSION AND CONCLUSIONS

Lees (1946, 1969) and Balashov (1972) indicated that when ticks need to rid their bodies of excess water, a negative geotaxis develops, and they move up to the tips of the vegetation. A positive geotaxis reappears when the tick's water content is reduced and they then return to the ground.

The results of this investigation confirmed to a great extent these findings. It was shown that when the treated ticks were released in the field plots, the fully hydrated individuals were always active immediately on the first day of release. Activity decreased later, probably as a result of the loss of excess water. The dehydrated groups, however, crawled into the litter and remained inactive at soil level for up to two days during the hot dry season. The length of this period of inactivity at soil level appeared to depend on the rate of water uptake by the ticks and the degree of previous dehydration. Water uptake in turn depended on temperature and relative humidity fluctuations experienced by the ticks during the exposure period.

Low humidities coupled with high temperatures obviously increase the rate of water loss from ticks through evaporation (Lees, 1946). This high rate of water loss in questing ticks would quickly bring the water content of a fully hydrated tick below the equilibrium weight. That is the weight below which the tick tries to avoid further desicciation and above which the tick tries to avoid further hydration . As a result, the tick is driven back into the vegetation.

The ground was found to be generally the most favourable level of the habitat for water uptakeby ticks. During the year of investigation, 378 humidity recordings were taken at soil level during the hours of observation. Of these, only 53 (14%) showed humidities below the ticks' critical equilibium humidity (CEH) of 85% R.H., and most of these low humidities were between 60-85% R.H.

Critical Equilibrium Humidity (CEH) is the humidity at which ticks neither gain nor lose water; below it they lose and above it they gain water. At humidities nearing the CEH the rate of water loss would be relatively slow (Lees, 1946). It is almost certain that for much of the rest of the day not covered by the records (mostly night-time) the R.H. would have been above the CEH, so that ticks could replace the water lost during the day-time.

R. appendiculatus is certainly able to control its water content. Comparing the weight changes at the three levels of hydration during the three seasons, one can see (Figs. 25-30) that the 85% hydrated males, for example (Fig. 25), always took up more water during the rainy season and a little less during the cool dry season, while during the hot dry season they again took much less water. The females (Fig. 26) were similar and, infact, the old females in the open site lost about 3% by the second day during the hot dry season. Generally, it can be concluded that the 65% hydrated groups took up a small amount of water, irrespective of season.

