WATER RELATIONS OF THE TICKS *RHIPICEPHALUS APPENDICULATUS* NEUMANN, 1901 AND *RHIPICEPHALUS PULCHELLUS* GERSTACKER, 1873

by

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DECLARATION

I, ABDUL OMARI MONGI, hereby declare that 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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C O N T E N T S

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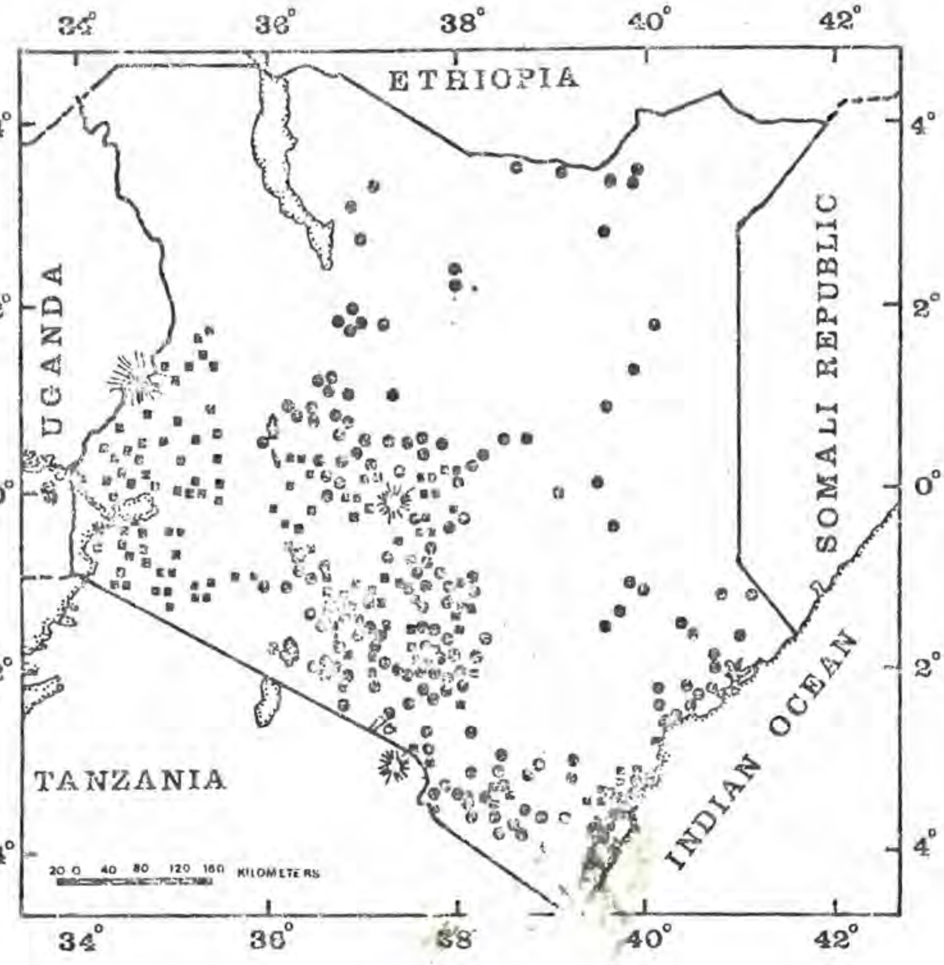
FIGURE 1

The map of Kenya showing the distribution of R. appendiculatus and R.pulchellus (from J. B. Walker, 1974).

FIG.1



R. appendiculatus (▪▪▪▪▪)

R. pullchellus (•••••)

A B S T R A C T

Fully hydrated, newly moulted, unfed nymphs and adults of Rhipicephalus appendiculatus and R.pulchellus were exposed to controlled relative humidities (RH) of 0%, 20%, 33%, 55%, 62%, 75%, 85% and 96% at 18°C, 23°C, 27°C and 31°C. Changes in weight of individual adults and nymphs, determined at regular intervals in batches of 50, resulted from water loss and water gain were found to be balanced near 85% RH, which is therefore the critical equilibrium humidity (CEH). It was found that the weight changes were independent of temperature.

Longevity was shortened at RHs below the CEH and water loss was most rapid at 33%, 20% and 0% RHs and was therefore the limiting factor to their survival. Mortality curves were constructed for each humidity. They showed an LD_{50} at 0% RH of about 6.5 days for female R.appendiculatus 6.8 days for female R.pulchellus and about 9.4 days for males of the two species.

Water vapour uptake from a near saturated atmosphere was studied using males and females of both species, and covering various parts of the body with paraffin wax (M.P. 44-45°C). It was shown that mouth-parts are major site of water vapour uptake.

Investigation of the lipid content of unfed adults of both species showed that lipid reserves were insufficient

on oxidation to provide enough water to contribute significantly to replacing water losses.

Cuticular permeability in both live and dead ticks at different rates of desiccation showed a curvilinear relationship to temperature. Females showed significantly greater water losses than males of the same species. Between species, *R.pulchellus* females consistently showed a significantly lower rate of water loss than *R.appendiculatus* females.

These findings help in explaining the distribution of the two species in nature, where *R.pulchellus* shows a preference for markedly arid habitats compared to *R. appendiculatus*.

CHAPTER I

INTRODUCTION

I.1: Water regulation by terrestrial arthropods

All terrestrial arthropods require to keep the proportion of water in their bodies constant within rather narrow limits. This is done by maintaining a balance between the water taken in through the mouth, the integument or through the spiracles and the water lost by excretion, by transpiration through the integument, and as a waste product of metobolism. The mechanisms involved are many and vary from species to species and whether the arthropods are found in dry or wet microhabitats.

Some insects can survive in dry places despite their small sizes because they possess a remarkably impermeable cuticle. In addition there are other physiological attributes which are important as are behaviour patterns which cause the insects to avoid unfavourable extremes of wetness or dryness. The investigations of (Arthur, 1951; Branagan, 1970; Hitchcock, 1955 and Newson pers. comm.) have shown that temperature and relative humidity govern the survival and development of ticks. Among the hazards confronting Rhipicephalids is the loss of water from their bodies, a problem common to all terrestial arthropods. These animals have many adaptations designed for the acquisition and conservation of water:

(a) A relatively impermeable integument

(b) Internal respiratory surfaces

(c) Relatively isoluble nitrogenous excretory products that can be eliminated as solids with minimum loss of water

(d) Active water vapour uptake

(e) Absorption of free water through the cuticle

(f) Utilisation of metabolic water especially from the oxidation of fat reserves (Kanungo, 1962; Edney, 1966; Noble - Nesbitt, 1969).

I.2: The critical equilibrium humidity

There is a critical equilibrium humidity (CEH) for each Arthropod species below which there is a net loss of water vapour to the atmosphere, whilst above it lost moisture can be regained by the tick from the surrounding atmosphere (Lees, 1946; Stampa, 1959; Browning, 1954; Balashov, 1960 and Knülle, 1974). These workers have shown that ticks possess the ability to take up water vapour from the air and also retain their water above a certain relative humidity, CEH. Lees (1946, 1964) investigated the effect of ageing on the water transport mechanism of the sheep tick <u>Ixodes ricinus</u> and discovered that the CEH increases with age until the oldest specimens in which water vapour uptake occurs only in saturated air. He however, stated that the efficiency of active resistance of desiccation is probably determined by the quantity of reserve food in the body. Knülle and Devine (1972) showed that CEH is merely the point at which water vapour uptake, which is proceeding all the time is sufficient to compensate for concurrent losses due to transpiration.

I.3: Water loss and cuticular permeability

Arthropods differ enormously in their powers of resistance to desiccation, depending upon their capacity for ventilatory control and more importantly upon the integument against which these powers operate. When they are exposed to a subsaturated atmosphere there will be a gradient of vapour pressure set up between the integument, at or near which water is present in liquid form, and the ambient air. Since the integument of the insect is not completely impermeable, water will evaporate from it and diffuse into the general atmosphere along the established gradient.

Ramsay (1935), Leighly (1937) and Beament (1961) found that the rate at which evaporation takes place depends upon three major factors:

(a) on the permeability to water of the transpiring membrane,

(b) on the temperature of the transpiring surface which will affect the rate of diffusion of moleculars of water,

(c) on the activity gradient between the insect surface and the general atmosphere.

The phenomenon is not simple, as the permeability of the transpiring surface varies widely for different parts of the insect. In ticks and other relatively small terrestrial Acarina water loss is especially critical because of their large evaporating surface in relation to the quantity of water which they contain. This important relationship was first recognized by Kennedy (1927) who pointed out that all other parameters remaining constant, the water content is a function of the volume of the animal whereas evaporation is a function of surface area. Thus the smaller the animal the more rapidly will its water content be depleted by evaporation. Ecologically it is important to know the rate at which animals lose water in a particular environment and to discover why evaporation rates differ between individual species. This question can only be resolved when the resistance of the cuticle to the passage of water is known so that the resistance can be correlated with particular structures or mechanisms in the integument. Lees (1947) found that the rate of water loss was nearly affected by the entire humidity range. Knülle and Devine (1972) demonstrated that in the larvae of Dermacentor variabilis, the movement of water from the tick into the atmosphere was heavily impeded by the resistance of the integument in particular the wax layer of the epicuticle.

As defined by Beament (1961) the permeability of a membrane is the rate at which a diffusant traverses a stated transporting agency. Measurement of the transpiration gives the rate, and the transporting agency usually can be regarded as the difference in the concentration of the diffusant at the two surfaces of the membrane, which is determined in part by the rate of evaporation. However, in most natural circumstances it cannot be evaluated.

I.4: Water vapour uptake

Many insects are capable of absorbing water at a substantial rate directly through the integument (Mellanby, 1932; Ludwig, 1937; Winston and Nelson, 1961; Edney, 1966). Noble-Nesbitt, (1971) demonstrated in *Thermobia domestica* that occlusion of the anus prevented uptake of water from the atmosphere. The rectum of insects has also been found to reabsorb water from the faeces (Lindsay, 1940; Beament 1964; Okasha, 1971). Little work of this kind has been done on the Acari, and the site and mechanism by which water vapour is extracted from the environment need to be surveyed in detail.

Since the uptake is affected against a formidable gradient of activity it must be an active process. However, the mechanism involved in this process has not been established, but a number of interesting possibilities have been suggested (Beament, 1964, 1965; Winston, 1967; Winston and Beament, 1969).

Knülle (1974) showed that in Dermacentor variabilis the mouth-parts are the main site of water vapour uptake. Beament (1954, 1961) found that the water can enter the cuticle more readily than it will pass out. He also stated that many arthropods and their eggs obtain water through their external surfaces directly from their surroundings and in a few instances it is certain that this involves an active process in which metabolic work is done to obtain the water. This is supported by the work of Knülle and Devine (1972) using tritiated water where it was found that the movement of water vapour from the atmosphere into the tick decreases with the activity of the water vapour in the air.

Knülle (1966) demonstrated that the partially dehydrated tick larvae transport water vapour actively from the atmosphere into the body above 85% RH a limit which was designated as CEH (Knülle and Wharton 1964: Hair, 1975).

I.5: Water content and dry weight

The body water content of several insects has been shown to have significance in relation to starvation and rate of metabolism at different temperatures and humidities (Pyne, 1926; Robinson, 1928; and Buxton 1930, 1932).

Mellanby (1932a, 1932b) demonstrated that starving mealworms Tenebrio molitor bedbugs Cimex lectularius and blood-sucking bugs Rhodnius prolixus regulate their rate of metabolism to maintain a constant percentage of water in the body at certain temperatures and humidities to which they are adapted. Both of these conditions, survival and regulation of body water in relation to metabolism at different temperatures and RHs are significant aspects of the problem of adjustment to seasonal weather fluctuations.

Hair (1975) made a comparison of three species of ticks, Amblyomma americanum, A.maculatum and Dermacentor variabilis in their ability to resist dehydration and maintain water balance. He found that A.americanum showed a preference for moist microhabitats because of its greater susceptibility to water loss than the other two species which showed preference for arid microhabitats. It is probable that the results of this investigation on changes in water content and dry weight of adult ticks, may offer an explanation of the ticks water regulation.

I.6: Lipids

The subject of lipid conversion into metabolic water has been investigated for many years by several workers (Lees, 1946, 1948; Gilby, 1957, 1961; Balashov, 1961; Clayton, 1964). But it remains unsolved in arthropods other than insects. Bursell (1959) for instance demonstrated that starving tsetse flies, metabolic water contributes about 1% of the total reserve;

while 25% of the water present in the eggs of <u>Eurygaster sp</u>. at the end of embryogenesis is found to be of metabolic origin.

In review by (Adrewartha and Birch,(1954),Edney, (1957),and Barton,(1964), it was pointed out that the metabolic water may figure as the sole item of water gain; but the observed results could be achieved as well by regulation of transpiratory and excretory losses which are known to excercise control in many insects.

Babcock (1917) showed that although oxidation of any stored lipid material must produce a considerable quantity of water, many animals use it to eliminate introgenous waste in solution. Those animals with isoluble excreta can therefore conserve water.

A fundamental question concerning the physiological role of lipids in water balance is the amount distributed between the exoskeleton and other tissues. Thus Lawrence (1967) working on <u>Schistocerca gregaria</u> showed that the exact amount varies not only with the physiological state and mode of life of the insect but also with the method of extraction. Further confusion arises over whether the results are expressed in terms of dry weight, wet weight or lean dry weight.

Recently Bart (1973) showed that ticks undergoing repeated water replenishment in the natural environment may be at a disadvantage in terms of metabolite conservation compared to ticks secluded in microhabitats with humidities above the CEH. But he concluded that the actual humidity itself was not significant.

The effects of relative humidity on arthropod metabolism have also been observed over relatively brief intervals by measuring the rate of oxygen consumption. Kanungo (1965) demonstrated that the oxygen consumption of desiccated versus fully hydrated mites, Echinolaelaps echidninus did not differ significantly at 98% RH, although the dehydrated mites gained weight. He concluded that the differential consumption of oxygen allegedly associated with water absorption probably represents only a minute fraction of the total energy involved in metabolism. Sweatman and Koussa (1968) observed that the rate of oxygen consumption of engorged female Rhipicephalus sanguineus tended to increase slightly with saturation deficit.

Cook (1972) measured the oxygen consumption of hydrated and desiccated Ornithodoros concanensis at various humidities above and below the CEH; and showed that the overall difference in metabolism of the two groups was not significant. However, the rate of oxygen consumption of the desiccated was significantly greater at 75% and 85% RH than at 50% and 90% RH. He therefore suggested that water uptake at intermediate humidities was perhaps at the expense of increased metabolism. Mellanby (1932) showed differential metabolism in dehydrated and starved bed bugs Cimex lectularius under prolonged exposure to various RHs. He examined the levels of fat and uric acid and found that the rates of metabolite utilisation did not differ significantly between the humidity treatments.

It is evident therefore that RHs experienced in the macroclimate and microclimate of the habitat are major factors in determining distribution and abundance of arthropods.

I.7: Objective of the research project

Tick-borne diseases are recognized as the major constraint to cattle productivity in the East African industry. The most important of these is East Coast Fever (ECF), of which the haemoprotozoan Theileria parva (Theiler) is the causative organism and the vector is Rhipicephalus appendiculatus Neumann, 1901.

There are about 30 million cattle in East Africa and most of them are kept in the ECF affected zones. Mortality from ECF has been estimated as 30-50% for calves,but upto 90% for adults which have not previously been exposed to the disease (FAO, 1976) and there is no commercially available treatment for the disease at present. There are many other tick-borne diseases affecting Man and his domestic animals which have local or general importance. In many cases the relationship between tick and disease is often not well understood. The losses caused by these diseases may be sudden and clearly seen. However, there are other less obvious, but persistent, effects which in total are probably of greater importance, and emphasize the need for tick control measures.

In order to control or prevent these diseases, many African countries are forced to spend heavily on tick control measures, mainly dipping and spraying, the effectiveness of which is greatly threatened by the development of resistance by the ticks to the acaricides in use. Yet exact details of the factors controlling tick distribution and activity are not thoroughly understood and much of the control effort may be misplaced.

The present study was therefore designed to investigate the effects of some environmental factors such as temperature and relative humidity on the water balance of the tick *Rhipicephalus appendiculatus* Newmann 1901, and *R. pulchellus* Gerstacker 1873, species with identical life cycles but occupying complimentary niches (Walker, 1974; Figure 1). The results will be of value in investigating survival, seasonal fluctuations and geographical distribution of these two species leading to a more rational and economic tick control programmes.

CHAPTER II

MATERIALS AND METHODS

II.1: Ticks

Rhipicephalus appendiculatus ticks were obtained from a laboratory colony at EAVRO, Muguga, all of which are of Kenyan origin and were maintained using the method of Bailey (1960). Engorged females of *R.pulchellus* were field collected from Longoswa in Kajiado District and bred into large numbers at Muguga.

All stages of the tick were fed in batches on the ears of Chinchilla Cross rabbits in cloth bags (Bailey, 1960; Irvin and Brocklesby, 1970). In order to eliminate any age-specific effects, only ticks 2-3 weeks old were used during my investigation. After moulting, the ticks were stored in 75x25mm flat bottomed glass tubes plugged with cotton wool which were held in aluminium cans containing damp sand, and kept in the dark at 27-28^{o}C and 85% RH.

Ticks were handled on a white enamel tray placed over a larger one containing water to trap any which tried to escape. They were manipulated only with a fine camel hair brush to avoid possible damage of the cuticle. Counting was done using a hand tally on a sheet of squared paper.

II.2: Tick storage for experimental purposes

The glass vials in which the unfed ticks were stored were thoroughly washed with detergent and then sterilized in order to kill fungi which normally appear at higher humidities and kill the ticks. Before use in experiments, they were kept in a desiccator at 27°C and 96% RH for 18 days.

II.3: Criteria for assessment of live and dead ticks

In their studies of water balance in larval ticks, Londt and Whitehead (1972) presumed death to have taken place when larvae could not move after stimulation by pressure from a needle, or when they floated in a weak soap solution. In my investigations three effective methods were adopted:

(a) Gently warming the vial with the palm of the hand or using a waterbath at 37°C.

(b) Breathing into the vial, since CO_2 is known to stimulate ticks.

(c) Touching any part of the tick with the tip of a camel hair brush.

After performing each of the above methods of stimulation, the ticks were observed under a binocular dissecting microscope. Those which did not respond by showing movement were counted as dead.

II.4: Temperature control and measurement

The temperatures were thermostatically controlled. They were provided by a "Hotpack incubator" Model.35270; through the manipulation of the temperature control switches with the aid of the instruction manual to the required temperature.

The Kilner jars in which the experiments were conducted at set relative humidities were then placed in the incubator. The temperature inside the incubator was monitored using an electrical resistance thermometer (Yellow Spring Instrument CO., Model 44 TD). The limits of any long-term fluctuations in temperature were recorded with a maximum/minimum mercury thermometer. Except when there was a failure of the main electrical supply, the temperature inside the incubator remained within $\pm$ 0.5^{o}C of the selected temperature.

II.5: Humidity control and measurement

Constant humidities were provided in still air. These were obtained in small, identically shaped desiccators considered adequate because they could provide a sealed atmosphere. The desiccators contained the appropriate saturated salt solution with an excess of solid (Winston and Bates, 1960) leaving a liquid layer of 4-5 mm above the solid salt. Table 1 shows the salts used together with the temperature ranges within which stable RHs were expected.

Salts were preferred because they are known to give stable, or nearly stable, RHs over a wide range of temperatures. They are reliable, easy to calibrate and do not require constant stirring (which liquid buffers would) although there is the possibility of a layer of unsaturated liquid forming at the surface of the salt solution. The

TABLE 1

Show the stability of relative humidity values over saturated salt solutions at various temperatures.

After Winston and Bates (1960).

TABLE 1

SALT	TEMPERATURE IN ^{o}C						
	2	5	10	15	20	25	30
Potassium sulphate K_2SO_4	99.0	98.5	98.5	99.0	98.0	97.5	96.5
Potassium chloride KCl	88.0	-	88.0	86.5	85.0	85.0	84.5
Sodium chloride NaCl	75.0	75.0	76.5	76.0	76.6	75.5	75.5
Sodium nitrite $NaNO_2$	-	-	-	-	65.0	64.0	63.0
Calcium nitrite $Ca(NO_3).4H_2O$	66.0	-	-	56. 0	55.5	50.5	47.0
Glucose	60.0	-	57.0	-	55.0	55.0	-
Magnesium chloride $MgCl_2.6H_2O$	35.0	34.5	34.0	34.0	33.0	32.5	32.5
Potassium acetate KC_2H_3O	23.0	-	21.0	-	20.0	22.5	22.0
Phosphorous pentoxide P_2O_5	00.0	-	00.0	00.0	00.0	00.0	00.0

- No value given

salts are safe to handle and, once prepared, the saturated solution can be used a number of times as they do not deteriorate as quickly as single phase buffers.

Commercially available cobalt thiocyanate paper was used to estimate RH. The stock of paper was always stored in the dark in sealed containers. Pieces measuring 1.5x1.5 cm were cut from the stock and suspended for two hours in the atmosphere to be measured. They were then folded into two and immediately transferred into liquid paraffin to prevent further changes in colour. The colour of the paper was then assessed aginst permanent glass colour standards provided by Lovibond Comparator discs used in a Lovibond Comparator Model 1000. The appropriate correction was then applied for papers matched at temperatures other than 20°C Solomon (1956).

Humidities greater than 96% were provided by distilled water. It is assumed that the RH was close to 98% since condensation was not observed.

II.6: Water loss, mortality, and critical equilibrium humidity

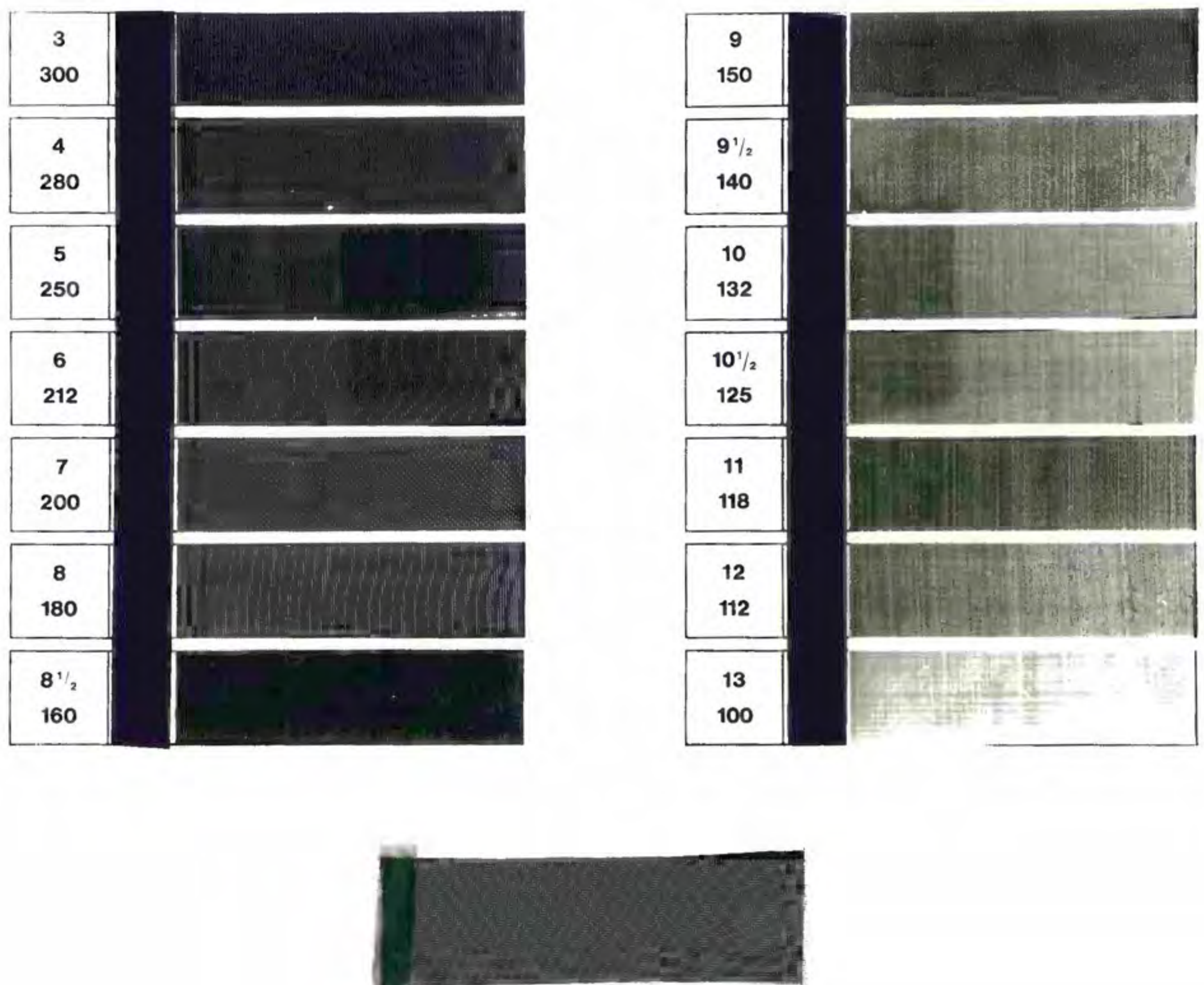
To determine water loss as well as CEH, ticks were exposed to 98% RH until they became fully hydrated. Before and after exposure, individual adults or groups of about 50 nymphs were confined in sealed numbered nylon packets (about 2cmx1cm, Plate 1). The ticks were then exposed to RHs of 0%, 20%, 33%, 55%, 62%, 75%, 85% and 96%, at 18°C.

PLATE 1

Photographs of specimens of nylon gauze including that used in this study, No.5. The second figure in each case is the pore size in microns.

The nylon cloth used was "NyBolt" Swiss silk bolting cloth Mfg Co. Ltd Zurich.

Plate 1


3
300
4
280
5
250
6
212
7
200
8
180
8½
160
9
150
9½
140
10
132
10½
125
11
118
12
112
13
100

23°C, 27°C and 31°C. Weighing was done on an Oertling analytical balance Model 407 to the nearest 0.01 mg. The ticks were weighed daily and any dead ticks noted. It was first established that the bags themselves were unaffected by changes in humidity. Each measurement was done in less than one minute so that gains or losses of moisture were negligible. The weight changes were expressed as percentage of the original weight. Curves characteristic of each RH were prepared. The RH value when weight change is zero was taken as CEH as defined earlier.

II.7: Site of water uptake

Unfed ticks of uniform size and assumed to be in the same physiological state were prepared as before, by storage for 2-3 weeks at 96% RH and 27°C until no further gain in weight occurred. This also allowed time for the complete elimination of all solid excretory material. The ticks were then dehydrated at 0% RH until they had lost about 27-33% of their initial weight and were assumed to be physiologically in need of water. Paraffin wax (M.P. 44-45°C) was then applied to various parts of the integument. The ticks were restrained by pressing them gently onto adhesive tape with the area to be treated exposed to view. In order to prevent the small amount of molten wax that was to be used from solidifying before it could be applied, the following method was developed.

A speck of wax was held with fine watch-makers forceps. The forceps were heated by transfer from an electric soldering iron controlled at 55°C by a rheostat. The droplet of molten wax which formed at the tip of the forceps could then be accurately directed to the site to be blocked and solidified as soon as the heat was removed. It was also possible to spread the wax evenly using the heated tips of the forceps Figure 2. The following parts of the body were covered:

- (i) anus
- (ii) spiracles
- (iii) entire ventral surface
- (iv) entire dorsal surface
- (v) mouthparts
- (vi) whole body
- (vii) untreated positive controls

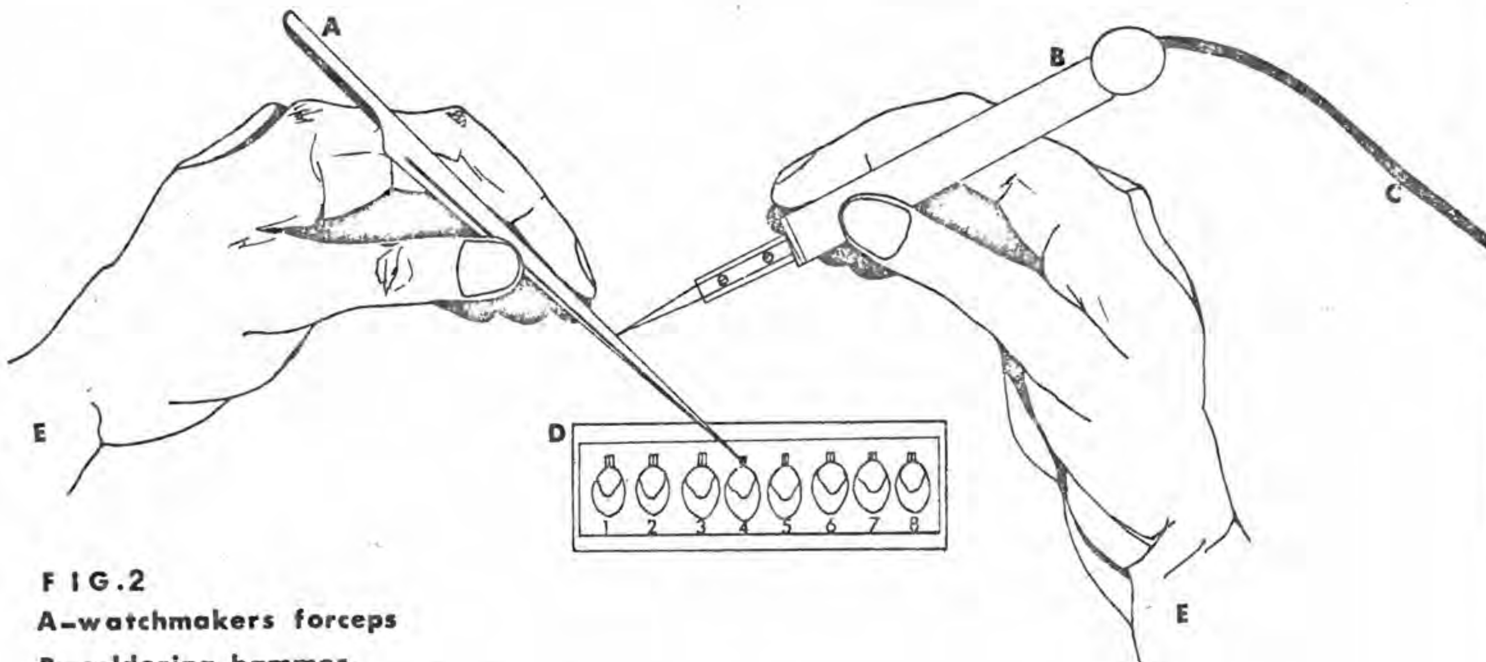
Item (vi) was performed in order to confirm that the wax was completely impermeable to water. Five replicates of each treatment were prepared and were then simultaneously exposed again to 96% RH and 27^{o}C. They were weighed daily for 12 days and the weight changes were expressed as percentage gains. Water vapour uptake curves were plotted and three-way analysis of variance performed to help in interpreting the results.

II.8: Measurement of cuticular permeability

The apparatus used is shown diagramatically in Figure 3. The temperature of the waterbath was controlled thermostatically and therefore maintained the required air stream at constant temperatures (Within $\pm$ 0.02^{o}C). The RH of the air being drawn through the exposure chamber was reduced to 0% by bubbling it through concentrated sulphuric

FIGURE 2

Diagramatic presentation of the method of wax application to the ticks' site to be blocked.



F I G.2
A-watchmakers forceps
B-soldering hammer
C-electric cable leading to a rheostat
D-ticks placed on a double sticker tape
E-left and right hands

FIGURE 3

The apparatus used for studying the permeability of the tick cuticule in dry air at different temperatures

A - flat-bottomed flask containing conc. H_2S0_4.

B & C - gas bottles containing conc. H_2S0_4.

D - spray trap flat-bottomed flask with glass wool.

E - air flow meter, range 0-1000 cc per minute.

G - copper coil.

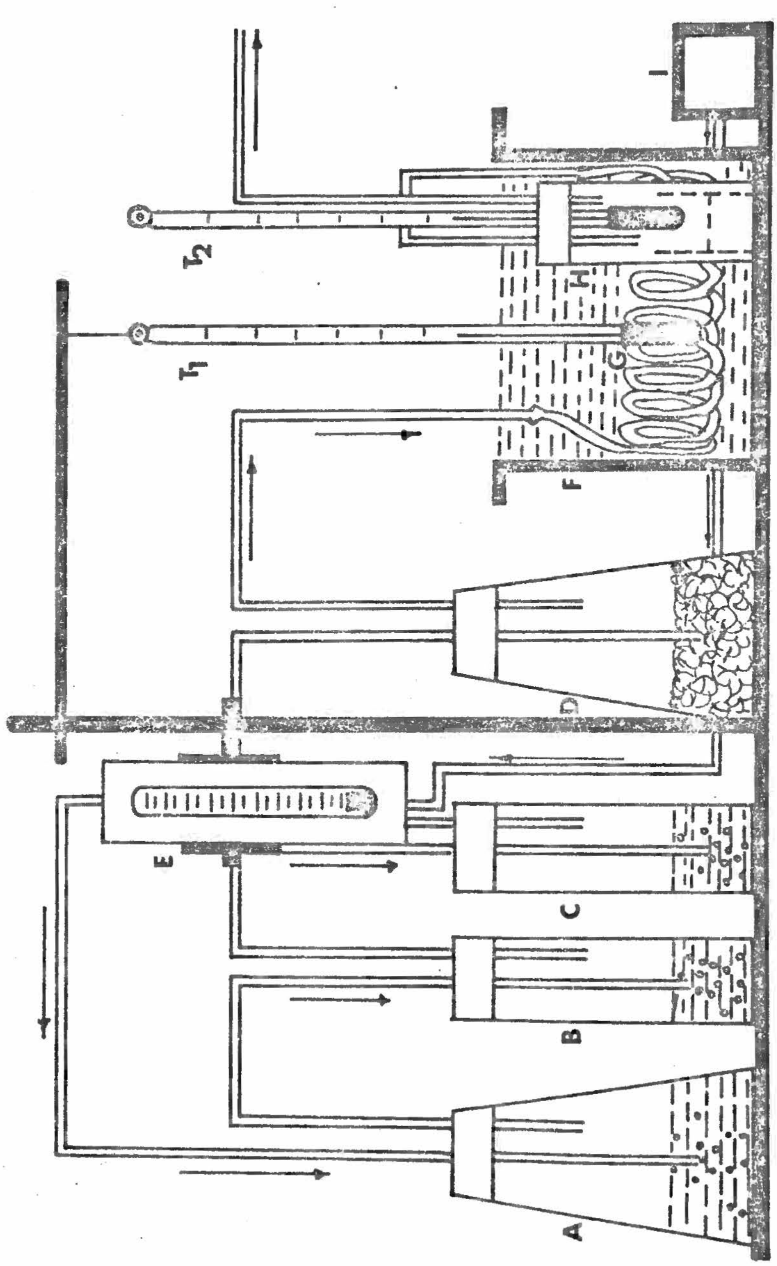
H - tick exposure chamber.

I - aquarium air pump.

T_1&T_2 -thermometers.

Temperatures used ranged from 10 - 70°C

FIG. 3



acid. Any aerosol droplets of acid were then removed in the fibre glass trap. A metered flow of 500 mℓ per minute was given by a small electric aquarium pump. It was assumed that it would be easier to maintain a stream of absolutely dry air than one at a low, but fluctuating RH. It was assumed that the shape of the exposure chamber had no effect on the rate of water loss from the ticks and also that the concentration of water vapour at a fixed small distance would also be constant.

According to Obenchain (1976) the rate of water loss from the tick surface is given by the equation:

$$= \log_{10} \left(W^{\frac{1}{3}}/S^{\frac{1}{2}}\right)$$

Where W = weight change in mg

S = scutal index (see below)

Both live and freshly killed ticks were used. Ammonia vapour was chosen for killing the ticks because it is known to have no effect on the cuticular waxes. Fresh ticks were used on each occasion.

II.9: Scutal index

Estimation of the effective surface area of a tick is difficult. Obenchain (1976) has shown that measurement of the sclerotized parts of the body is the most effective way of assessing its size. This is vital to an understanding of water balance, as explained earlier.

The scutal index (SI) is the product of the length of the scutum in the midline and its width between the eyes, obtained by measuring superimposed images of the tick scutum with a millimeter rule over a dissecting microscope fitted with a drawing tube. The image of the scutum of each tick used in the experiment was measured, and the relative measurements were expressed in ocular units (o.u), which were converted into mm reading by a conversion factor 1.00 o.u = 2.53 mm. Thus the SI and weight change of each individual tick were calculated and the cuticular permeability determined.

II.10: Depletion of food reserves

Since only the changes in lipid content for the two species on successive days of exposure at 0% RH was required, it was measured in the following manner.

Eleven groups, each of about 50 newly moulted ticks, were kept at 96% RH and 27°C, as before, to acquire full hydration. The ticks, now assumed to be all in the same state of water balance, were weighed on day 0 (initial live weight) and exposed to 0% RH. One group at a time was removed daily and weighed and then dried to constant weight at 60°C in a 2.5x10.0 cm Soxhlet extracting thimble. (The thimble had previously been dried to constant weight at 60°C for three days). Lipids were then extracted by boiling the dried, ticks together with the extraction thimble in diethyl ether in a Soxhlet apparatus for 36 hours. The thimble and the dried ticks were again weighed after further drying to constant weight at 60°C. The difference in weight gave the diethyl ether soluble lipids and this was expressed as percent dry weight.

II.11: Water and dry weight content determination

Fully hydrated ticks were prepared as before, were weighed on day 0 (initial live weight) and 11 groups, each of about 50 ticks were exposed to 0% RH and 27°C. One group at a time was removed daily and dried 60°C until no further loss of weight occurred, giving a final dry weight. The live weight, water content and dry weight of each sample were expressed as percentages of the initial live weight.

CHAPTER III

RESULTS

III.1: The effect of different humidities on water loss and CEH

The results of the calculations are given in Tables 2-20 and are shown graphically in Figures 4a-8c for proper interpretation.

The ticks, despite standardization, still varied in size, therefore only relative comparisons of water loss are given and the observations have been expressed as percent weight changes of the initial weight. Data for the nymphs of R.pulchellus were not obtained as the immature stages were not available when needed. Similarly, an insufficient number of nymphs of R.appendiculatus were obtained, and have only been presented for 18°C, 27°C and 31°C, over the entire humidity range. Mortality has also been observed at 23°C for the two species.

At all temperatures very little difference in the rates of water loss there was at 33%, 20% and 0% RHs. For the three curves plotted, at 0% RH, the rate of water loss was greater than at other humidities studied. Exposure to 20% and 0% RHs caused severe water loss at all temperatures, and both sexes of the two species had lost 60-64% of their original body weight by day 14. The nymphs had started dying by day 6 and by day 9, most of them were dead. The trend of water loss in the nymphs at these humidities was rather striking.

There was a rapid rate of water loss for the first three days at all temperatures, and thereafter a gradual loss until day 8 and 9 for nymphs exposed at 31°C where the curve starts levelling off Figures 8a-8c. This levelling off process was also seen at 55% and 33% RHs starting on day 11 and 12 of the period of exposure, and suggests that whatever body fluids were present in the nymphs were completely exhausted, leaving dry matter only.

An almost identical pattern of water loss was observed in males exposed to 62% and 55% RHs and in some cases for nymphs exposed to 62% and 75% RHs at all temperatures used. However, it should be noted that the pattern of water loss for nymphs and females of the two species exposed to 20% and 0% RHs was more rapid than that caused by exposure to 55% and 33% RHs at 31°C.

The general tendency of the rate of water loss as shown by the curves suggests a relationship between water loss and RHs below 85%. Below this value the ticks are unable to maintain their water status and the rate of water loss is much more rapid. However, the degree of water loss at both 75% and 62% RHs and in some cases at 62% and 55%RHs seem to be the same.

III.2: The critical equilibrium humidity

By plotting the gain or loss in weight with atmos-

TABLE 2-3

Mean weight changes of male and female *R.pulchellus* respectively (expressed as percentage of the initial weight) during exposure to different RHs at 18^{o}C.