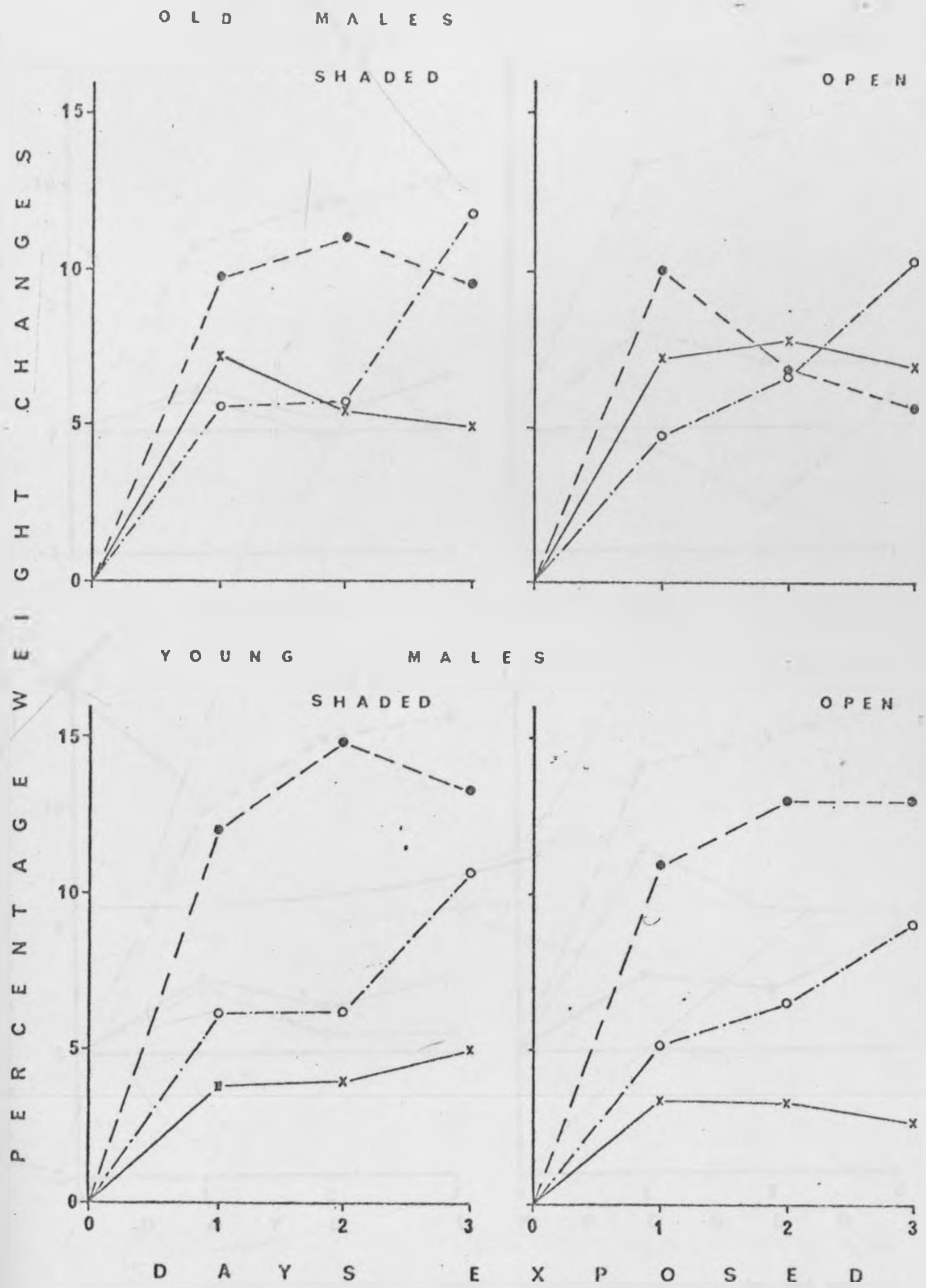

Fig.25. Seasonal comparison of daily weight changes by old and young male R.appendiculatus of 65% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----●---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