TABLE 2

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-12.50	-16.91	-22.60	-28.97	-33.87	-36.32	-39.09
	± SE	0.62	0.55	1.14	0.90	1.51	0.99	0.89
20%RH	Mean %	-10.10	-12.46	-14.87	-17.73	-21.49	-24.49	-29.34
	± SE	0.38	0.50	0.81	0.95	1.44	1.93	2.29
33%RH	Mean %	-9.84	-12.20	-13.66	-16.60	-19.39	-23.91	-28.99
	± SE	0.92	0.92	0.91	1.03	1.60	1.76	1.22
55%RH	Mean %	-4.01	-6.52	-9.78	-13.06	-15.23	-19.26	-21.14
	± SE	0.57	0.59	0.64	0.42	0.35	0.39	0.61
62%RH	Mean %	-3.63	-4.80	-5.65	-6.07	-6.57	-7.07	-7.60
	± SE	0.41	0.38	0.36	0.55	0.49	0.49	0.53
75%RH	Mean %	-3.55	-4.77	-5.21	-6.58	-6.96	-7.21	-7.71
	± SE	0.29	0.37	0.31	0.40	0.40	0.34	0.18
85%RH	Mean %	-1.99	-1.99	+2.00	-2.01	-2.02	-2.01	-2.01
	± SE	0.20	0.21	0.21	0.20	0.19	0.18	0.18
96%RH	Mean %	+2.88	+2.86	+3.06	+2.98	+3.01	+2.91	+2.90
	± SE	0.10	0.09	0.23	0.15	0.16	0.10	0.09

TABLE 2 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-42.47	-46.43	-50.83	-55.19	-57.68	-60.60	-62.81
	± SE	1.30	1.44	1.16	1.44	1.41	0.67	1.10
20%RH	Mean %	-31.12	-35.58	-39.38	-42.05	-45.77	-49.61	-51.60
	± SE	1.71	2.02	1.53	1.51	1.52	1.15	1.73
33%RH	Mean %	-31.77	-34.31	-35.86	-39.29	-42.22	-43.67	-44.58
	± SE	0.84	0.86	1.04	0.74	0.94	1.05	0.75
55%RH	Mean %	-24.61	-28.33	-27.90	-29.42	-31.36	-33.27	-33.71
	± SE	0.40	0.69	0.40	0.63	0.27	0.56	0.46
62%RH	Mean %	-7.85	-8.52	-9.27	-9.77	-10.78	-11.53	-12.02
	± SE	0.61	0.48	0.56	0.56	0.50	0.27	0.22
75%RH	Mean %	-8.11	-8.38	-8.85	-9.38	-9.94	-10.19	-10.71
	± SE	0.07	0.15	0.10	0.15	0.24	0.17	0.28
85%RH	Mean %	-2.02	-2.01	-2.01	-2.01	-2.00	-2.00	-2.01
	± SE	0.18	0.19	0.19	0.19	0.19	0.19	0.19
96%RH	Mean %	+2.97	+2.97	+2.92	+2.89	+2.94	+2.90	+2.88
	± SE	0.07	0.07	0.05	0.08	0.06	0.08	0.09

TABLE 3

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-11.29	-15.20	-18.11	-26.37	-32.78	-37.89	-40.24
	± SE	1.08	0.86	1.22	1.34	1.20	1.16	0.89
20%RH	Mean %	-8.94	-10.17	-13.41	-18.28	-21.58	-26.80	-32.08
	± SE	1.04	1.08	1.08	0.89	1.12	1.11	1.10
33%RH	Mean %	-8.76	-11.20	-12.98	-15.98	-19.20	-22.86	-26.33
	± SE	0.97	0.92	1.03	1.06	0.93	0.84	0.87
55%RH	Mean %	-5.07	-6.73	-8.74	-11.66	-14.82	-19.11	-20.33
	± SE	0.73	0.88	0.71	0.70	0.88	1.01	1.17
62%RH	Mean %	-4.11	-5.78	-7.86	-9.67	-12.97	-15.23	-18.41
	± SE	0.84	0.86	0.94	1.04	0.93	0.94	1.01
75%RH	Mean %	-3.08	-4.81	-5.34	-6.85	-7.06	-7.11	-7.34
	± SE	0.44	0.48	0.44	0.40	0.35	0.92	0.56
85%RH	Mean %	-1.24	-1.38	-1.24	-1.70	-1.68	-1.66	-1.70
	± SE	0.54	0.48	0.33	0.52	0.61	0.36	0.37
96%RH	Mean %	+1.81	+1.83	+1.97	+2.01	+2.06	+2.34	+2.34
	± SE	0.27	0.31	0.38	0.31	0.31	0.33	0.28

TABLE 3 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-43.67	-46.01	-49.36	-54.27	-58.00	-60.23	-62.51
	± SE	1.15	0.89	1.06	1.15	1.08	1.07	1.12
20%RH	Mean %	-34.14	-37.39	-41.90	-44.27	-46.75	-49.35	-52.08
	± SE	0.93	0.74	0.63	0.90	0.96	0.94	0.97
33%RH	Mean %	-31.80	-35.00	-37.16	-39.48	-41.41	-44.26	-46.07
	± SE	1.06	1.07	1.06	0.80	0.93	1.04	1.03
55%RH	Mean %	-24.90	-28.11	-30.27	-32.14	-33.20	-35.31	-37.02
	± SE	1.15	1.20	1.22	1.23	1.20	1.14	1.14
62%RH	Mean %	-20.31	-24.19	-27.18	-29.16	-30.24	-32.27	-33.72
	± SE	1.08	0.83	0.54	0.75	0.81	0.91	0.93
75%RH	Mean %	-7.80	-8.07	-8.86	-8.96	-9.47	-10.06	-10.16
	± SE	0.62	0.58	0.61	0.54	0.38	0.42	0.58
85%RH	Mean %	-1.94	-2.01	-2.03	-2.07	-2.11	-2.10	-2.12
	± SE	0.37	0.37	0.80	0.86	0.74	0.62	0.67
96%RH	Mean %	+2.35	+2.40	+2.40	+2.40	+2.41	+2.40	+2.44
	± SE	0.19	0.20	0.18	0.20	0.18	0.19	0.18

TABLE 4-5

Mean weight changes of male and female *R.appendiculatus* respectively (expressed as percentage of the initial weight) during exposure to different RHs at 18°C.

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-10.86	-14.64	-19.47	-25.62	-31.18	-38.01	-43.12
	± SE	0.50	0.83	0.67	0.69	0.97	1.50	2.51
20%RH	Mean %	-7.24	-10.70	-14.53	-18.22	-21.44	-27.48	-32.89
	± SE	0.47	0.48	1.12	1.17	1.16	1.42	1.19
33%RH	Mean %	-6.97	-8.52	-10.74	-14.03	-17.66	-20.03	-24.16
	± SE	0.59	0.67	0.53	0.98	1.29	1.08	0.72
55%RH	Mean %	-5.52	-6.58	-7.94	-8.88	-10.26	-11.35	-12.15
	± SE	0.45	0.30	0.46	0.50	0.72	0.70	0.92
62%RH	Mean %	-4.51	-5.32	-5.96	-6.93	-8.02	-8.72	-9.59
	± SE	0.36	0.39	0.44	0.52	0.42	0.29	0.52
75%RH	Mean %	-3.91	-4.58	-6.33	-7.04	-7.82	-8.10	-8.73
	± SE	0.22	0.57	0.54	0.84	0.84	0.97	1.08
85%RH	Mean %	-0.99	-0.99	-0.97	-0.76	-0.74	-0.73	-0.70
	± SE	0.28	0.27	0.27	0.28	0.30	0.28	0.29
96%RH	Mean %	+0.73	+0.60	+0.74	+0.82	+1.02	+1.05	+1.01
	± SE	0.30	0.32	0.29	0.23	0.20	0.21	0.25

TABLE 4 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-47.99	-52.44	-55.59	-59.91	-61.86	-62.73	-64.26
	± SE	1.31	0.56	1.16	0.97	0.67	0.46	0.70
20%RH	Mean %	-37.86	-42.44	-47.54	-51.32	-53.53	-55.74	-56.57
	± SE	1.43	1.97	2.63	3.19	3.33	3.21	3.02
33%RH	Mean %	-27.51	-32.51	-36.01	-39.52	-42.92	-46.20	-50.04
	± SE	1.09	2.17	1.61	1.31	1.32	1.49	0.91
55%RH	Mean %	-12.85	-14.30	-15.91	-17.29	-18.21	-19.62	-20.86
	± SE	0.84	0.79	0.97	1.30	1.26	0.88	0.72
62%RH	Mean %	-10.29	-10.95	-11.65	-11.81	-12.45	-12.69	-12.87
	± SE	0.54	0.52	0.56	0.61	0.64	0.66	0.53
75%RH	Mean %	-9.57	-9.92	-10.41	-10.62	-10.94	-11.07	-11.24
	± SE	1.31	1.06	0.96	0.79	0.76	0.70	0.68
85%RH	Mean %	-0.70	-0.68	-0.70	-0.70	-0.68	-0.69	-0.69
	± SE	0.29	0.28	0.28	0.27	0.26	0.26	0.26
96%RH	Mean %	+1.06	+1.10	+1.17	+1.09	+1.08	+1.07	+1.07
	± SE	0.24	0.21	0.17	0.22	0.19	0.18	0.19

TABLE 5

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-13.11	-16.84	-21.29	-28.88	-32.72	-38.20	-41.46
	± SE	0.52	0.72	0.93	0.84	0.81	0.51	0.47
20%RH	Mean %	-11.15	-15.43	-21.14	-28.86	-33.21	-38.08	-42.82
	± SE	0.44	0.69	0.33	0.76	0.99	0.81	0.87
33%RH	Mean %	-11.01	-14.32	-18.31	-23.79	-29.81	-32.92	-38.17
	± SE	0.53	0.41	0.54	0.91	0.73	1.19	0.84
55%RH	Mean %	-8.49	-10.12	-11.49	-12.44	-13.78	-15.29	-17.05
	± SE	0.38	0.57	0.65	0.90	0.96	1.00	1.09
62%RH	Mean %	-4.69	-6.67	-7.63	-7.80	-8.46	-9.17	-9.68
	± SE	0.64	0.45	0.38	0.39	0.46	0.29	0.33
75%RH	Mean %	-3.78	-4.06	-4.93	-5.15	-5.63	-6.04	-7.02
	± SE	0.18	0.20	0.20	0.24	0.28	0.24	0.23
85%RH	Mean %	-2.36	-2.27	-2.20	-2.33	-2.27	-2.20	-2.36
	± SE	0.49	0.52	0.41	0.43	0.42	0.48	0.43
96%RH	Mean %	+1.38	+1.29	+1.26	+1.40	+1.42	+1.46	+2.24
	± SE	0.38	0.34	0.39	0.38	0.38	0.37	0.37

TABLE 5 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-46.55	-50.65	-54.08	-59.03	-61.31	-63.27	-64.47
	± SE	0.75	0.67	1.00	0.75	0.94	0.76	0.39
20%RH	Mean %	-47.36	-50.14	-52.82	-56.31	-59.32	-60.47	-60.98
	± SE	0.97	0.72	0.43	0.96	0.66	0.47	0.64
33%RH	Mean %	-41.48	-44.10	-46.56	-49.72	-51.50	-52.56	-54.04
	± SE	0.55	1.25	1.53	0.29	0.41	0.46	0.38
55%RH	Mean %	-19.07	-20.47	-22.33	-24.56	-26.07	-27.23	-28.68
	± SE	1.03	1.02	1.06	1.83	1.87	2.03	2.17
62%RH	Mean %	-10.59	-11.76	-12.25	-12.70	-13.44	-13.74	-14.04
	± SE	0.47	0.51	0.47	0.44	0.28	0.33	0.35
75%RH	Mean %	-7.41	-8.02	-8.17	-8.92	-9.26	-9.58	-9.70
	± SE	0.32	0.28	0.24	0.27	0.30	0.31	0.33
85%RH	Mean %	-2.36	-2.36	-2.35	-2.37	-2.39	-2.33	-2.35
	± SE	0.45	0.46	0.43	0.39	0.43	0.42	0.42
96%RH	Mean %	+1.45	+1.32	+1.12	+1.18	+1.25	+1.27	+1.30
	± SE	0.34	0.32	0.42	0.44	0.46	0.46	0.44

TABLE 6-7

Mean weight changes of male and female *R.pulchellus* respectively (expressed as percentage of the initial weight) during exposure to different RHs at 23^{o}C.

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-11.95	-16.49	-20.73	-28.50	-33.19	-36.67	-41.00
	± SE	o.30	0.37	0.46	0.34	0.67	1.10	0.75
20%RH	Mean %	-10.54	-14.44	-17.66	-21.14	-26.96	-30.10	-35.40
	± SE	0.09	0.70	0.69	0.77	0.51	0.19	0.47
33%RH	Mean %	-8.92	-10.09	-14.54	-19.25	-23.22	-28.38	-31.54
	± SE	0.26	0.40	0.22	0.15	0.85	0.66	0.29
55%RH	Mean %	-3.67	-5.37	-8.21	-10.41	-12.33	-15.09	-17.91
	± SE	0.07	0.42	0.30	0.52	0.80	1.25	0.85
62%	Mean %	-3.41	-4.48	-5.27	-6.03	-6.88	-7.62	-8.70
	± SE	0.17	0.19	0.33	0.32	0.26	0.21	0.41
75%RH	Mean %	-2.31	-2.91	-3.72	-4.17	-4.82	-5.57	-6.12
	± SE	0.05	0.15	0.22	0.20	0.14	0.19	0.20
85%RH	Mean %	-1.23	-1.22	-1.22	-1.23	-1.23	-1.24	-1.24
	± SE	0.02	0.02	0.04	0.01	0.01	0.01	0.01
96%RH	Mean %	+2.61	+2.94	+2.96	+3.22	+3.38	+3.46	+3.66
	± SE	0.07	0.19	0.10	0.12	0.18	0.09	0.13

TABLE 6 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-44.75	-48.20	-51.74	-56.39	-59.30	-61.49	-62.23
	± SE	0.28	0.31	0.64	0.72	0.81	0.36	0.22
20%RH	Mean %	-38.83	-43.29	-46.82	-49.88	-52.91	-53.50	-55.06
	± SE	0.39	0.53	0.17	0.57	0.82	0.80	0.84
33%RH	Mean %	-34.92	-36.97	-40.14	-42.77	-45.22	-46.99	-57.23
	± SE	0.99	1.11	0.73	0.91	0.74	0.42	0.39
55%RH	Mean %	-20.80	-21.06	-23.87	-25.35	-27.67	-30.27	-33.14
	± SE	1.08	1.20	1.25	0.55	0.38	0.30	0.32
62%RH	Mean %	-9.84	-10.57	-10.86	-11.34	-11.72	-12.21	-12.47
	± SE	0.37	0.40	0.40	0.37	0.36	0.26	0.28
75%RH	Mean %	-6.72	-7.60	-8.08	-8.48	-8.72	-9.09	-9.66
	± SE	0.28	0.31	0.25	0.19	0.21	0.17	0.16
85%RH	Mean %	-1.24	-1.25	-1.25	-1.26	-1.26	-1.26	-1.26
	± SE	0.01	0.01	0.01	0.01	0.01	0.01	0.01
96%RH	Mean %	+3.57	+3.25	+3.46	+3.47	+3.44	+3.45	+3.38
	± SE	0.08	0.13	0.22	0.21	0.20	0.20	0.20

TABLE 7

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-10.82	-12.89	-20.85	-25.54	-30.56	-40.42	-45.80
	± SE	0.60	1.56	1.89	2.07	1.67	1.77	2.71
20%RH	Mean %	-9.18	-11.15	-17.07	-20.97	-25.11	-30.99	-35.59
	± SE	1.73	1.56	1.43	1.64	1.76	2.09	2.11
33%RH	Mean %	-8.66	-12.41	-14.98	-16.83	-18.74	-24.08	-29.25
	± SE	0.75	0.69	0.77	0.54	0.50	2.20	2.02
55%RH	Mean %	-3.57	-5.19	-7.29	-8.39	-9.64	-10.95	-12.24
	± SE	0.54	0.69	1.20	0.81	0.91	1.28	1.30
62%RH	Mean %	-2.89	-4.07	-4.96	-7.32	-8.89	-10.75	-12.23
	± SE	0.45	0.43	0.43	0.72	1.02	1.39	1.48
75%RH	Mean %	-2.55	-3.14	-5.07	-6.03	-6.50	-7.89	-7.98
	± SE	0.91	0.96	1.20	1.33	1.09	1.44	1.27
85%RH	Mean %	-0.45	-0.51	-0.55	-0.64	-0.75	-0.84	-0.75
	± SE	0.09	0.08	0.12	0.09	0.10	0.14	0.13
96%RH	Mean %	+3.22	+4.79	+5.12	+3.84	+5.18	+4.04	+6.29
	± SE	0.91	0.96	1.21	0.89	1.27	1.36	1.34

TABLE 7 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-50.77	-52.77	-56.30	-58.32	-58.96	-60.46	-61.05
	± SE	2.73	1.78	2.38	2.39	2.32	1.95	2.06
20%RH	Mean %	-41.89	-45.65	-49.21	-50.49	-52.93	-54.34	-55.62
	± SE	2.35	2.11	1.91	1.69	1.10	1.08	1.05
33%RH	Mean %	-34.41	-38.57	-42.74	-45.86	-49.10	-49.10	-50.56
	± SE	2.06	3.17	3.29	3.44	1.93	1.92	3.17
55%RH	Mean %	-13.29	-14.29	-15.24	-16.28	-16.92	-17.64	-18.34
	± SE	1.32	1.43	1.41	1.64	1.65	1.71	1.78
62%RH	Mean %	-14.22	-15.17	-16.20	-17.20	-18.11	-18.90	-19.21
	± SE	2.20	2.34	2.45	2.62	2.61	2.71	2.70
75%RH	Mean %	-9.00	-8.16	-9.13	-10.04	-10.06	-10.00	-11.02
	± SE	1.36	1.27	0.80	0.96	0.96	1.06	1.22
85%RH	Mean %	-0.72	-0.75	-0.75	-0.75	-0.75	-0.67	-0.77
	± SE	0.13	0.10	0.06	0.09	0.09	0.08	0.10
96%RH	Mean %	+4.16	+4.92	+2.91	+4.83	+3.03	+4.93	+4.53
	± SE	0.92	1.26	0.89	1.67	0.87	1.47	1.17

TABLE 8-9

Mean weight changes of male and female R.appendiculatus respectively (expressed as percentage of the initial weight) during exposure to different RHs at 23°C.

TABLE 8

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-11.29	-17.01	-22.86	-27.54	-32.31	-36.76	-39.44
	± SE	0.35	0.27	0.34	0.24	0.22	0.48	0.38
20%RH	Mean %	-10.51	-14.46	-17.67	-21.53	-25.96	-30.41	-35.43
	± SE	0.11	0.75	0.71	1.07	0.84	0.07	0.53
33%RH	Mean %	-9.57	-12.01	-15.69	-18.95	-23.14	-28.86	-33.45
	± SE	0.17	0.39	0.27	0.20	0.57	0.51	0.54
55%RH	Mean %	-3.10	-7.33	-10.33	-13.00	-16.38	-19.36	-21.18
	± SE	0.33	0.35	0.82	0.64	0.52	0.74	0.67
62%RH	Mean %	-3.96	-5.11	-6.34	-6.96	-7.75	-8.64	-9.38
	± SE	0.19	0.30	0.39	0.50	0.50	0.62	0.57
75%RH	Mean %	-3.22	-3.67	-4.28	-5.15	-6.04	-6.99	-7.20
	± SE	0.27	0.20	0.28	0.58	0.66	0.57	0.62
85%RH	Mean %	-1.17	-1.21	-1.22	-1.25	-1.28	-1.30	-1.32
	± SE	0.04	0.03	0.03	0.02	0.04	0.05	0.06
96%RH	Mean %	+2.39	+2.57	+2.54	+2.79	+3.37	+2.91	+3.67
	± SE	0.12	0.12	0.18	0.15	0.19	0.25	0.12

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-45.53	-49.25	-53.87	-55.47	-61.76	-62.98	-63.48
	± SE	0.72	0.25	0.36	0.51	0.80	0.57	0.42
20%RH	Mean %	-39.44	-42.97	-46.03	-50.17	-53.94	-56.15	-58.52
	± SE	0.21	1.73	1.72	1.02	1.18	1.17	1.16
33%RH	Mean %	-34.70	-37.02	-40.45	-44.02	-47.78	-50.39	-52.25
	± SE	0.65	0.45	0.37	0.97	0.55	0.36	0.24
55%RH	Mean %	-24.71	-26.48	-27.76	-30.09	-31.49	-32.70	-34.33
	± SE	1.06	0.72	1.13	0.81	0.53	0.41	0.35
62%RH	Mean %	-10.26	-11.08	-11.99	-12.76	-13.57	-14.21	-14.53
	± SE	0.47	0.58	0.62	0.37	0.27	0.26	0.18
75%RH	Mean %	-8.00	-8.26	-8.66	-9.32	-9.82	-10.19	-10.70
	± SE	0.68	0.69	0.57	0.47	0.43	0.38	0.46
85%RH	Mean %	-1.32	-1.31	-1.33	-1.30	-1.29	-1.34	-1.32
	± SE	0.05	0.05	0.06	0.05	0.05	0.06	0.04
96%RH	Mean %	+3.52	+2.59	+2.39	+2.45	+2.68	+3.68	+3.93
	± SE	0.17	0.16	0.18	0.19	0.23	0.16	0.25

TABLE 9

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-10.07	-16.08	-18.12	-20.94	-28.94	-32.57	-37.53
	± SE	0.98	1.46	1.66	1.79	1.65	1.11	2.61
20%RH	Mean %	-11.82	-13.31	-18.52	-20.59	-27.40	-32.58	-41.49
	± SE	2.12	2.40	2.16	2.37	3.34	2.68	1.30
33%RH	Mean %	-8.89	-10.20	-15.76	-18.31	-23.74	-28.01	-31.44
	± SE	1.82	2.06	1.61	0.96	1.07	1.30	1.63
55%RH	Mean %	-3.53	-6.87	-8.07	-11.88	-15.64	-19.45	-23.33
	± SE	1.08	1.44	1.68	1.45	2.37	3.69	3.89
62%RH	Mean %	-2.02	-2.84	-3.74	-7.08	-10.93	-11.69	-13.18
	± SE	0.41	0.49	0.56	1.09	1.58	1.94	1.94
75%RH	Mean %	-2.07	-2.18	-3.86	-5.88	-7.79	-8.06	-8.86
	± SE	0.81	0.80	1.07	0.81	1.13	1.08	1.08
85%RH	Mean %	-0.26	-0.24	-0.40	-0.32	-0.26	-0.23	-0.21
	± SE	0.07	0.09	0.08	0.08	0.16	0.07	0.04
96%RH	Mean %	+0.94	+2.49	+3.77	+3.06	+4.17	+3.96	+2.38
	± SE	0.34	0.58	0.81	1.43	1.07	1.13	0.95

TABLE 9 Cont.