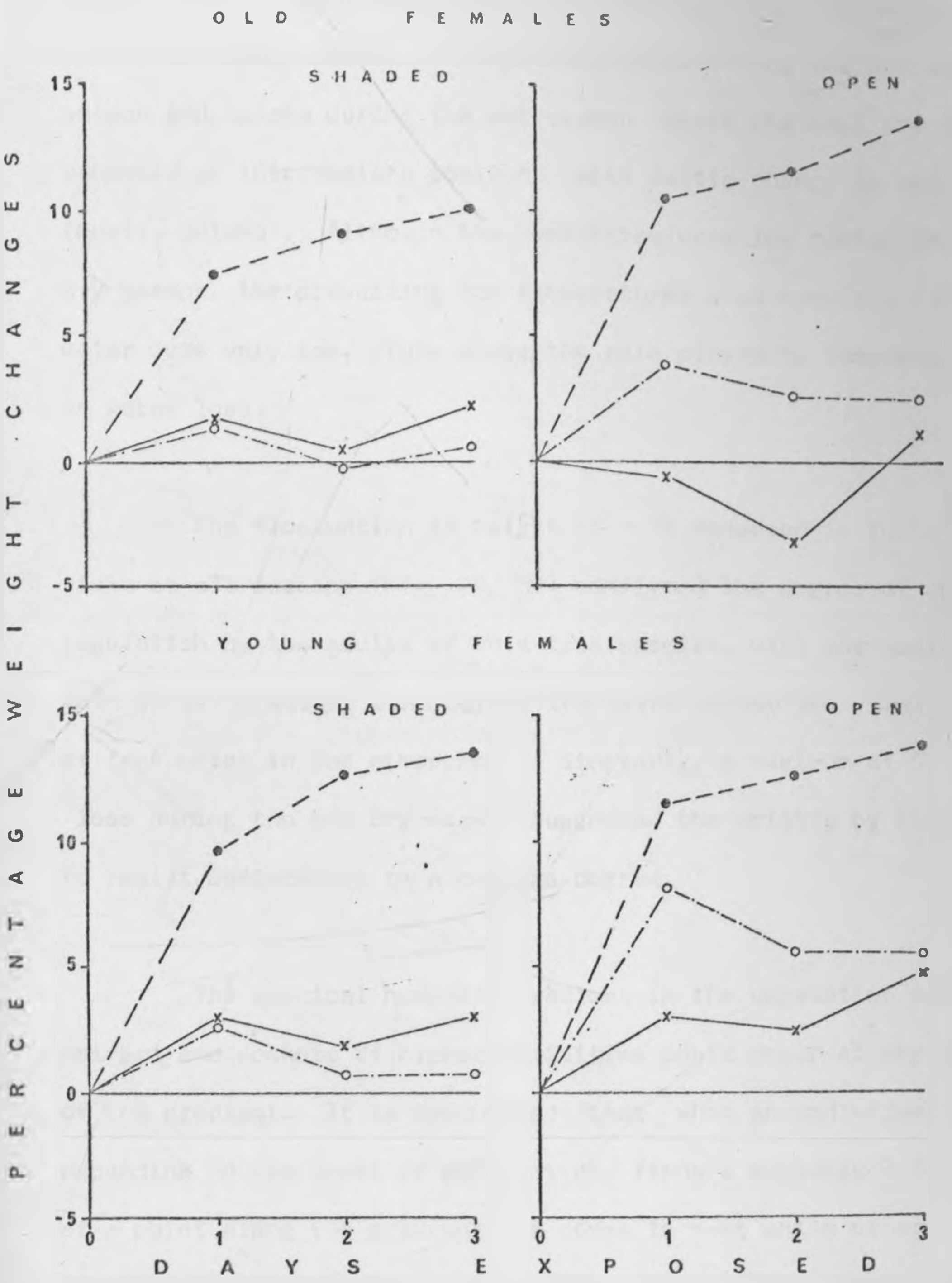

Fig. 26. Seasonal comparison of daily weight changes by the old and young female, R. appendiculatus of 65% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----●---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

The males of 85% hydration level (Fig. 27) took up water in all three seasons, with most in the rainy season. The females (Fig. 28) had a more characteristic response in the three seasons. As can be seen, there was always water loss during the hot dry season and uptake during the wet season, while the cool dry season occupied an intermediate position with little change in weight (mostly uptake). Although the humidities were low during the cool dry season, the prevailing low temperatures also made the rate of water loss very low. This shows the role played by temperature on water loss.

The fluctuation in weight of ± 5% observed in fully hydrated ticks at all seasons (Figs. 29, 30) confirmed the degree of water regulation by the adults of this tick species, with the maximum extra gain of 5% in weight even during the rainy season when there is a lot of free water in the atmosphere. Similarly, a maximum of 5% weight loss during the hot dry season suggested the ability by this species to resist desiccation by a certain degree.

The vertical humidity gradient in the vegetation may not be uniform and pockets of higher humidities could occur at any level of the gradient. It is postulated that when an individual tick, depending on its level of dehydration, finds a suitable R.H. at a point along the gradient, it comes to rest while other, less fortunate ticks may continue to be driven down towards the soil level. This may be especially so during the dry seasons.

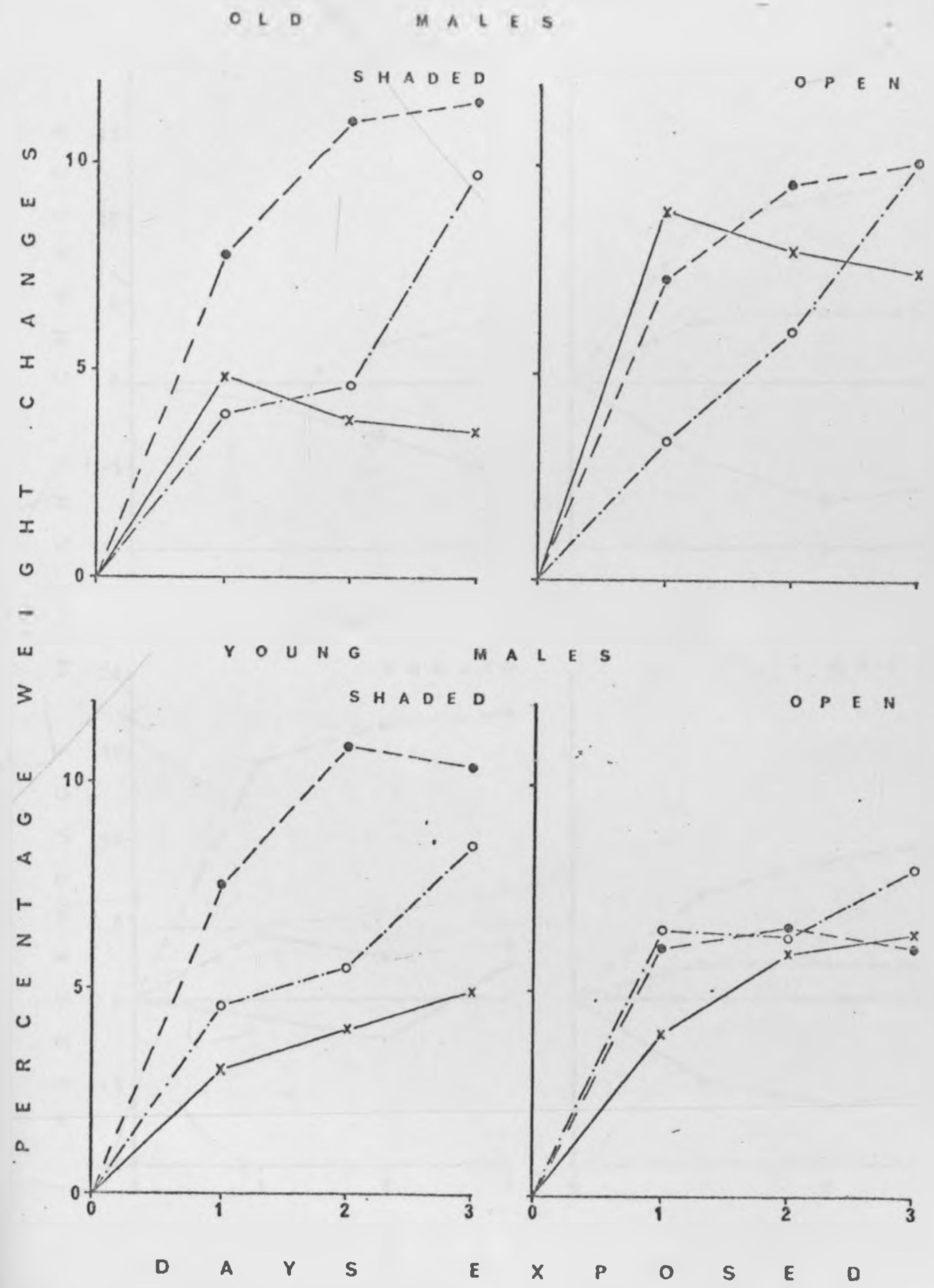

Fig.27 Seasonal comparison of daily weight changes by old and young male R. appendiculatus of 85% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----●---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