TREATMENT		8	9	10	11	12	13	14
		DAYS OF EXPOSURE						
0%RH	Mean %	-44.10	-46.63	-51.79	-55.85	-61.01	-62.29	-62.68
	± SE	1.98	2.01	1.83	1.68	1.63	1.88	1.98
20%RH	Mean %	-47.88	-54.20	-54.57	-54.36	-56.96	-59.52	-61.58
	± SE	3.01	3.22	4.41	2.37	3.33	2.33	2.52
33%RH	Mean %	-38.67	-40.40	-45.68	-49.30	-52.11	-55.06	-55.06
	± SE	1.98	1.27	1.30	1.30	1.40	1.47	1.47
55%RH	Mean %	-24.33	-28.07	-30.15	-31.91	-34.35	-34.93	-33.84
	± SE	3.95	4.33	5.03	5.62	6.78	6.99	8.19
62%RH	Mean %	-14.93	-16.53	-17.65	-19.38	-20.42	-21.42	-21.42
	± SE	2.19	2.52	2.91	3.06	3.25	3.17	3.22
75%RH	Mean %	-9.16	-9.83	-9.96	-10.00	-10.18	-10.39	-10.64
	± SE	1.11	0.82	0.83	0.91	0.93	0.93	0.93
85%RH	Mean %	-0.34	-0.29	-0.28	-0.23	-0.24	-0.29	-0.32
	± SE	0.07	0.08	0.07	0.05	0.08	0.09	0.09
96%RH	Mean %	+2.57	+2.17	+1.81	+1.95	+2.07	+2.49	+2.30
	± SE	0.52	0.65	1.09	1.36	1.32	1.24	1.39

TABLE 10-11

Mean weight changes of male and female R.pulchellus respectively (expressed as percentage of the initial weight) during exposure to different RHs at 27°C.

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-8.26	-12.96	-17.98	-22.74	-27.68	-32.03	-36.43
	± SE	1.71	1.55	2.18	1.64	1.31	0.97	0.91
20%RH	Mean %	-6.21	-8.97	-11.95	-16.85	-20.39	-24.74	-31.65
	± SE	1.24	1.86	2.05	1.80	2.56	3.18	3.42
33%RH	Mean %	-5.27	-7.57	-11.06	-15.07	-19.69	-23.91	-28.26
	± SE	0.88	0.76	1.02	1.46	1.78	1.53	1.97
55%RH	Mean %	-5.72	-7.29	-9.81	-12.11	-13.06	-13.88	-15.04
	± SE	1.08	0.92	1.41	2.52	2.36	2.27	2.41
62%RH	Mean %	-3.76	-4.97	-5.95	-7.32	-8.45	-8.70	-10.04
	± SE	0.45	0.46	0.62	0.65	0.50	0.55	0.78
75%RH	Mean %	-3.40	-4.22	-5.71	-6.96	-7.73	-8.69	-9.59
	± SE	0.42	0.43	0.49	0.76	0.62	0.36	0.29
85%RH	Mean %	-2.87	-2.87	-2.64	-2.62	-2.61	-2.60	-2.57
	± SE	0.31	0.31	0.23	0.23	0.22	0.22	0.22
96%RH	Mean %	+2.54	+2.23	+2.40	+2.51	+2.59	+2.61	+2.60
	± SE	0.37	0.44	0.38	0.33	0.32	0.31	0.23

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-40.27	-45.50	-48.29	-56.86	-59.97	-62.54	-63.13
	± SE	0.59	1.24	1.67	1.90	1.60	0.79	0.73
20%RH	Mean %	-36.46	-40.86	-45.83	-51.58	-55.98	-56.97	-57.88
	± SE	3.88	3.65	2.46	3.25	2.67	2.38	2.14
33%RH	Mean %	-32.46	-37.70	-42.33	-48.68	-51.33	-53.58	-55.80
	± SE	2.00	2.74	2.81	3.24	2.79	2.65	2.00
55%RH	Mean %	-16.87	-18.19	-19.68	-21.68	-23.32	-23.62	-24.02
	± SE	2.41	2.48	2.06	1.34	0.89	0.78	0.73
62%RH	Mean %	-11.08	-12.02	-12.66	-12.89	-13.19	-13.39	-13.67
	± SE	0.71	0.73	0.61	0.56	0.48	0.52	0.40
75%RH	Mean %	-10.55	-11.00	-12.00	-12.36	-12.98	-13.19	-13.23
	± SE	0.26	0.20	0.64	0.54	0.73	0.84	0.80
85%RH	Mean %	-2.55	-2.48	-2.46	-2.38	-2.36	-2.34	-2.33
	± SE	0.23	0.24	0.24	0.19	0.19	0.20	0.20
96%RH	Mean %	+2.98	+2.74	+2.74	+2.63	+2.59	+2.61	+2.64
	± SE	0.36	0.28	0.27	0.30	0.29	0.28	0.26

TABLE 11

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-13.02	-18.39	-22.57	-30.13	-33.77	-37.79	-40.72
	± SE	0.36	0.36	0.26	0.39	0.66	0.76	0.30
20%RH	Mean %	-12.61	-16.97	-20.47	-24.71	-29.58	-32.51	-36.71
	± SE	0.55	1.00	1.80	1.44	0.86	0.89	0.41
33%RH	Mean %	-11.45	-14.26	-17.74	-21.25	-28.57	-31.08	-36.68
	± SE	0.42	0.33	0.30	0.40	0.34	0.55	0.54
55%RH	Mean %	-8.24	-9.48	-10.62	-12.17	-13.91	-16.13	-17.70
	± SE	0.24	0.30	0.60	0.83	1.05	1.08	0.91
62%RH	Mean %	-4.33	-5.71	-7.27	-8.24	-9.14	-9.79	-11.58
	± SE	0.27	0.48	0.36	0.37	0.33	0.26	0.21
75%RH	Mean %	-3.44	-3.72	-4.56	-4.83	-5.47	-6.11	-6.66
	± SE	0.20	0.19	0.10	0.02	0.17	0.18	0.23
85%RH	Mean %	-1.83	-1.88	-1.90	-1.91	-1.93	-2.01	-2.01
	± SE	0.12	0.14	0.14	0.14	0.13	0.12	0.12
96%RH	Mean %	+2.97	+3.07	+3.08	+3.19	+3.43	+3.10	+2.78
	± SE	0.06	0.05	0.23	0.18	0.37	0.21	0.06

TABLE 11 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-44.18	-49.58	-53.33	-58.39	-60.62	-62.84	-63.09
	± SE	0.71	0.40	0.44	0.51	0.49	0.31	0.13
20%RH	Mean %	-38.95	-45.30	-50.41	-52.34	-54.67	-55.43	-56.01
	± SE	0.45	0.38	0.38	0.34	0.43	0.20	0.06
33%RH	Mean %	-41.06	-41.08	-44.65	-48.65	-51.76	-53.85	-54.90
	± SE	0.55	0.48	0.31	0.40	0.50	0.16	0.12
55%RH	Mean %	-19.81	-22.19	-24.88	-28.44	-30.89	-33.25	-34.30
	± SE	1.16	0.72	0.48	0.77	0.70	0.54	0.51
62%RH	Mean %	-12.43	-13.18	-13.70	-14.35	-14.79	-15.09	-15.31
	± SE	0.25	0.15	0.08	0.10	0.13	0.15	0.13
75%RH	Mean %	-7.50	-8.27	-8.94	-9.23	-9.48	-9.68	-9.85
	± SE	0.18	0.22	0.11	0.15	0.17	0.14	0.13
85%RH	Mean %	-1.97	-1.97	-1.98	-1.98	-1.97	-1.97	-1.97
	± SE	0.12	0.11	0.11	0.11	0.11	0.11	0.11
96%RH	Mean %	+2.80	+2.84	+2.91	+2.90	+2.86	+2.95	+3.00
	± SE	0.12	0.06	0.09	0.05	0.06	0.07	0.06

TABLE 12-13

Mean weight changes of male and female *R.appendiculatus* respectively (expressed as percentage of the initial weight) during exposure to different RHs at 27°C.

TABLE 12

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-10.09	-13.37	-18.89	-25.37	-30.44	-36.64	-41.15
	± SE	0.93	0.68	0.45	0.75	0.71	0.86	0.72
20%RH	Mean %	-7.06	-12.98	-17.83	-20.96	-25.01	-29.24	-43.05
	± SE	0.45	0.97	1.04	1.54	1.61	1.35	1.33
33%RH	Mean %	-6.23	-8.04	-10.75	-14.41	-20.23	-24.55	-29.32
	± SE	0.98	1.60	1.91	2.11	2.16	2.14	3.31
55%RH	Mean %	-4.18	-5.92	-6.94	-8.24	-9.21	-10.83	-12.58
	± SE	0.63	0.37	0.37	0.47	0.82	0.45	0.58
62%RH	Mean %	-4.52	-5.46	-6.52	-7.54	-8.52	-9.61	-10.71
	± SE	0.49	0.61	0.70	0.92	1.22	1.25	1.19
75%RH	Mean %	-3.55	-4.08	-5.26	-6.17	-7.41	-7.92	-8.88
	± SE	0.15	0.30	0.68	0.93	1.45	1.48	1.31
85%RH	Mean %	-2.55	-2.56	-2.57	-3.20	-2.93	-3.20	-2.94
	± SE	0.13	0.52	0.33	0.88	0.32	0.85	0.76
96%RH	Mean %	+2.30	+2.32	+2.37	+2.46	+2.41	+1.93	+2.31
	± SE	0.28	0.40	0.42	0.37	0.44	0.54	0.40

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-46.91	-51.44	-54.53	-58.01	-62.22	-63.34	-63.99
	± SE	1.31	0.84	1.51	1.25	1.91	1.34	0.85
20%RH	Mean %	-34.05	-40.15	-42.97	-45.87	-51.41	-53.34	-60.76
	± SE	1.33	0.83	0.92	1.92	1.05	1.47	0.99
33%RH	Mean %	-33.59	-37.15	-41.77	-45.48	-46.82	-48.59	-49.79
	± SE	3.16	3.05	2.99	1.24	1.63	0.92	0.82
55%RH	Mean %	-14.39	-15.54	-17.26	-22.61	-21.91	-22.61	-23.09
	± SE	1.02	1.01	1.08	0.79	0.88	0.79	0.60
62%RH	Mean %	-11.09	-11.47	-12.32	-12.42	-13.25	-13.66	-13.98
	± SE	1.22	1.35	1.73	1.73	1.57	1.46	1.42
75%RH	Mean %	-9.08	-9.01	-9.83	-10.83	-11.39	-11.50	-12.03
	± SE	1.46	1.50	1.23	0.75	0.71	0.72	0.81
85%RH	Mean %	-3.02	-3.26	-3.13	-3.23	-3.10	-2.93	-2.59
	± SE	0.70	0.63	0.60	0.57	0.89	0.20	0.55
96%RH	Mean %	+2.17	+2.28	+2.15	+2.36	+2.16	+2.06	+1.82
	± SE	0.37	0.35	0.40	0.33	0.43	0.62	0.53

TABLE 13

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-12.09	-16.20	-22.95	-29.36	-35.04	-37.59	-41.26
	± SE	0.36	0.96	0.37	0.36	0.85	0.84	0.49
20%RH	Mean %	-12.72	-18.60	-23.72	-27.37	-31.30	-34.06	-36.84
	± SE	0.39	0.69	1.30	1.35	1.11	0.95	1.07
33%RH	Mean %	-12.34	-15.30	-17.89	-22.99	-26.81	-31.21	-36.15
	± SE	0.25	0.23	0.22	0.52	0.46	0.43	0.23
55%RH	Mean %	-8.13	-9.47	-10.96	-12.42	-14.37	-19.04	-22.16
	± SE	0.16	0.42	0.19	0.25	0.21	0.26	0.54
62%RH	Mean %	-0.43	-5.15	-6.44	-7.90	-9.53	-10.70	-11.86
	± SE	0.27	0.26	0.17	0.36	0.17	0.36	0.31
75%RH	Mean %	-3.06	-3.55	-4.55	-5.60	-6.63	-7.56	-7.72
	± SE	0.15	0.20	0.22	0.21	0.21	0.22	0.18
85%RH	Mean %	-1.78	-1.82	-1.82	-1.81	-1.84	-1.83	-1.80
	± SE	0.07	0.09	0.09	0.10	0.09	0.07	0.08
96%RH	Mean %	+3.25	+2.97	+3.31	+2.95	+2.96	+3.40	+2.78
	± SE	0.32	0.27	0.19	0.25	0.20	0.28	0.17

TABLE 13 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-44.58	-48.59	-52.06	-57.40	-59.10	-61.91	-63.19
	± SE	0.29	0.37	0.64	0.49	0.61	0.50	0.83
20%RH	Mean %	-41.05	-46.17	-50.34	-52.00	-53.34	-55.80	-56.12
	± SE	0.56	0.27	0.48	0.49	0.35	1.00	1.09
33%RH	Mean %	-39.93	-44.93	-48.62	-50.40	-52.42	-54.15	-55.67
	± SE	1.44	1.64	0.92	0.89	1.19	0.37	0.65
55%RH	Mean %	-24.93	-28.31	-30.57	-32.66	-33.60	-33.91	-35.08
	± SE	0.83	0.64	0.60	0.96	0.80	0.53	0.82
62%RH	Mean %	-12.70	-13.21	-13.44	-13.64	-13.77	-13.78	-14.07
	± SE	0.11	0.09	0.16	0.18	0.23	0.34	0.43
75%RH	Mean %	-8.00	-8.24	-8.62	-8.93	-9.21	-10.55	-12.18
	± SE	0.18	0.16	0.17	0.26	0.27	0.23	0.49
85%RH	Mean %	-1.83	-1.83	-1.85	-1.87	-1.90	-1.85	-1.86
	± SE	0.10	0.10	0.09	0.09	0.08	0.09	0.09
96%RH	Mean %	+2.90	+2.93	+2.83	+2.82	+3.06	+2.95	+2.91
	± SE	0.27	0.28	0.20	0.18	0.23	0.09	0.11

TABLE 14-15

Mean weight changes of male and female R.pulchellus respectively (expressed as percentage of the initial weight) during exposure to different RHs at 31°C.

TABLE 14

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-9.46	-12.28	-15.15	-19.55	-26.38	-33.51	-38.68
	± SE	0.61	0.93	0.82	0.75	1.21	1.52	1.52
20%RH	Mean %	-8.67	-13.02	-16.25	-20.93	-26.89	-31.57	-35.90
	± SE	0.66	0.28	0.86	1.04	1.24	1.27	1.00
33%RH	Mean %	-8.59	-11.83	-14.56	-17.48	-20.30	-23.66	-28.91
	± SE	0.36	0.60	0.41	0.58	0.63	1.15	1.47
55%RH	Mean %	-8.39	-9.92	-11.56	-13.01	-14.00	-15.99	-18.32
	± SE	0.32	0.55	0.65	0.46	0.34	0.47	1.01
62%RH	Mean %	-8.18	-10.72	-11.77	-13.24	-14.62	-15.81	-16.55
	± SE	0.57	0.37	0.36	0.35	0.52	0.24	0.34
75%RH	Mean %	-6.67	-9.02	-10.31	-11.71	-12.53	-13.47	-14.16
	± SE	0.32	0.44	0.47	0.60	0.57	0.41	0.39
85%RH	Mean %	-3.47	-3.51	-3.53	-3.58	-3.66	-3.69	-3.71
	± SE	0.29	0.30	0.30	0.30	0.31	0.31	0.30
96%RH	Mean %	+2.84	+2.84	+2.94	+2.93	+3.00	+3.00	+2.98
	± SE	0.18	0.20	0.20	0.20	0.21	0.21	0.21

TABLE 14 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-45.79	-49.89	-52.88	-57.20	-60.54	-62.72	-63.69
	± SE	2.19	1.47	1.44	1.15	1.16	0.65	0.60
20%RH	Mean %	-39.62	-42.96	-48.85	-53.74	-59.20	-61.10	-62.11
	± SE	0.44	0.77	0.38	0.41	0.27	0.36	0.53
33%RH	Mean %	-32.97	-38.13	-42.52	-45.89	-49.68	-50.47	-50.83
	± SE	1.08	0.64	0.72	0.74	0.24	0.20	0.14
55%RH	Mean %	-20.16	-24.16	-26.69	-27.86	-28.51	-28.83	-30.05
	± SE	0.94	0.94	1.81	1.81	1.76	1.56	1.34
62%RH	Mean %	-18.81	-20.38	-21.09	-22.26	-22.91	-23.63	-24.45
	± SE	0.28	0.43	0.42	0.50	0.43	0.41	0.19
75%RH	Mean %	-14.67	-15.40	-15.93	-16.37	-16.99	-17.43	-17.88
	± SE	0.32	0.38	0.34	0.33	0.19	0.13	0.24
85%RH	Mean %	-3.76	-3.77	-3.79	-3.77	-3.78	-3.82	-3.80
	± SE	0.34	0.34	0.34	0.34	0.33	0.32	0.34
96%RH	Mean %	+3.06	+3.10	+3.12	+3.14	+3.14	+3.14	+3.15
	± SE	0.21	0.18	0.18	0.16	0.16	0.16	0.16

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-11.86	-17.16	-22.17	-28.70	-33.60	-37.07	-41.35
	± SE	0.99	0.48	0.80	1.33	0.74	0.72	0.78
20%RH	Mean %	-10.28	-15.64	-19.74	-24.46	-29.93	-31.31	-36.79
	± SE	0.66	0.61	0.74	1.33	1.06	1.47	2.24
33%RH	Mean %	-13.92	-16.46	-19.96	-25.50	-30.46	-36.18	-41.38
	± SE	0.51	0.65	0.57	0.51	0.74	0.92	0.82
55%RH	Mean %	-7.60	-10.10	-11.97	-14.32	-16.38	-18.90	-21.31
	± SE	0.66	0.54	0.81	1.57	1.76	1.62	2.46
62%RH	Mean %	-6.84	-8.53	-9.38	-11.17	-12.44	-13.58	-14.93
	± SE	0.43	0.71	0.83	0.63	0.89	0.77	0.62
75%RH	Mean %	-3.98	-5.21	-6.70	-7.52	-8.38	-9.15	-10.47
	± SE	0.52	0.57	0.63	0.85	0.76	0.99	1.16
85%RH	Mean %	-3.78	-3.79	-3.56	-3.69	-3.71	-3.94	-3.83
	± SE	0.20	0.23	0.39	0.33	0.34	0.33	0.42
96%RH	Mean %	+2.90	+2.91	+2.95	+2.98	+3.03	+3.06	+3.01
	± SE	0.05	0.06	0.05	0.05	0.09	0.09	0.06

TABLE 15 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-45.51	-49.43	-53.74	-57.67	-60.76	-62.94	-63.20
	± SE	1.05	0.52	0.82	1.18	0.56	0.83	0.80
20%RH	Mean %	-41.82	-46.21	-51.24	-52.72	-57.53	-59.18	-60.12
	± SE	0.53	0.78	0.44	0.77	1.21	0.65	0.43
33%RH	Mean %	-45.63	-50.25	-51.46	-53.01	-53.90	-54.82	-57.42
	± SE	1.10	1.76	1.61	1.24	1.33	1.62	1.32
55%RH	Mean %	-25.13	-27.72	-30.99	-31.99	-34.49	-35.40	-36.95
	± SE	1.73	1.29	1.12	1.23	1.44	1.30	1.30
62%RH	Mean %	-15.46	-17.08	-18.55	-20.22	-21.61	-22.33	-23.89
	± SE	0.71	0.94	1.43	1.40	0.94	0.86	0.72
75%RH	Mean %	-11.07	-11.98	-12.92	-13.14	-13.68	-13.96	-14.50
	± SE	1.05	1.06	0.70	0.75	0.63	0.69	0.80
85%RH	Mean %	-3.68	-3.66	-3.77	-3.86	-3.78	-3.59	-3.70
	± SE	0.37	0.35	0.30	0.32	0.30	0.41	0.36
96%RH	Mean %	+3.04	+3.05	+3.04	+3.04	+3.04	+3.05	+3.06
	± SE	0.09	0.10	0.10	0.10	0.10	0.09	0.09

TABLE 16-17

Mean weight changes of male and female R.appendiculatus respectively (expressed as percentage of the initial weight) during exposure to different RHs at 31°C.