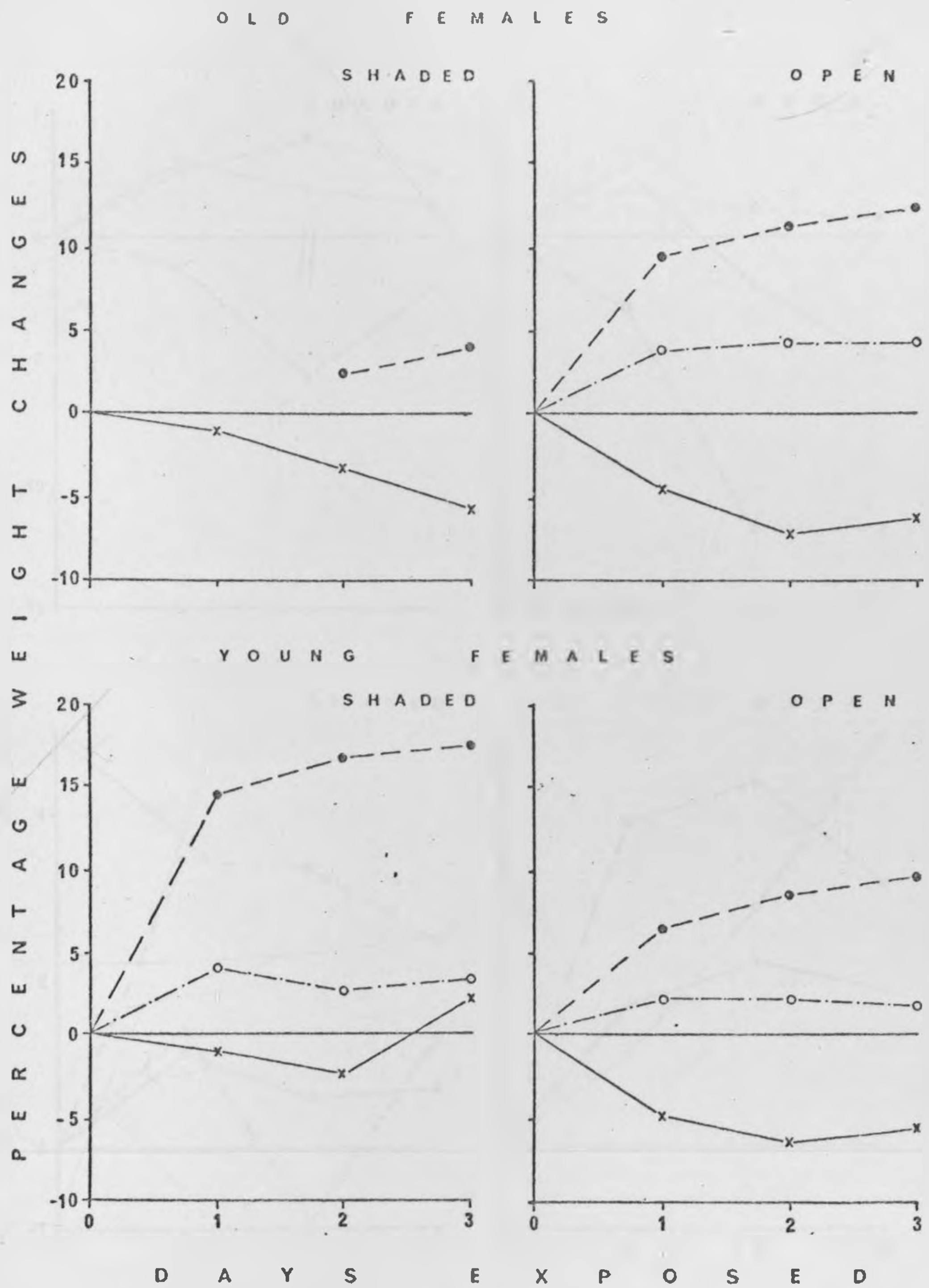

Fig.28. Seasonal comparison of daily weight changes by the old and young female R.appendiculatus of 85% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----●---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