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-10.88	-14.87	-18.99	-25.05	-32.05	-37.62	-41.68
	± SE	0.51	0.48	0.58	0.94	0.55	0.35	0.67
20%RH	Mean %	-8.16	-11.39	-14.07	-17.57	-21.17	-26.05	-29.93
	± SE	0.32	0.88	1.41	1.54	1.53	1.68	1.87
33%RH	Mean %	-7.87	-11.77	-15.23	-18.50	-22.21	-27.72	-35.21
	± SE	0.62	0.81	1.09	1.07	1.19	1.27	1.73
55%RH	Mean %	-8.10	-9.89	-12.14	-14.33	-15.98	-19.40	-20.94
	± SE	0.58	0.44	0.46	0.33	1.00	0.59	0.86
62%RH	Mean %	-6.89	-8.74	-9.84	-13.39	-13.59	-14.50	-15.57
	± SE	0.16	0.29	0.25	1.79	0.55	0.31	0.39
75%RH	Mean %	-5.55	-8.16	-9.23	-10.19	-10.65	-12.29	-13.49
	± SE	0.41	0.56	0.54	0.46	0.45	0.38	0.26
85%RH	Mean %	-2.77	-2.83	-2.97	-2.89	-2.92	-2.98	-3.01
	± SE	0.20	0.22	0.29	0.22	0.21	0.21	0.21
96%RH	Mean %	+2.22	+2.43	+2.41	+2.46	+2.43	+2.48	+2.50
	± SE	0.33	0.42	0.43	0.43	0.43	0.43	0.43

TABLE 16 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-48.17	-52.37	-57.22	-61.78	-63.45	-64.19	-64.48
	± SE	0.57	0.67	1.20	1.16	0.93	0.40	0.40
20%RH	Mean %	-34.52	-38.67	-42.36	-46.08	-51.18	-58.35	-60.01
	± SE	1.47	0.92	0.61	1.11	1.03	2.03	1.61
33%RH	Mean %	-36.68	-40.93	-45.02	-48.11	-50.06	-50.49	-50.93
	± SE	1.38	1.08	1.37	0.71	0.15	0.30	0.25
55%RH	Mean %	-20.99	-21.70	-21.98	-21.95	-22.47	-22.97	-23.24
	± SE	1.01	1.06	1.11	1.14	1.14	1.23	1.18
62%RH	Mean %	-17.49	-18.25	-19.06	-20.17	-20.67	-21.50	-22.12
	± SE	0.49	0.68	0.88	1.06	1.08	0.98	1.14
75%RH	Mean %	-13.50	-14.42	-14.41	-14.92	-15.37	-15.60	-16.33
	± SE	0.19	0.36	0.25	0.31	0.41	0.43	0.41
85%RH	Mean %	-3.10	-3.12	-3.18	-3.21	-3.15	-3.17	-4.08
	± SE	0.19	0.18	0.16	0.16	0.19	0.19	0.92
96%RH	Mean %	+2.60	+2.61	+2.59	+2.58	+2.58	+2.57	+2.54
	± SE	0.42	0.46	0.46	0.46	0.46	0.47	0.47

TABLE 17

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-13.38	-18.73	-23.94	-29.96	-35.37	-39.97	-46.37
	± SE	0.38	0.35	0.51	0.66	1.11	0.58	1.44
20%RH	Mean %	-12.74	-16.36	-20.65	-26.42	-30.53	-35.71	-40.12
	± SE	0.62	0.29	0.53	0.65	0.61	1.41	1.08
33%RH	Mean %	-9.84	-15.65	-20.09	-25.27	-29.94	-34.78	-39.08
	± SE	0.52	0.67	0.80	1.41	0.84	0.59	0.46
55%RH	Mean %	-8.62	-11.00	-12.89	-16.20	-19.15	-20.88	-22.97
	± SE	0.51	0.52	0.65	1.30	1.72	1.63	1.91
62%RH	Mean %	-6.38	-8.14	-9.71	-10.67	-12.92	-15.21	-16.11
	± SE	0.26	0.43	0.77	0.76	1.28	0.92	1.21
75%RH	Mean %	-4.80	-6.93	-9.09	-9.80	-11.22	-12.79	-13.58
	± SE	0.41	0.30	0.43	0.52	0.75	0.43	0.38
85%RH	Mean %	-2.91	-3.04	-3.18	-3.14	-3.16	-3.87	-3.13
	± SE	0.22	0.24	0.24	0.30	0.31	0.55	0.41
96%RH	Mean %	+2.50	+2.46	+2.69	+2.65	+2.56	+2.59	+2.55
	± SE	0.54	0.48	0.51	0.46	0.44	0.52	0.32

TABLE 17 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-49.82	-54.46	-57.65	-60.89	-62.11	-63.63	-64.52
	± SE	1.10	1.76	1.52	0.85	0.47	0.36	0.58
20%RH	Mean %	-43.67	-47.68	-51.12	-54.09	-57.69	-59.87	-61.38
	± SE	0.92	0.79	0.67	1.09	1.15	0.82	0.74
33%RH	Mean %	-41.97	-47.36	-50.82	-52.61	-54.89	-55.30	-57.35
	± SE	0.53	1.29	0.32	0.57	0.58	0.77	0.45
55%RH	Mean %	-25.99	-29.04	-32.74	-34.88	-37.53	-38.72	-39.71
	± SE	1.97	2.08	1.73	1.92	1.60	1.86	1.92
62%RH	Mean %	-6.38	-8.14	-9.71	-10.67	-12.92	-15.21	-16.11
	± SE	1.04	1.06	0.96	0.69	0.24	0.45	0.43
75% RH	Mean %	-14.83	-15.47	-15.95	-16.86	-17.15	-17.23	-17.28
	± SE	0.59	0.67	0.67	0.73	0.77	0.74	0.74
85%RH	Mean %	-3.18	-4.12	-3.52	-3.42	-3.35	-3.55	-3.44
	± SE	0.39	0.80	0.37	0.45	0.39	0.42	0.46
96%RH	Mean %	+1.99	+2.14	+2.17	+2.22	+2.12	+2.22	+2.40
	± SE	0.35	0.23	0.31	0.34	0.36	0.36	0.46

TABLE 18-20

Mean weight changes of nymphs of *R.appendiculatus* (expressed as percentage of the initial weight) during exposure to different RHs at 18°C, 27°C and 31°C respectively.

TABLE 1[illegible]

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-30.41	-35.99	-33.68	-40.84	-42.13	-45.90	-47.88
	± SE	2.15	2.02	2.13	1.94	1.59	1.92	2.08
20%RH	Mean %	-20.06	-22.64	-24.08	-26.61	-29.02	-30.37	-34.59
	± SE	0.93	1.01	1.08	1.25	1.44	1.52	1.76
33%RH	Mean %	-19.06	-22.64	-23.99	-25.36	-28.22	-29.25	-30.29
	± SE	2.19	2.09	2.20	2.04	2.01	2.02	1.84
55%RH	Mean %	-12.98	-13.08	-15.23	-18.11	-22.18	-23.68	-26.68
	± SE	1.88	1.51	1.88	2.72	2.96	2.51	2.52
62%RH	Mean %	-10.66	-11.90	-12.41	-13.43	-14.98	-15.99	-16.83
	± SE	0.75	0.67	0.69	0.55	0.77	0.37	0.54
75%RH	Mean %	-8.32	-10.34	-12.09	-13.37	-13.28	-15.80	-16.36
	± SE	1.28	1.24	1.17	1.19	1.19	1.27	1.52
85%RH	Mean %	-2.35	-2.06	-2.94	-3.22	-3.68	-3.51	-3.76
	± SE	1.22	1.05	0.83	0.97	1.24	1.24	1.36
96%RH	Mean %	+1.63	+2.69	+2.25	+2.41	+2.27	+2.69	+3.02
	± SE	0.80	0.33	0.41	0.81	0.44	0.51	0.61

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-50.58	-55.42	-56.00	-59.38	-59.38	-61.10	-61.13
	± SE	2.02	1.07	0.80	1.24	1.70	0.48	0.48
20%RH	Mean %	-35.55	-37.25	-40.39	-42.49	-45.09	-48.96	-53.56
	± SE	3.03	1.99	2.24	2.17	2.01	2.06	2.22
33%RH	Mean %	-31.98	-34.41	-36.38	-38.57	-40.45	-42.74	-45.86
	± SE	2.15	2.06	2.10	2.17	2.29	2.44	2.75
55%RH	Mean %	-27.51	-29.76	-30.79	-32.83	-35.91	-37.01	-37.36
	± SE	2.58	3.09	2.79	2.59	2.76	2.88	3.08
62%RH	Mean %	-18.66	-18.74	-19.31	-20.53	-20.97	-22.12	-23.52
	± SE	0.48	0.50	0.67	0.66	0.64	0.46	0.37
75%RH	Mean %	-16.76	-17.26	-18.31	-18.26	-18.61	-19.88	-20.28
	± SE	1.44	1.09	1.06	0.91	0.91	0.88	1.06
85%RH	Mean %	-3.19	-3.91	-3.31	-3.86	-3.31	-3.55	-3.60
	± SE	2.58	2.09	2.59	1.76	1.88	1.08	1.15
96%RH	Mean %	+2.64	+2.79	+2.83	+2.40	+2.94	+2.66	+2.92
	± SE	0.41	0.30	0.36	0.26	0.56	0.25	0.36

TABLE 19

TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-31.31	-38.39	-39.93	-41.75	-44.71	-48.85	-50.77
	± SE	0.61	0.51	0.38	0.43	0.93	0.65	0.42
20%RH	Mean %	-21.82	-25.51	-29.49	-32.24	-35.83	-38.79	-42.84
	± SE	0.44	0. 75	0.34	0.35	0.77	0.63	0.70
33%RH	Mean %	-18.47	-22.70	-23.85	-26.00	-28.78	-32.15	-36.05
	± SE	0.24	0.71	0.55	0.34	0.31	1.14	1.66
55%RH	Mean %	-13.51	-15.00	-16.57	-18.55	-21.32	-24.54	-27.87
	± SE	0.20	0.22	0.13	0.36	0.40	0.30	0.61
62%RH	Mean %	-9.38	-11.12	-11.16	-16.72	-19.21	-20.38	-20.79
	± SE	0.46	0.43	0.42	0.66	0.12	0.38	0.26
75%RH	Mean %	-11.15	-12.02	-13.18	-13.58	-14.23	-15.25	-16.04
	± SE	0.17	0.16	0.23	0.20	0.32	0.49	0.37
85%RH	Mean %	-1.70	-1.91	-2.62	-3.22	-3.51	-3.59	-3.48
	± SE	0.35	0.33	0.49	0.56	0.62	0.65	0.72
96%RH	Mean %	+2.62	+3.11	+3.44	+3.35	+3.56	+3.50	+3.57
	± SE	0.35	0.29	0.20	0.21	0.17	0.29	0.11

TABLE 15 Cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-54.40	-57.53	-61.83	-62.32	-63.63	-63.12	-63.25
	± SE	0.25	0.42	0.50	0.32	0.41	0.34	0.29
20%RH	Mean %	-45.71	-50.04	-52.84	-56.19	-57.45	-57.58	-57.06
	± SE	0.77	1.17	1.20	1.01	1.05	0.77	0.77
33%RH	Mean %	-37.39	-38.47	-42.91	-45.09	-46.42	-47.78	-48.87
	± SE	1.44	0.55	0.77	0.76	1.10	0.67	0.67
55%RH	Mean %	-30.33	-33.73	-37.32	-39.43	-39.94	-40.95	-41.24
	± SE	0.44	0.94	0.44	0.23	0.19	0.23	0.22
62%RH	Mean %	-21.39	-21.94	-22.49	-22.63	-22.78	-23.04	-23.36
	± SE	0.39	0.38	0.47	0.48	0.47	0.53	0.59
75%RH	Mean %	-16.85	-17.76	-18.90	-19.67	-20.32	-21.37	-21.80
	± SE	0.51	0.42	0.42	0.43	0.57	0.47	0.35
85% RH	Mean %	-3.72	-3.59	-3.75	-3.78	-3.66	-4.13	-3.86
	± SE	0.58	0.70	0.57	0.55	0.51	0.48	0.37
96%RH	Mean %	+3.61	+3.40	+3.62	+3.72	+3.70	+3.57	+3.62
	± SE	0.14	0.08	0.13	0.17	0.15	0.12	0.13

TABLE 20

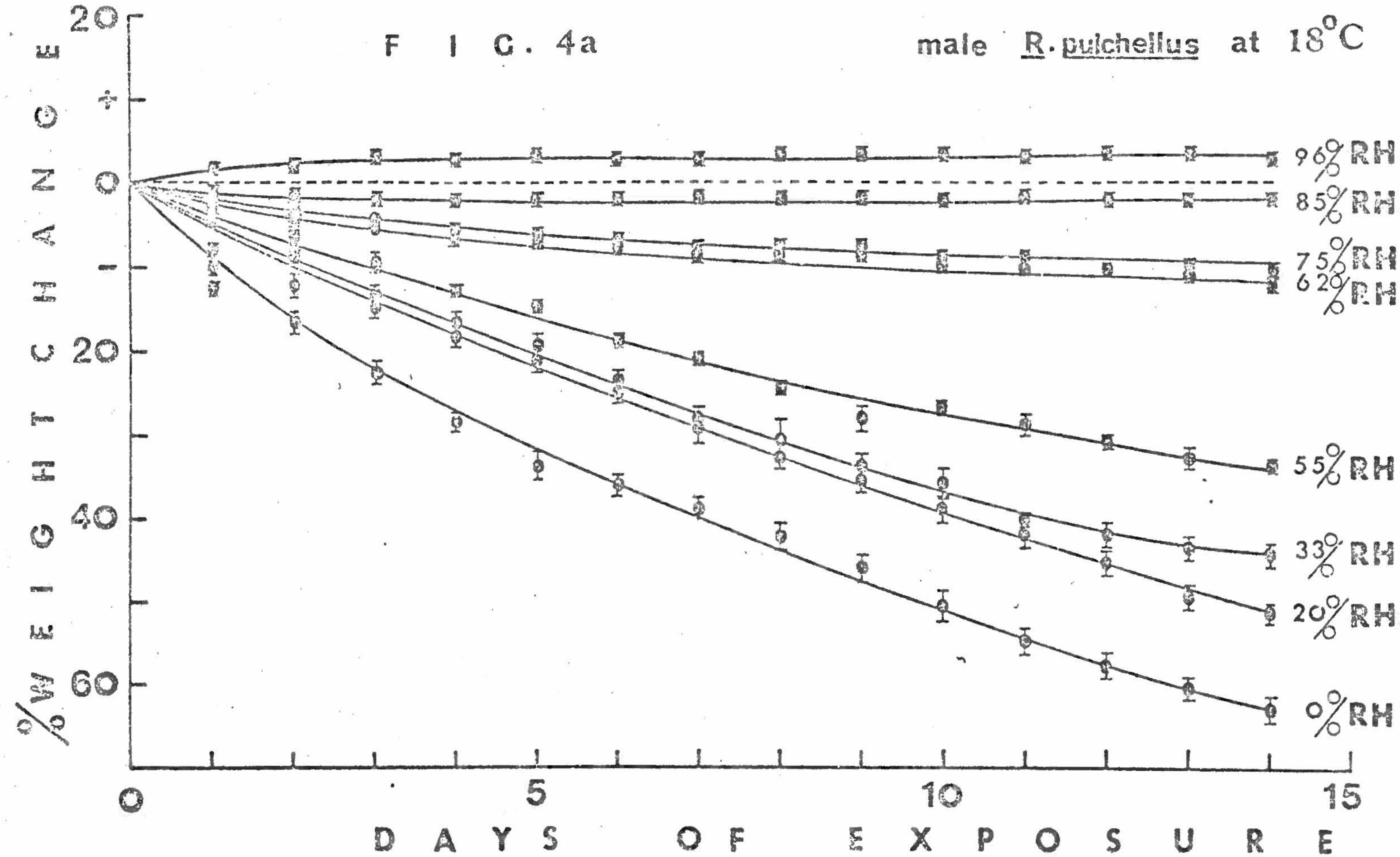
TREATMENT		DAYS OF EXPOSURE						
		1	2	3	4	5	6	7
0%RH	Mean %	-31.68	-39.97	-42.15	-47.54	-51.39	-55.09	-64.86
	± SE	2.15	1.79	2.41	2.24	2.98	3.01	2.66
20%RH	Mean %	-19.26	-23.15	-31.55	-35.33	-39.42	-44.47	-50.43
	± SE	1.78	2.57	3.00	2.16	1.90	1.81	1.91
33%RH	Mean %	-19.00	-22.61	-30.23	-34.59	-37.73	-41.50	-43.98
	± SE	2.72	3.32	2.43	2.78	3.44	3.45	3.41
55%RH	Mean %	-13.03	-15.87	-20.87	-27.84	-30.09	-35.70	-39.96
	± SE	1.16	1.23	0.81	1.69	1.43	1.10	1.51
62%RH	Mean %	-11.71	-11.89	-11.84	-12.85	-12.92	-13.99	-15.69
	± SE	0.60	0.97	1.17	1.32	1.44	1.08	1.06
75%RH	Mean %	-10.36	-11.67	-11.06	-11.82	-12.85	-13.73	-14.93
	± SE	1.58	1.38	1.33	2.91	3.25	3.72	3.66
85%RH	Mean %	-2.98	-3.08	-3.19	-3.25	-2.93	-2.93	-2.31
	± SE	0.42	0.42	0.45	0.60	0.61	0.48	0.38
96%RH	Mean %	+3.92	+4.75	+3.93	+3.22	+3.00	+3.19	+2.80
	± SE	1.61	1.43	0.81	1.69	2.63	1.02	1.02

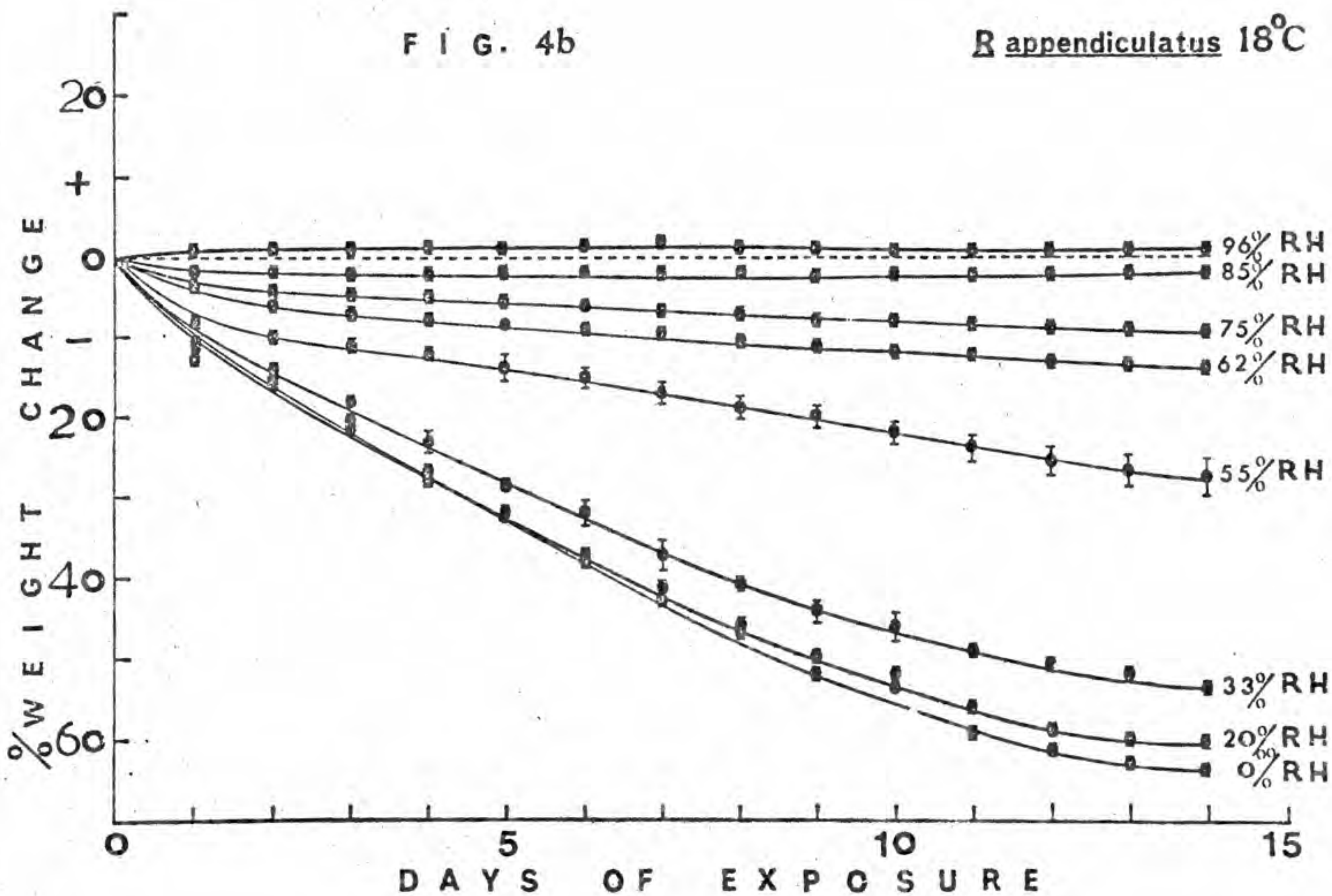
TABLE 20 cont.

TREATMENT		DAYS OF EXPOSURE						
		8	9	10	11	12	13	14
0%RH	Mean %	-70.17	-73.56	-75.01	-74.02	-73.74	-73.80	-73.80
	± SE	2.09	1.53	1.35	1.78	1.73	1.77	1.82
20%RH	Mean %	-58.64	-64.70	-67.21	-67.71	-68.20	-68.75	-71.26
	± SE	2.23	0.95	1.49	1.43	1.19	0.93	1.32
33%RH	Mean %	-49.94	-53.81	-56.46	-58.19	-58.37	-58.44	-58.68
	± SE	3.81	3.66	3.38	3.47	3.40	3.36	3.29
55%RH	Mean %	-42.13	-49.07	-51.11	-55.63	-57.52	-58.06	-58.14
	± SE	1.25	1.21	1.21	1.20	1.20	1.23	1.22
62%RH	Mean %	-16.07	-17.87	-18.69	-18.88	-19.65	-19.80	-21.93
	± SE	1.08	1.12	1.17	1.30	1.32	1.17	1.08
75%RH	Mean %	-15.98	-14.54	-16.37	-16.33	-16.34	-18.84	-19.88
	± SE	3.50	3.75	3.23	3.20	3.20	3.34	3.03
85%RH	Mean %	-2.29	-2.27	-2.23	-2.38	-2.18	-2.15	-2.12
	± SE	0.35	0.33	0.26	0.20	0.31	0.36	0.48
96%RH	Mean %	+3.59	+3.85	+2.17	+3.13	+3.23	+3.45	+3.26
	± SE	0.58	1.10	1.51	1.25	1.55	1.21	1.21

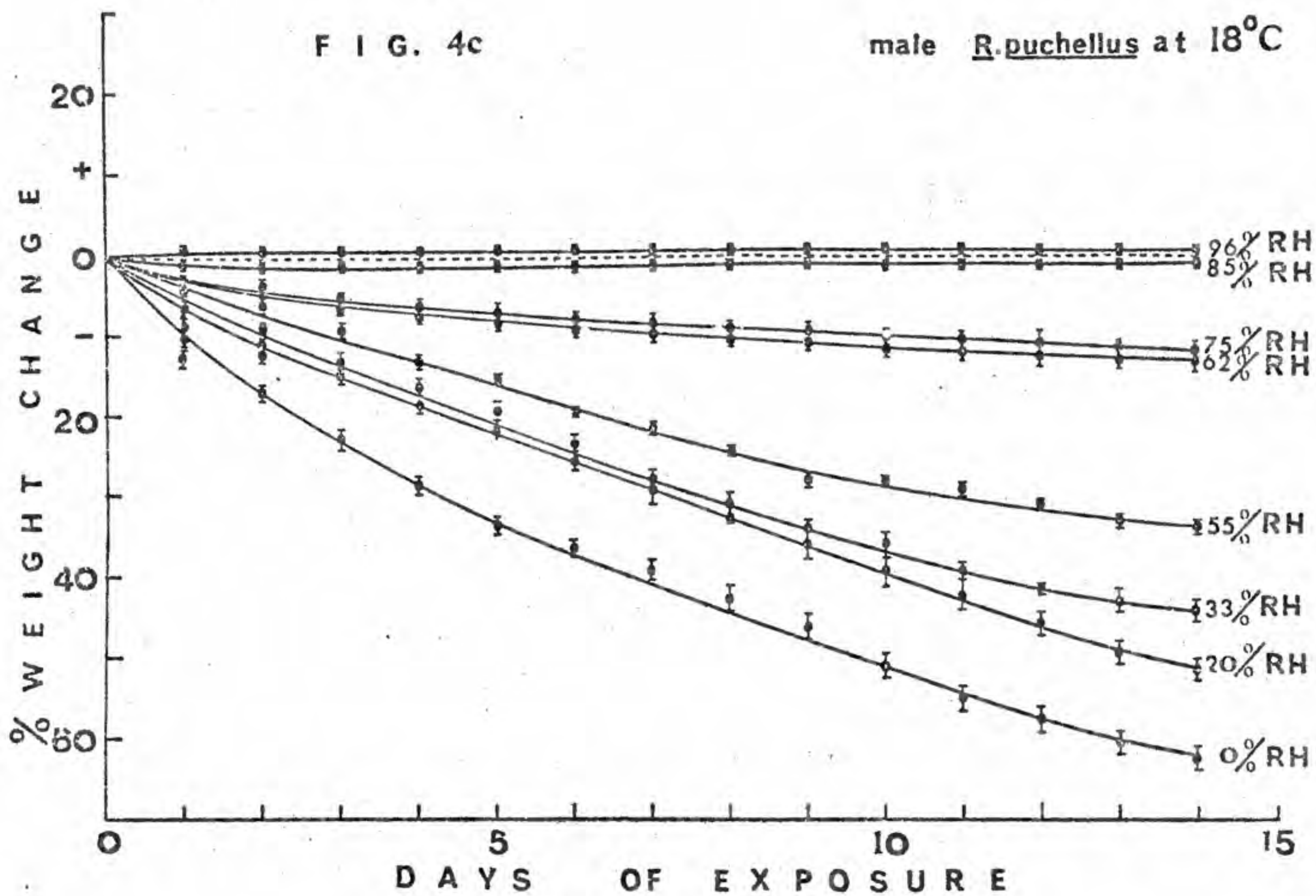
FIGURES 4a - 4d

Weight changes of adult *R.appendiculatus* and *R.pulchellus* after exposure to 8 relative humidities (RHs) at 18^{o}C. The bars indicate $\pm$ S.E.

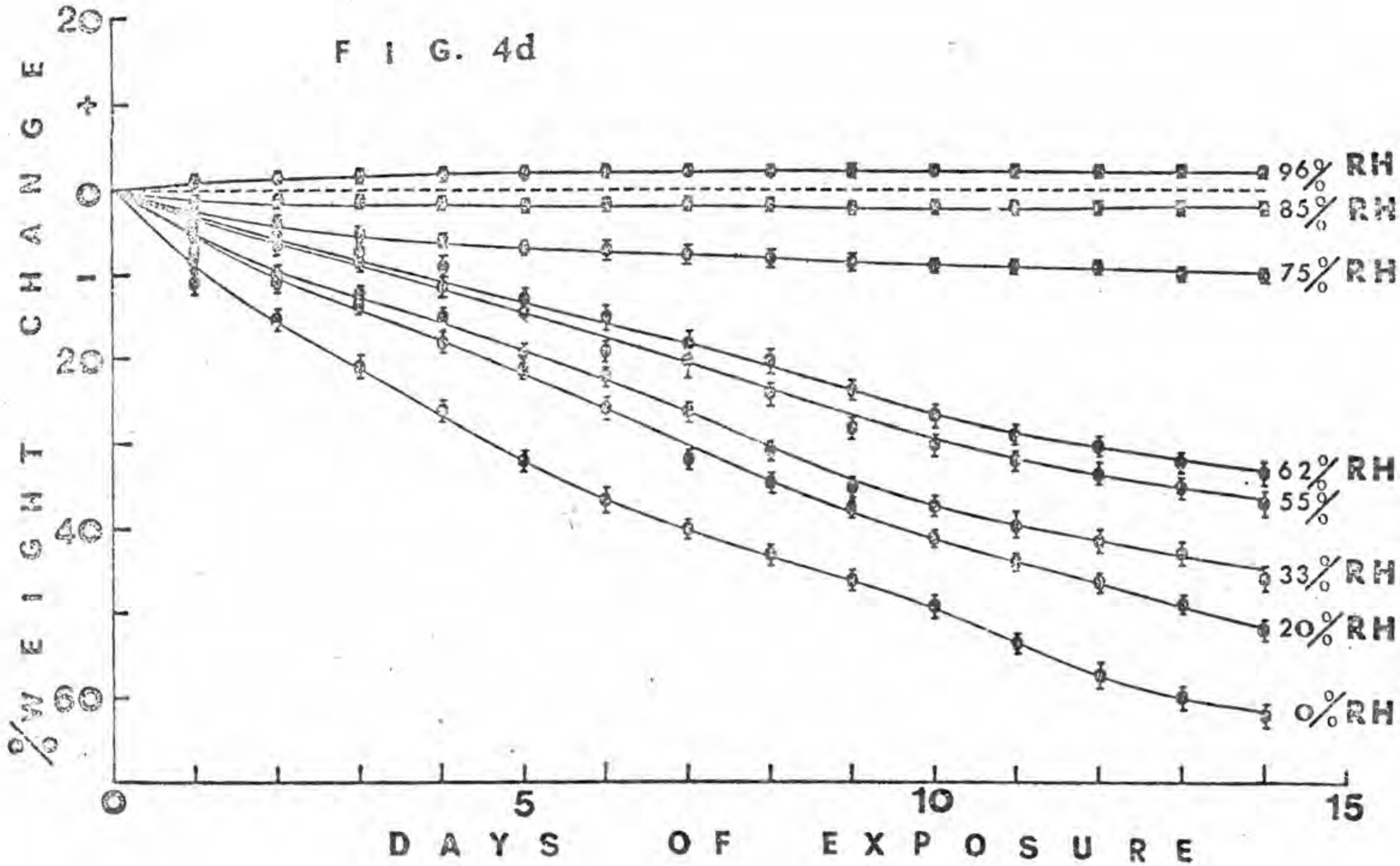

F I G. 4a
male R. pulchellus at 18°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE



F I G. 4b
R appendiculatus 18°C
20
+
0
-
20
40
60
% WEIGHT CHANGE
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

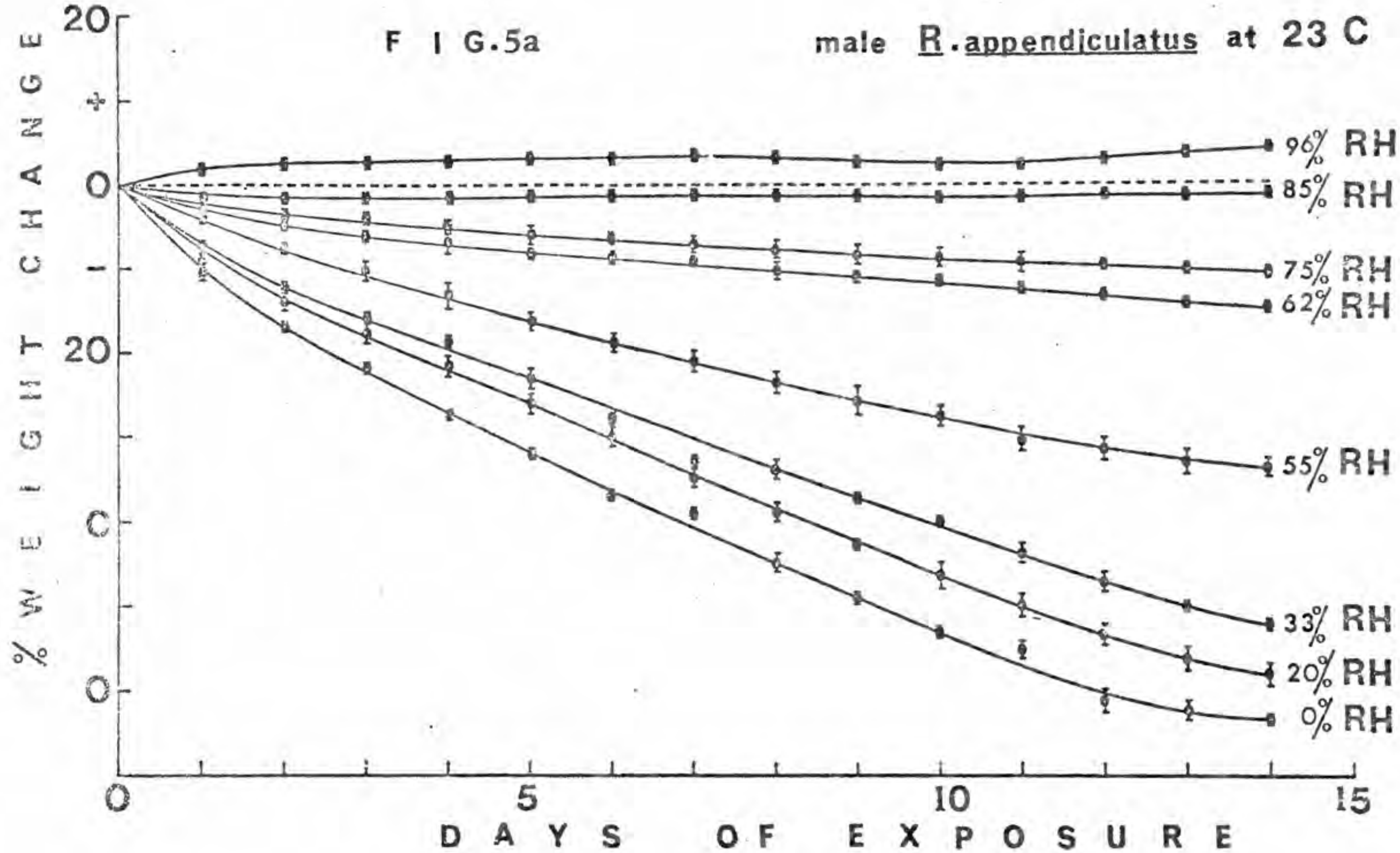

F I G. 4c
male R.puchellus at 18°C
20
+
0
-
20
40
60
% WEIGHT CHANGE
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