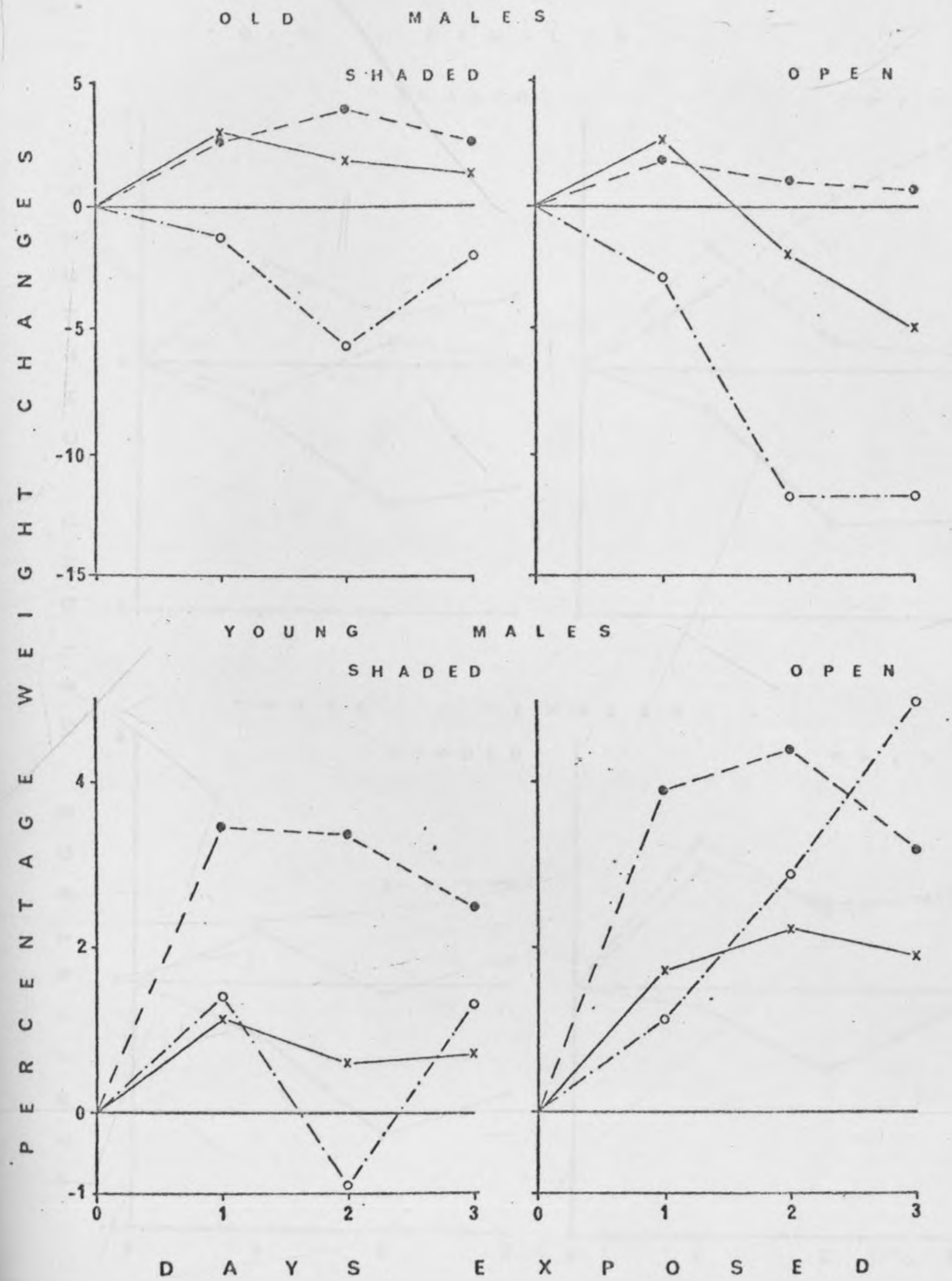

Fig.29. Seasonal comparison of daily weight changes by the old and young male R.appendiculatus of 100% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----•---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