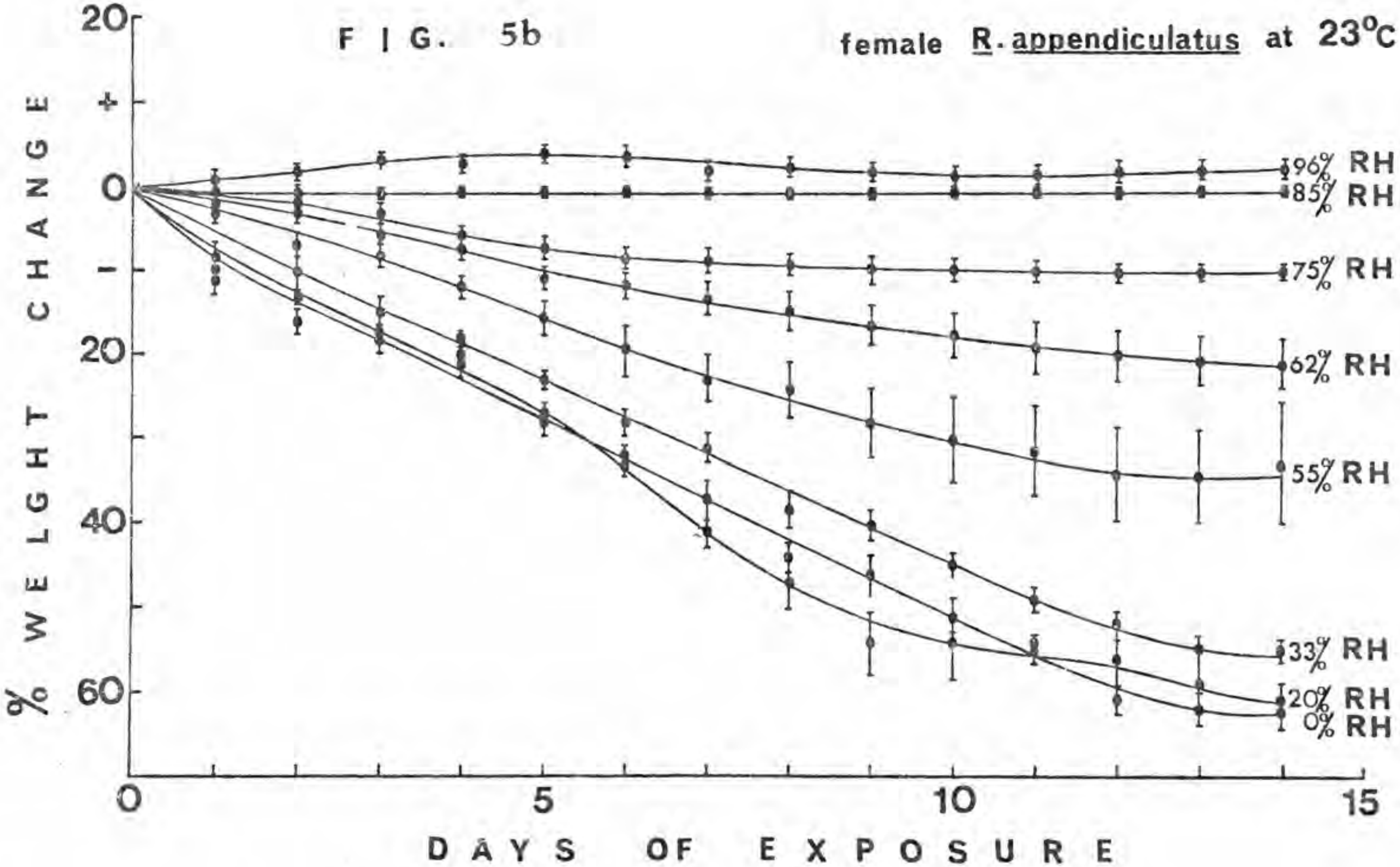
female *R.appendiculatus* at 18°C

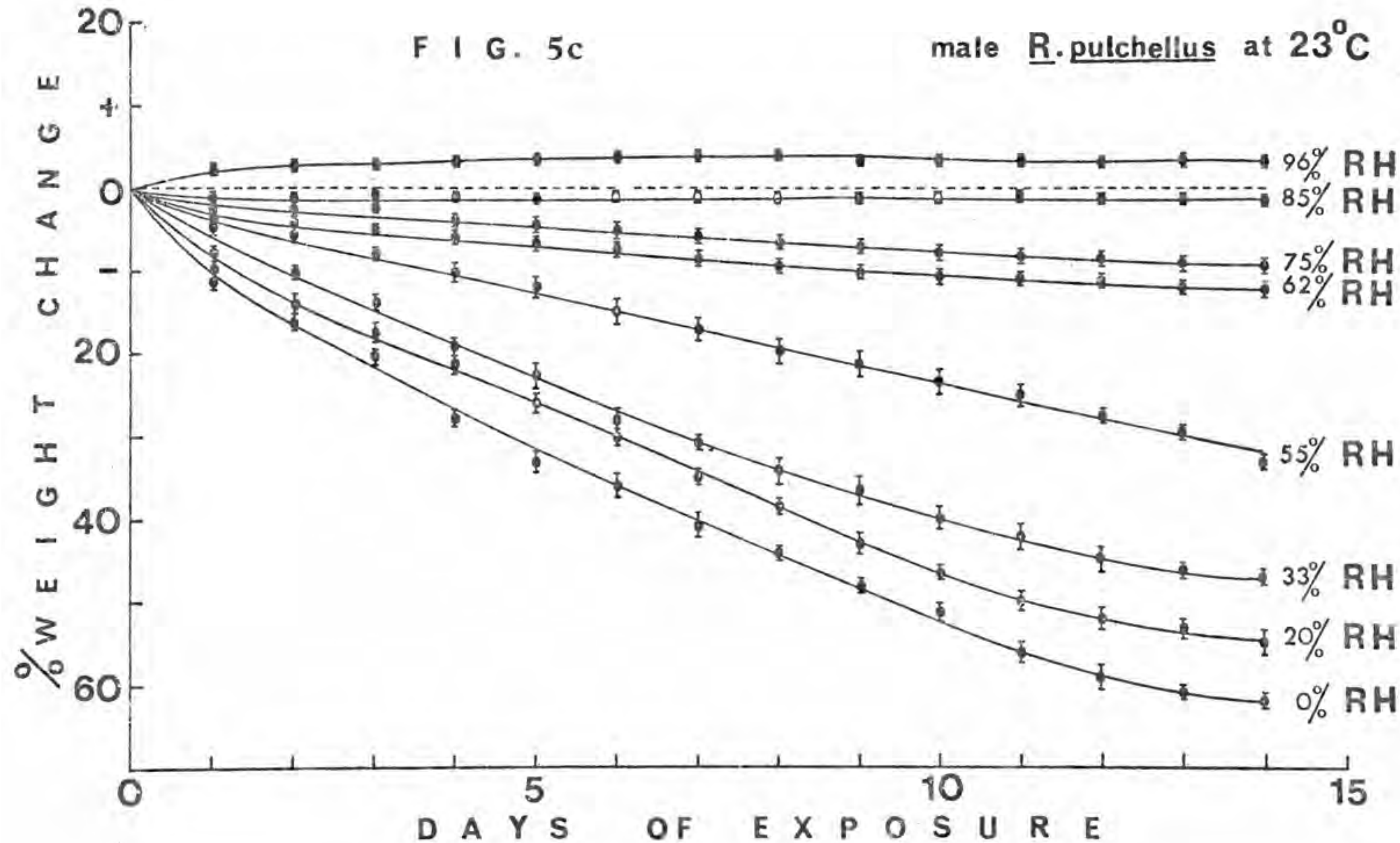


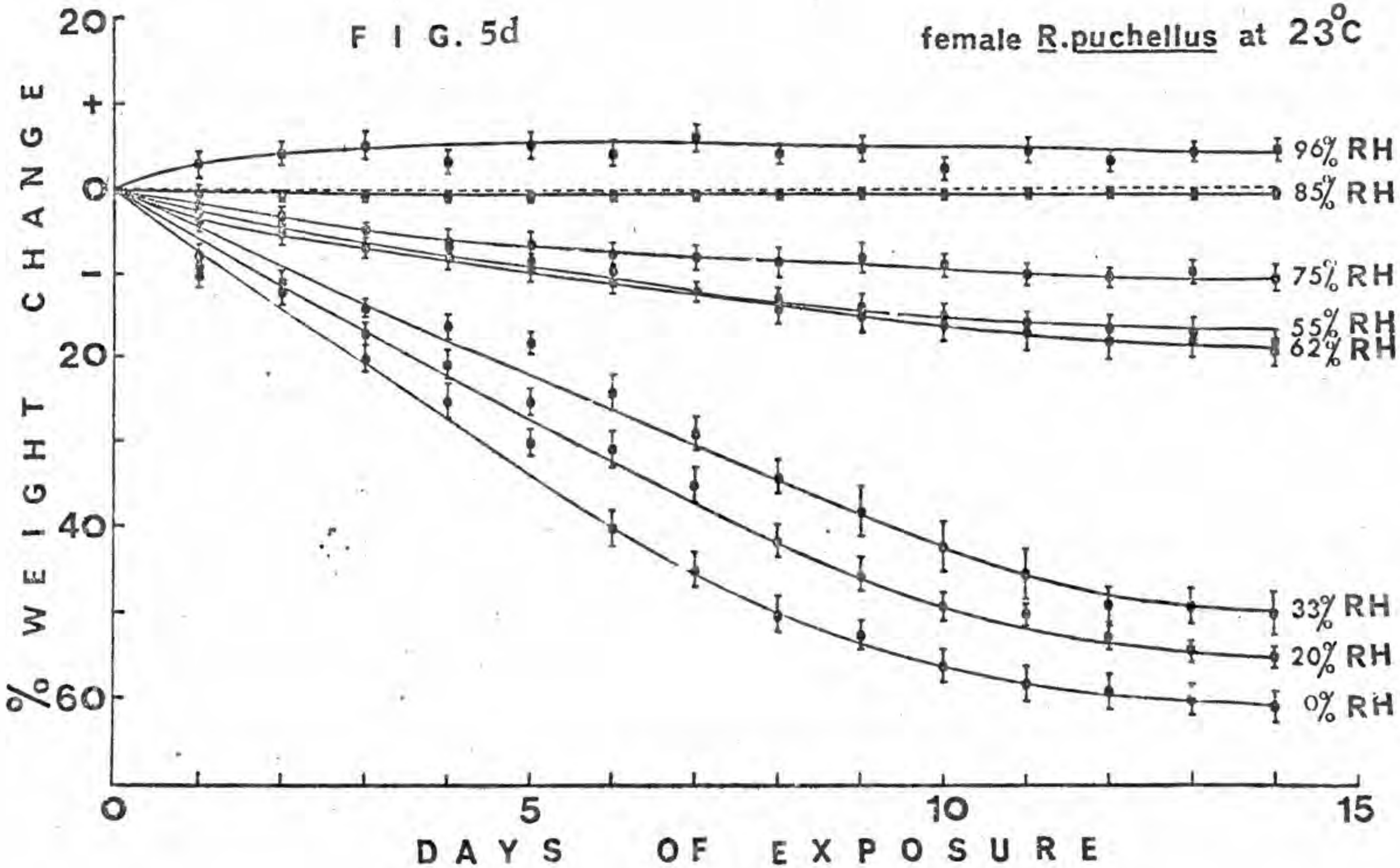
FIGURES 5a - 5d

Weight changes of adult R.appendiculatus and R.pulchellus after exposure to 8 relative humidities (RHs) at 23^{o}C. The bars indicate $\pm$ S.E.


F I G.5a
male R.appendiculatus at 23 C
% WEIGHT CHANGE
20
+
0
-
20
C
0
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

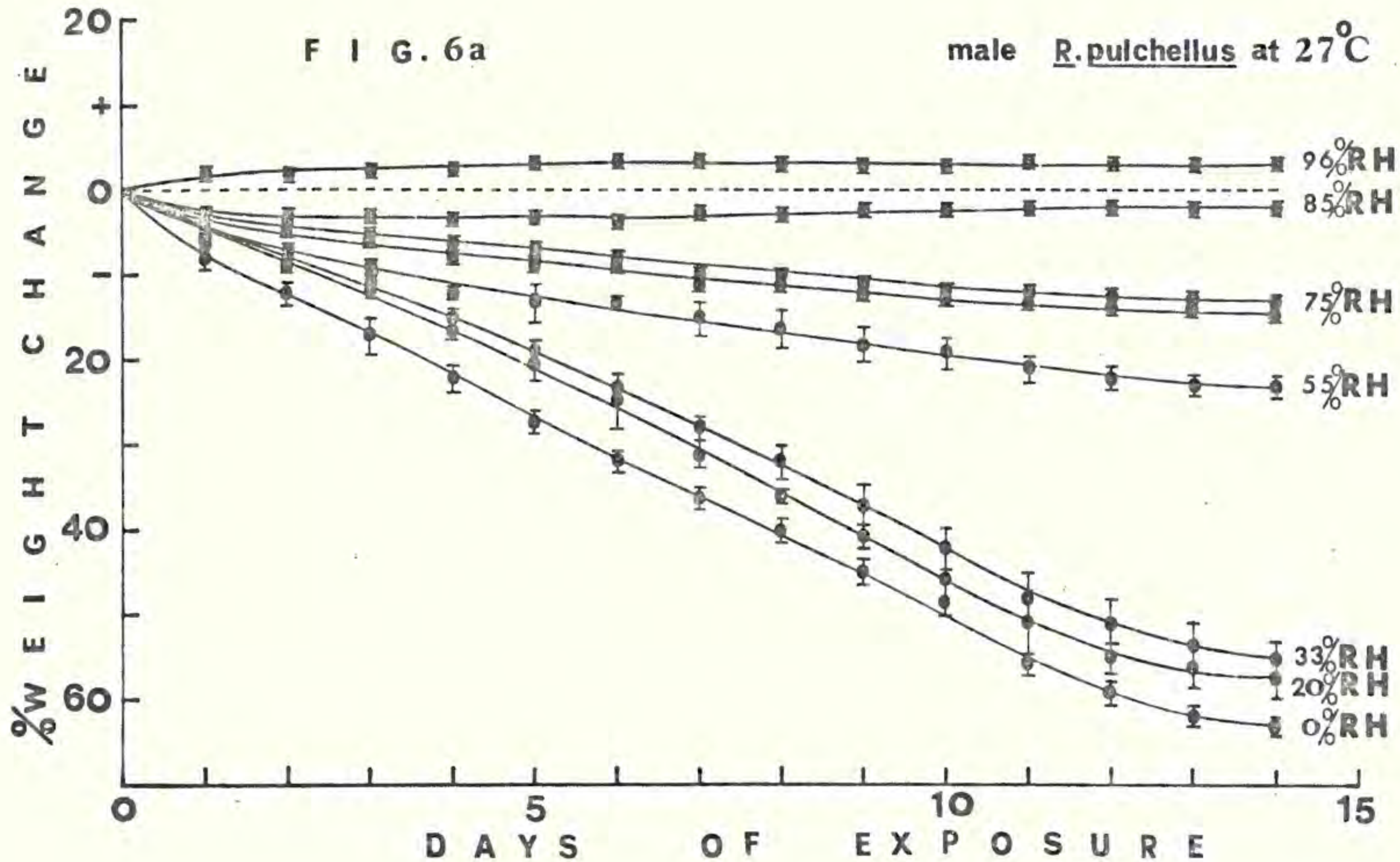

F I G. 5b
female R. appendiculatus at 23°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE


F I G. 5c
male R. pulchellus at 23°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

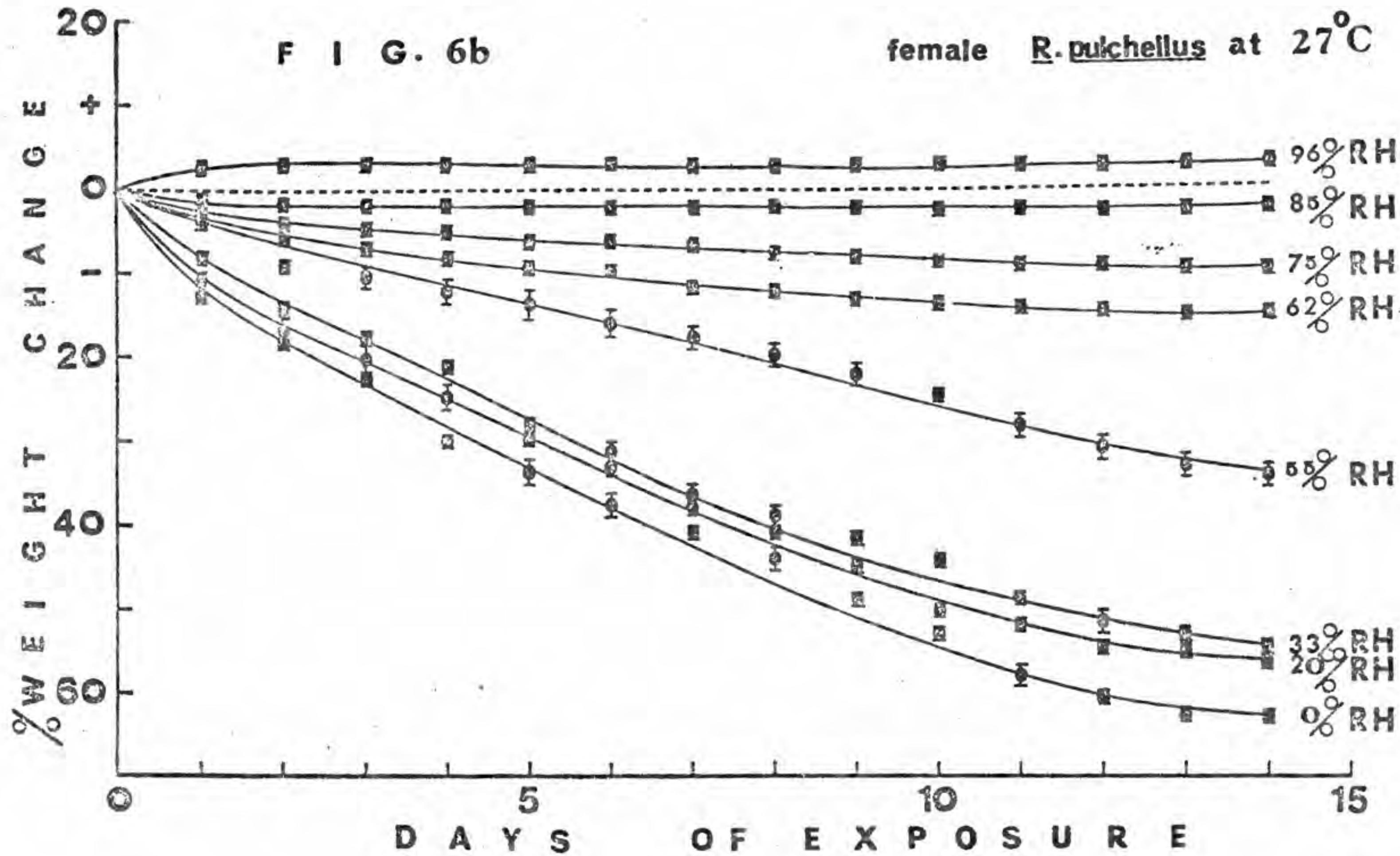

F I G. 5d
female R.puchellus at 23°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
55% RH
62% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

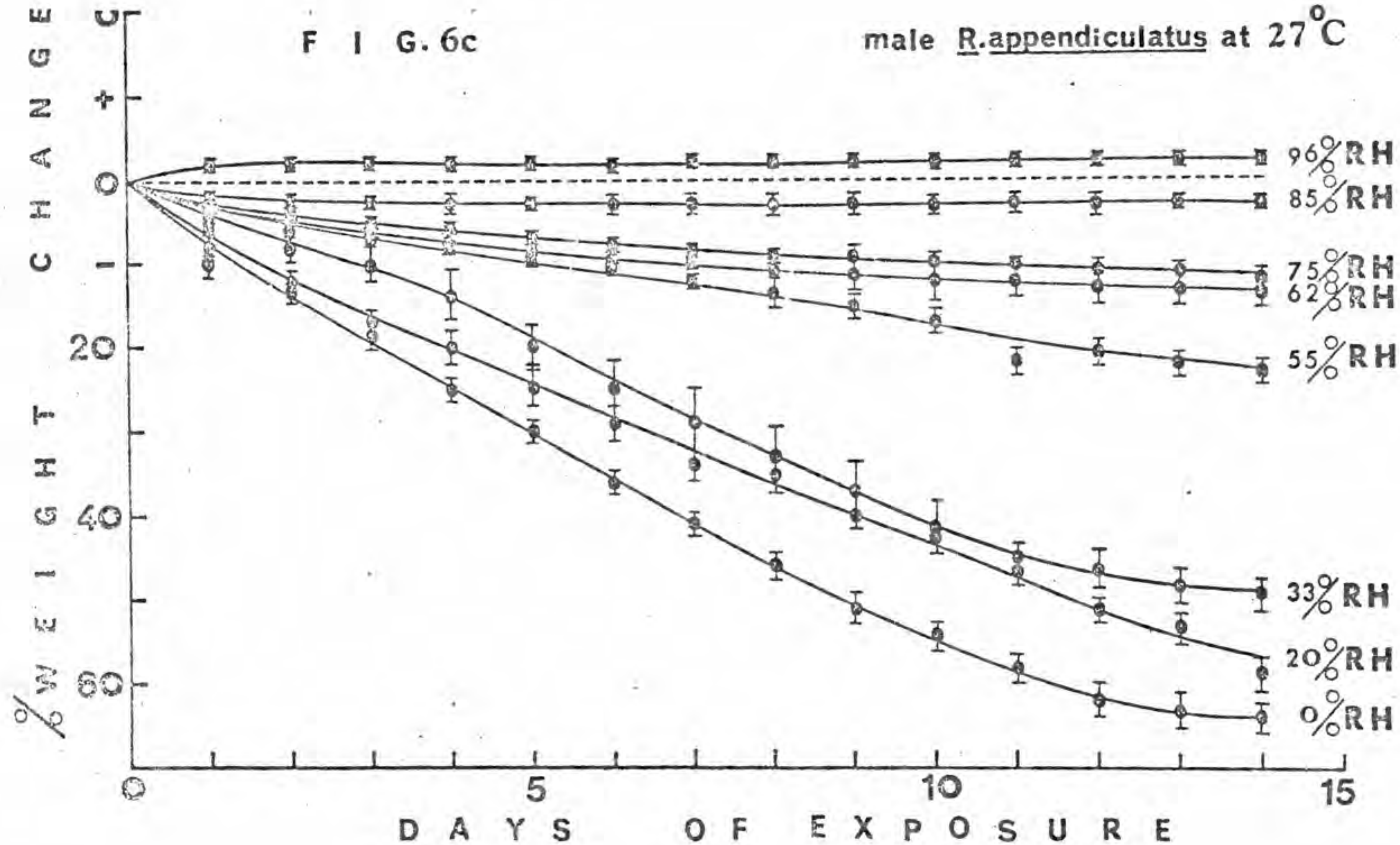
FIGURES 6a - 6d

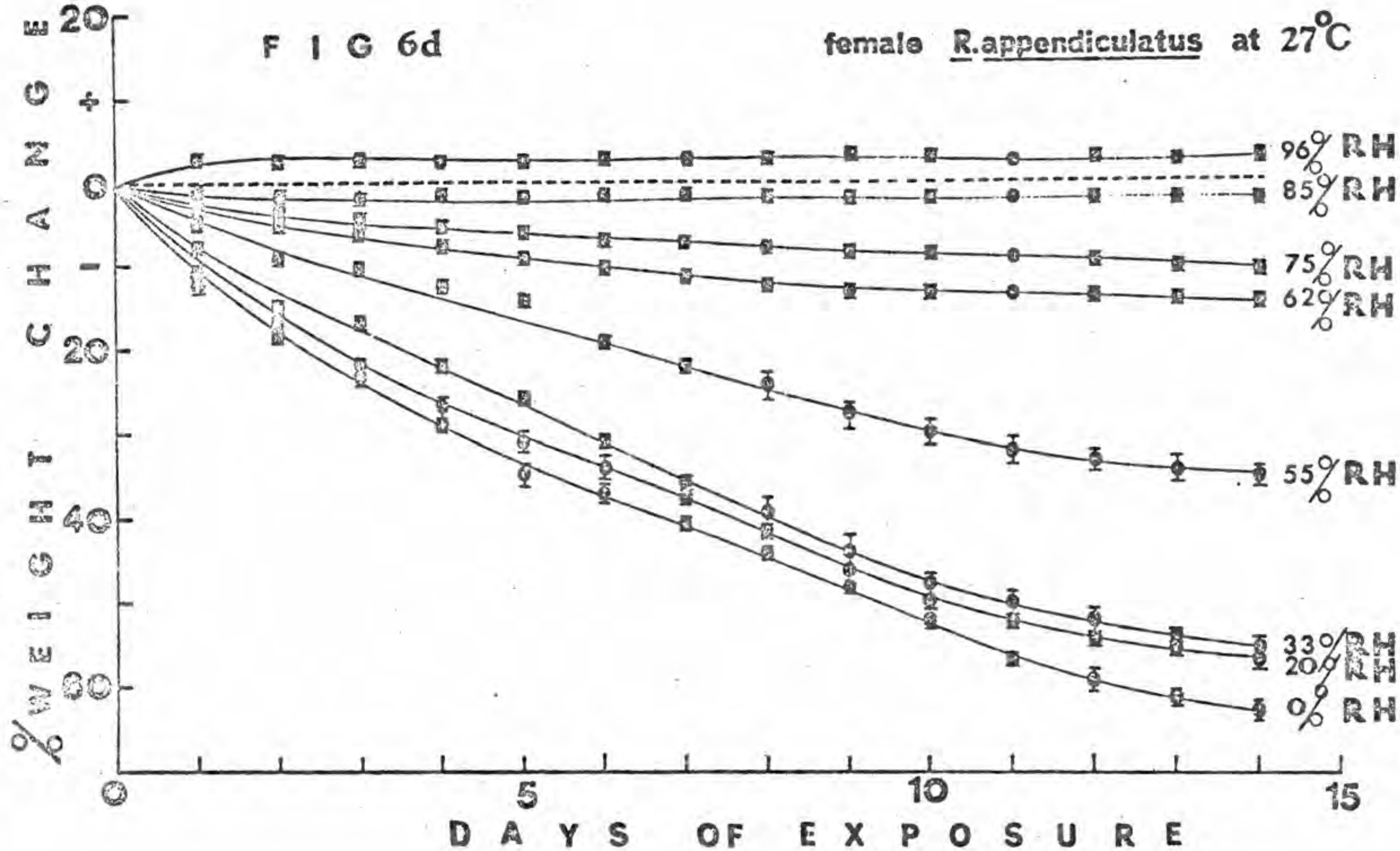
Weight changes of adult *R.appendiculatus* and *R.pulchellus* after exposure to 8 relative humidities (RHs) at 27°C. The bars indicate ± S.E.