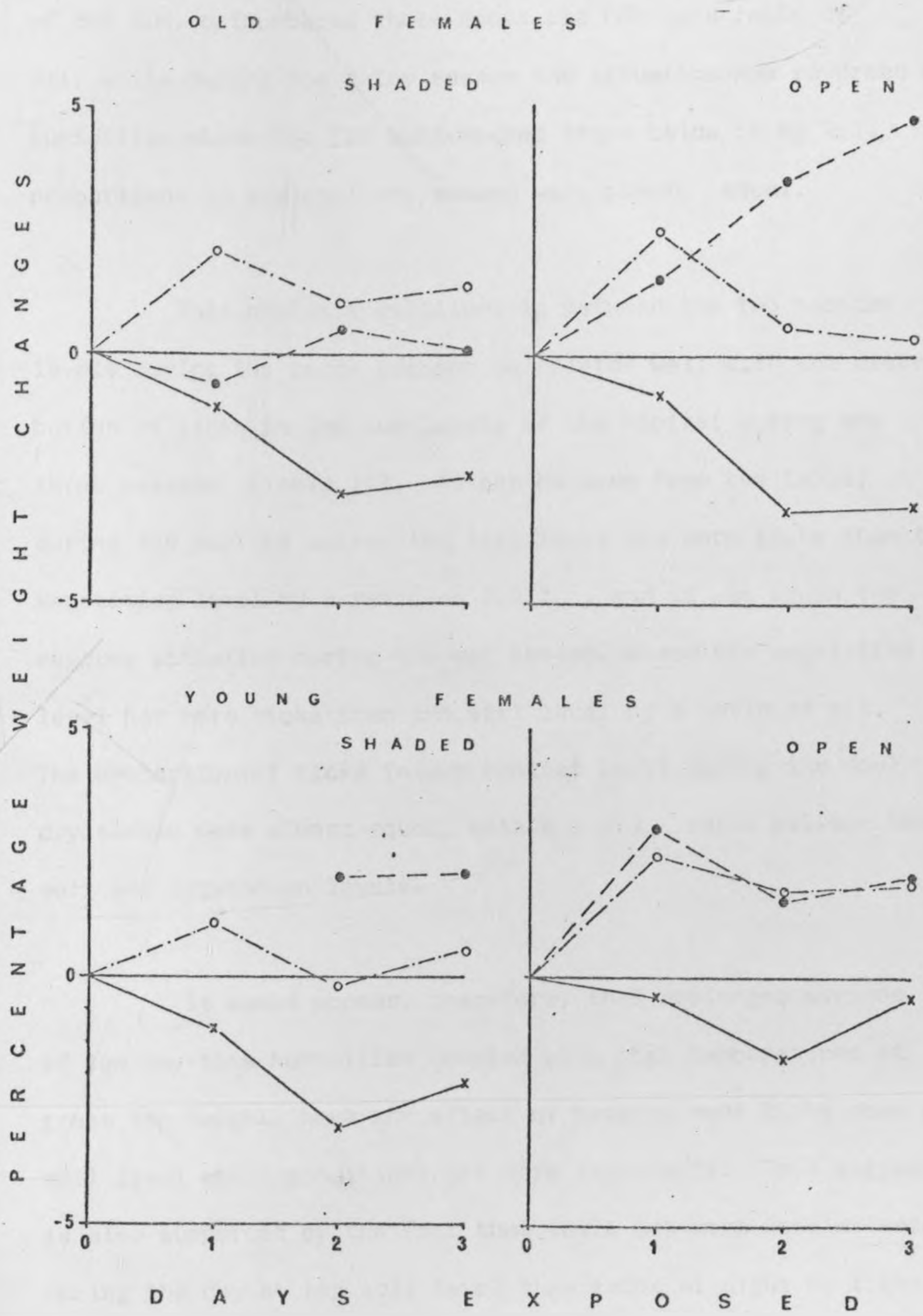

Fig.30. Seasonal comparison of daily weight changes by the old and young female. *R appendiculatus* of 100% hydration state exposed in the field for three days. Open and shaded sites compared.
Key: ----●---- rainy season
—·—o—·— cool dry season
——x—— hot dry season

During the hot dry season grass top height, R.H. recordings lower than the critical equilibrium humidity (CEH) of 85% R.H. outnumbered those above the CEH by a ratio of 3:1, while during the rainy season the situation was reversed and humidities above the CEH outnumbered those below it by 2:1. The proportions in the cool dry season were almost equal.

This humidity relationship between the two habitat levels during the three seasons correlates well with the distribution of ticks in the two levels of the habitat during the three seasons (Table 17). As can be seen from the table, during the hot dry season the soil level had more ticks than the vegetation level by a ratio of 2.5:1, and it was again the reverse situation during the wet season, where the vegetation level had more ticks than the soil level by a ratio of 6:1. The proportions of ticks in each habitat level during the cool dry season were almost equal, with a 1.5:1 ratio between the soil and vegetation levels.

It would appear, therefore, that prolonged periods of low day-time humidities coupled with high temperatures at grass top height, have the effect of keeping most ticks down at soil level where conditions are more favourable. This suggestion is also supported by the fact that there was more loss of water during the day at top soil level than gains at night by ticks. (Figs.14, 16). During the wet season, however, there was more uptake than loss (Figs. 17-19) and ticks at soil level may be in danger of becoming over hydrated. They may, infact, need to expose themselves to dehydration as a matter of necessity. During the cool dry season gains and losses of water are balanced and, as has been observed, the ticks were evenly distributed between the vegetation and the soil.

Tick activity was concentrated at high humidities (Fig. 13) which also confirms the suggestions of Lees (1946, 1969) and Balashov (1972) that when there is excess water in the tick there is correspondingly high activity. It was also clear that temperature plays a very important role in the initiation of activity (Fig. 12). There seemed to be limits (20°C - 30°C) outside of which the ticks responded negatively. This negative response is probably independent of the water content of the tick or the relative humidity of the environment.

Responses to these limiting temperatures can be seen in the field results (Figs. 9-11). Daily tick activity was highest between 20°C - 30°C. When the temperature went above 30°C there was a marked decrease in activity (Figs. 9, 10) which was particularly marked in the middle of the day during the hot dry season in the open site. As the temperature fell from the maximum towards the optimum, tick activity again increased but then decreased once more as the lower limit was approached towards evening. If the upper limit is not exceeded, tick activity may remain high for prolonged periods during the day (Figs. 9, 11) e.g. in the shaded site (Fig. 11) when there was continuous high activity from 1030-1630 hours.

In the open site during the hot dry season (Fig. 9) the optimum temperature was reached early in the day and there was correspondingly early activity starting at 0830 hours. This was soon reduced, however, when the higher limit was approached at 1230 hours.

Hence, daily increase in activity may be delayed or hestened in parallel with the changes in temperature towards the optimum.

It therefore, appears that although temperature changes trigger activity, only fully hydrated ticks are responsive. Thus the observed failure of dehydrated ticks to climb the vegetation for 1-2 days after introduction to the experimental plots suggests that until the tick is approaching full hydration, it is indifferent to temperature changes and will remain at the bottom of the vegetation.

As mentioned earlier, during the hottest part of the day, most ticks on the vegetation were seen on the lower surfaces of the leaves or grass blades. They could, however, be easily activated when they promptly moved onto the upper leaf surfaces. Some, indeed, climbed rapidly as high as they could on the nearest stem and started questing. However, after short intervals most of them returned to the protection of the thicker vegetation, in response perhaps, to unfavourable high ambient temperature.

Although there is at present no way to determine the age of a tick in the field it appears from the present experiments that most of the active ticks are old. The significant difference shown in the analysis of variance (Table 15) between the different water contents and age and the significant interaction of seasons and water content, and similarly the significant difference shown by the sign test between ages and between hydration levels, all indicate that the water content and the age of the tick are the critical factors in tick regulatory activity. This suggestion contrasts with that of Lees (1946) that as the tick ages it becomes less efficient in water uptake and more susceptable to desiccation. Thus one would expect that the older ticks would not only be losing water more rapidly but would be unable to recover so much during the night, and would thus be forced to remain at the bottom of the vegetation for most of the time. The lack of significant difference between the climbing activity of the two sexes (Table 16) suggests that they have a similar ability to regulate their water content . Indeed, in nature males and females appear on the vegetation in equal numbers.

There is significant interaction of season and water content (Table 16); during the wet season the rate of water uptake is faster and higher than during the dry seasons.

Although the number of active ticks was only just significantly different (P=0.05) when the two sites were compared, it should be noted that activity in the open site tended to be in brief high peaks compared with lower and more extended periods of activity in the shaded site (Figs. 9-11).

The following general conclusions can be drawn:-

a) The distinct seasonal activity pattern of *R. appendiculatus* adults, with a well marked peak during the rainy season, may be attributed to the following:-

i) Most ticks are found on the upper part of the vegetation and are thus readily available, and easily activated by a passing host, during the rainy season.

ii) Most ticks are found at soil level during the hot dry season conserving or replenishing their water content, and are very reluctant to become active when they have a low water content. Hence low activity in natural populations during the hot dry season.

iii) The intermediate picture shown in natural field populations for activity in the cool dry season agrees with the intermediate level of water regulation, with not so much loss nor so much gain.

b) The regular daily activity patterns appear to be produced by the interaction of the water content of the ticks with the daily cycle of temperature and humidity. Ticks that are fully hydrated respond to increase in temperature from the lower thresholds to the optimum. If this optimum is exceeded and the higher threshold is reached there is a decrease in the number of active ticks. Otherwise, a high level of activity continues until the temperature starts to drop towards the lower threshold, when activity also decreases and the night level of activity is reached.

When the ambient temperature starts to increase, the temperature deep down in the vegetation increases more slowly and thus the response of the ticks, and their appearance on the tips of the vegetation would also be delayed. However, ticks that are already in the upper part of the vegetation would be stimulated sooner since the increase in temperature would reach them more quickly. It is possibly true that the activated ticks from the soil level may not even reach the tips of the vegetation before they find high temperatures at the middle of the vegetation which drive them back down again.

Although R. appendiculatus adults did not respond to light or darkness changes by moving, the questing behaviour shown by the ticks when the lights were turned off was similar to that reported in Ixodes ricinus by Lees (1948). This may be similar to the response shown by a tick to the shadow cast by a large host.

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