F I G. 6a   male R. pulchellus at 27°C

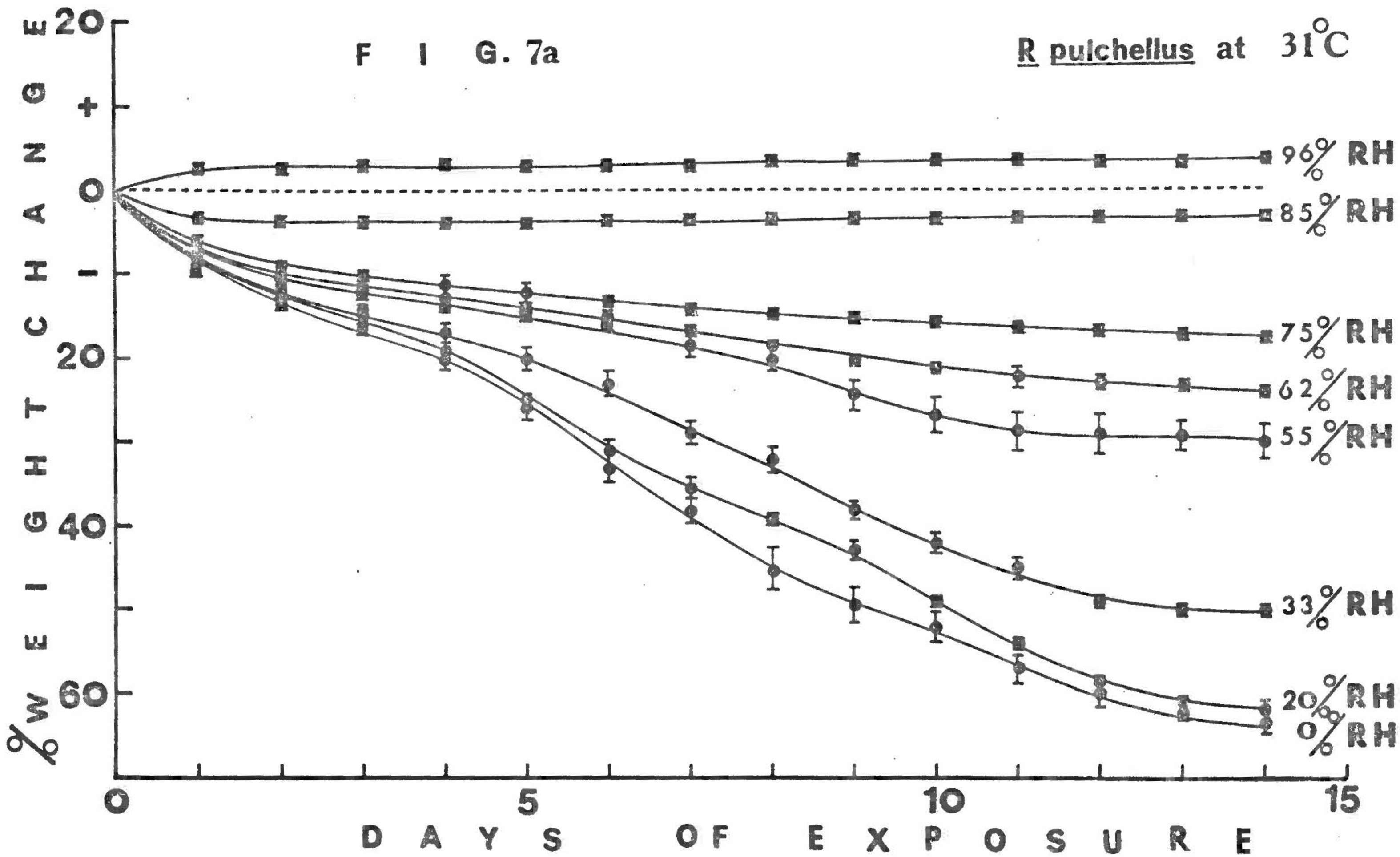

F I G. 6b
female R. pulchellus at 27°C
% WEIGHT CHANGE
+
-
20
0
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE


F I G. 6c
male R.appendiculatus at 27°C
% WEIGHT CHANGE
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE


F I G 6d
female R.appendiculatus at 27°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

FIGURES 7a - 7d

Weight changes of adult *R.appendiculatus* and *R.pulchellus* after exposure to 8 relative humidities (RHs) at 31°C. The bars indicate $\pm$ S.E.


F I G. 7a
R pulchellus at 31°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

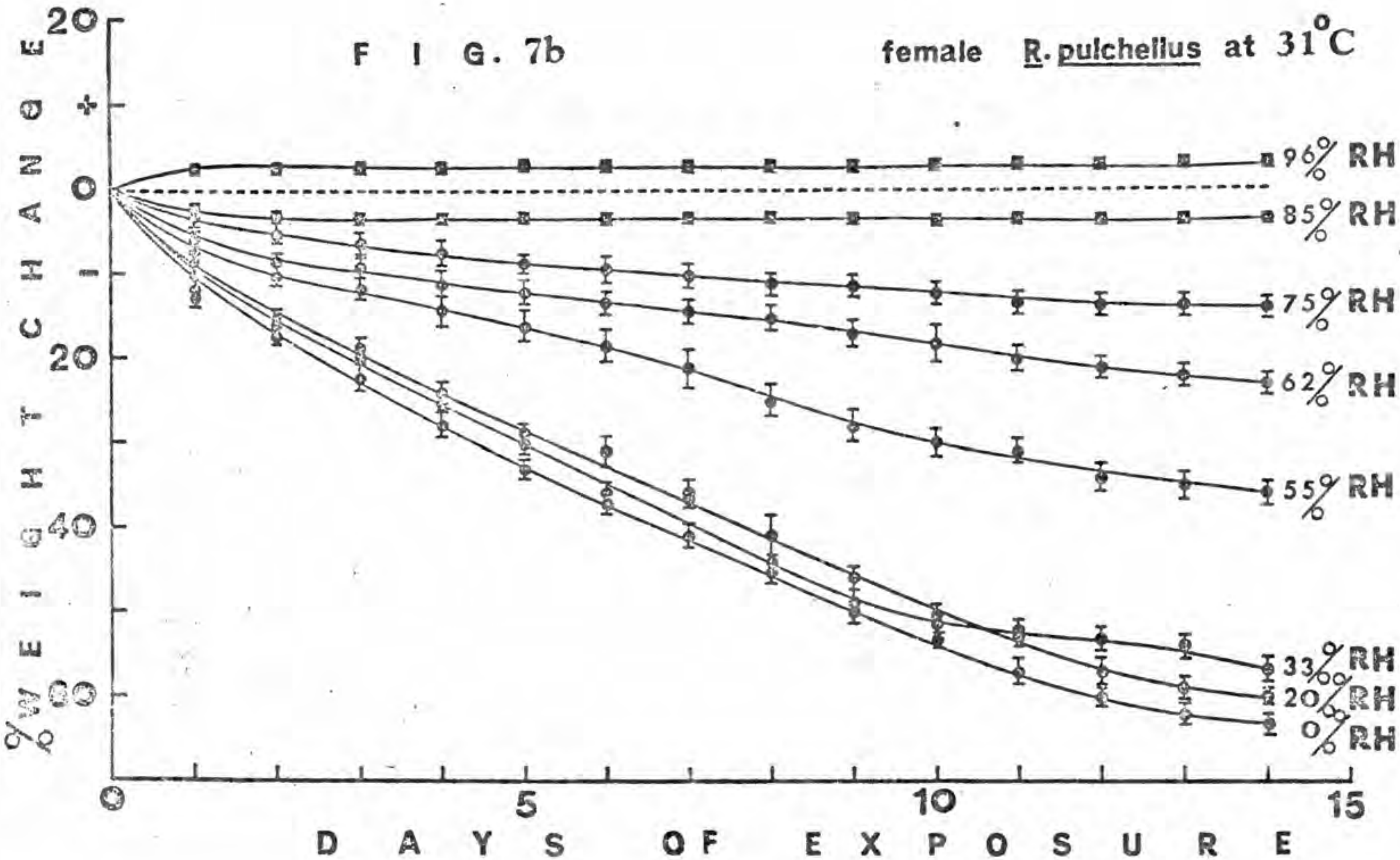
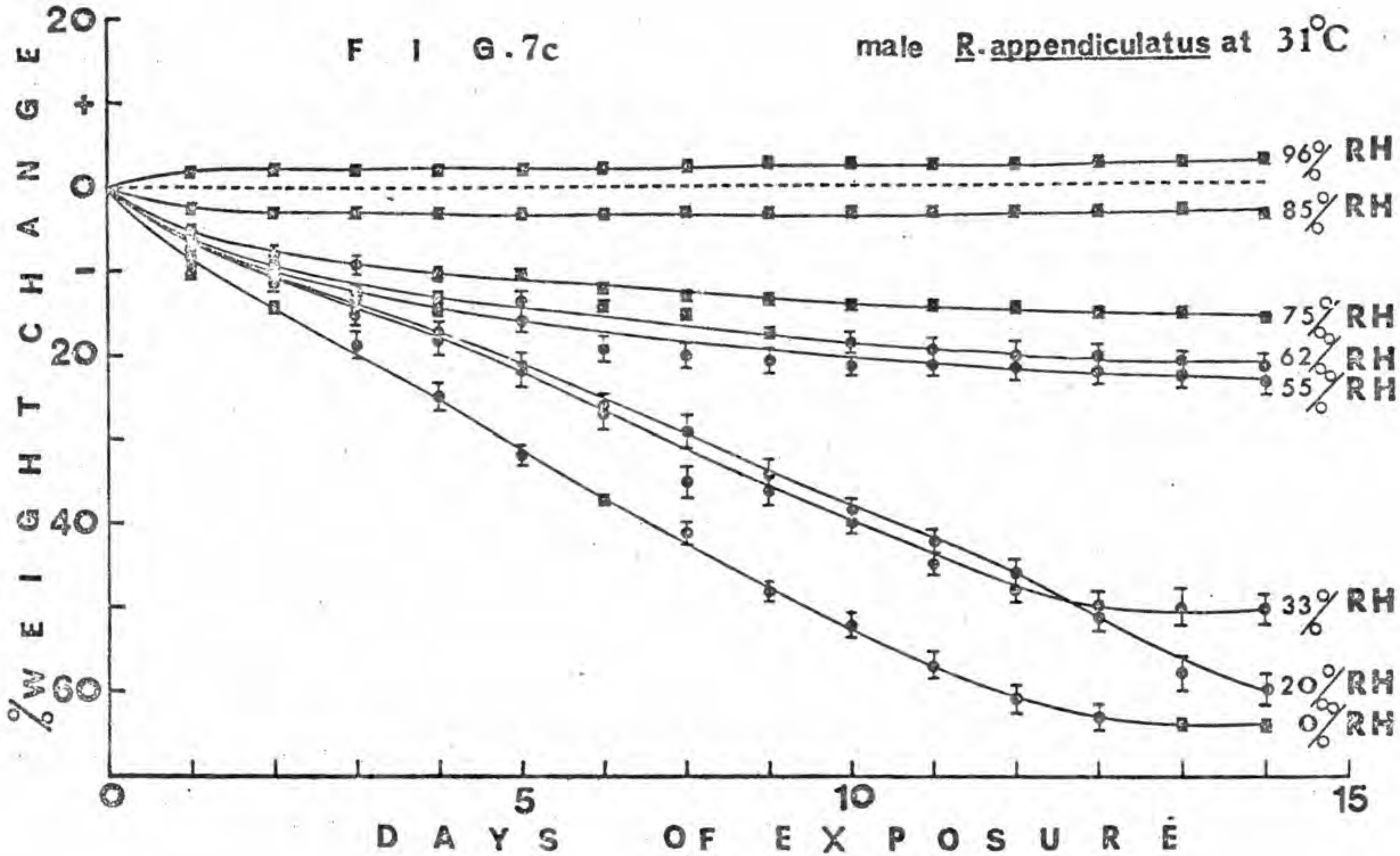
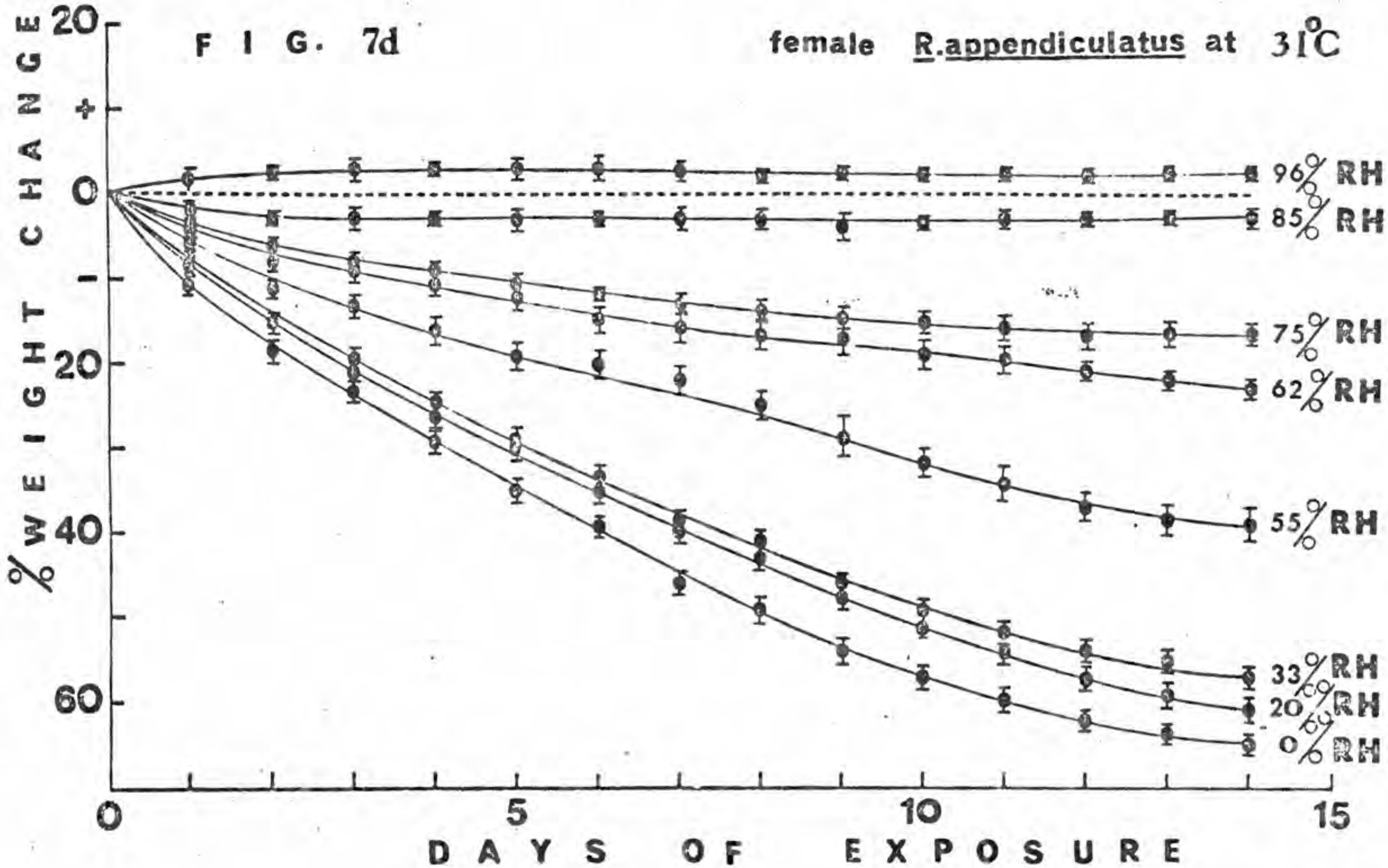


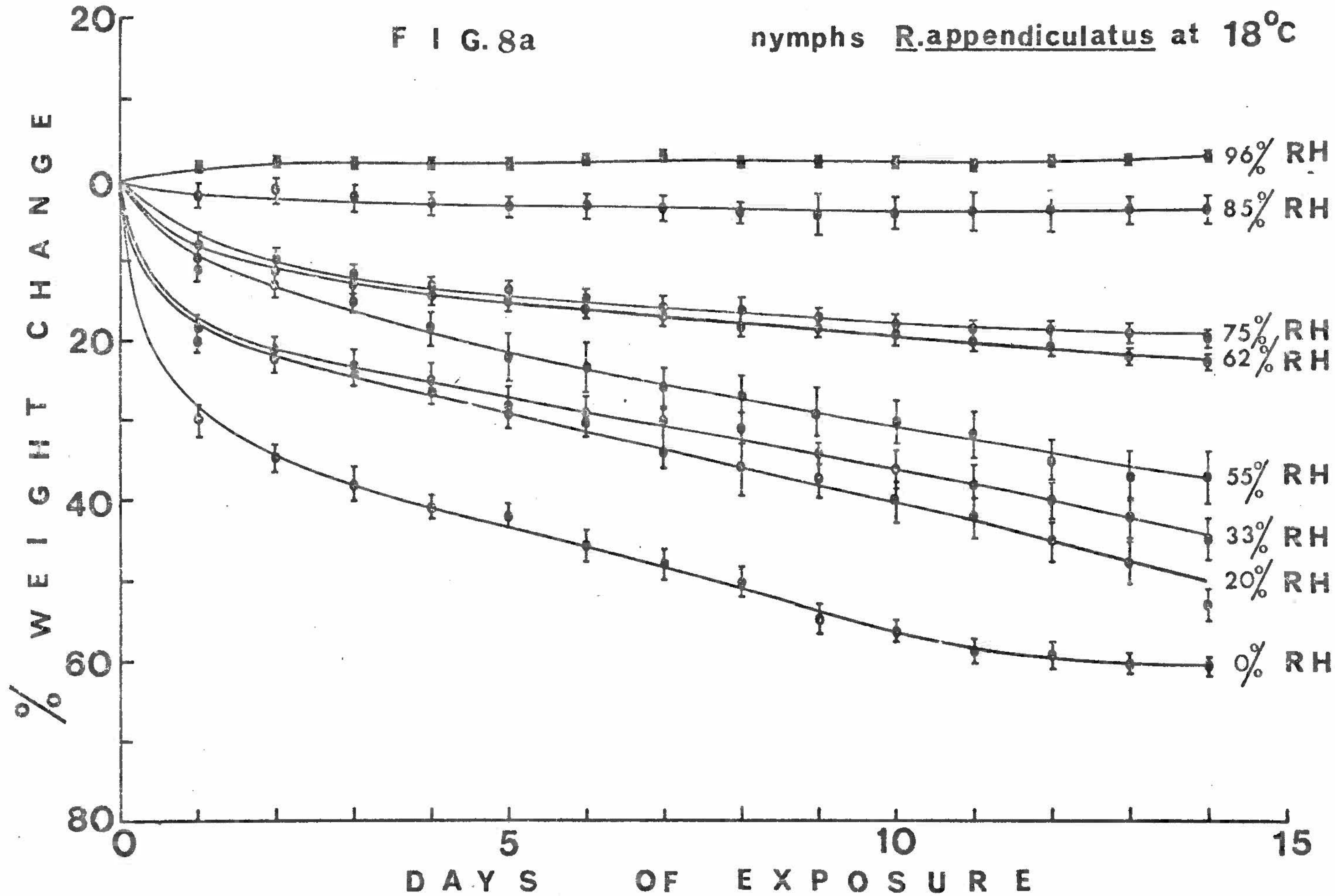
FIG. 7b female R. pulchellus at 31°C

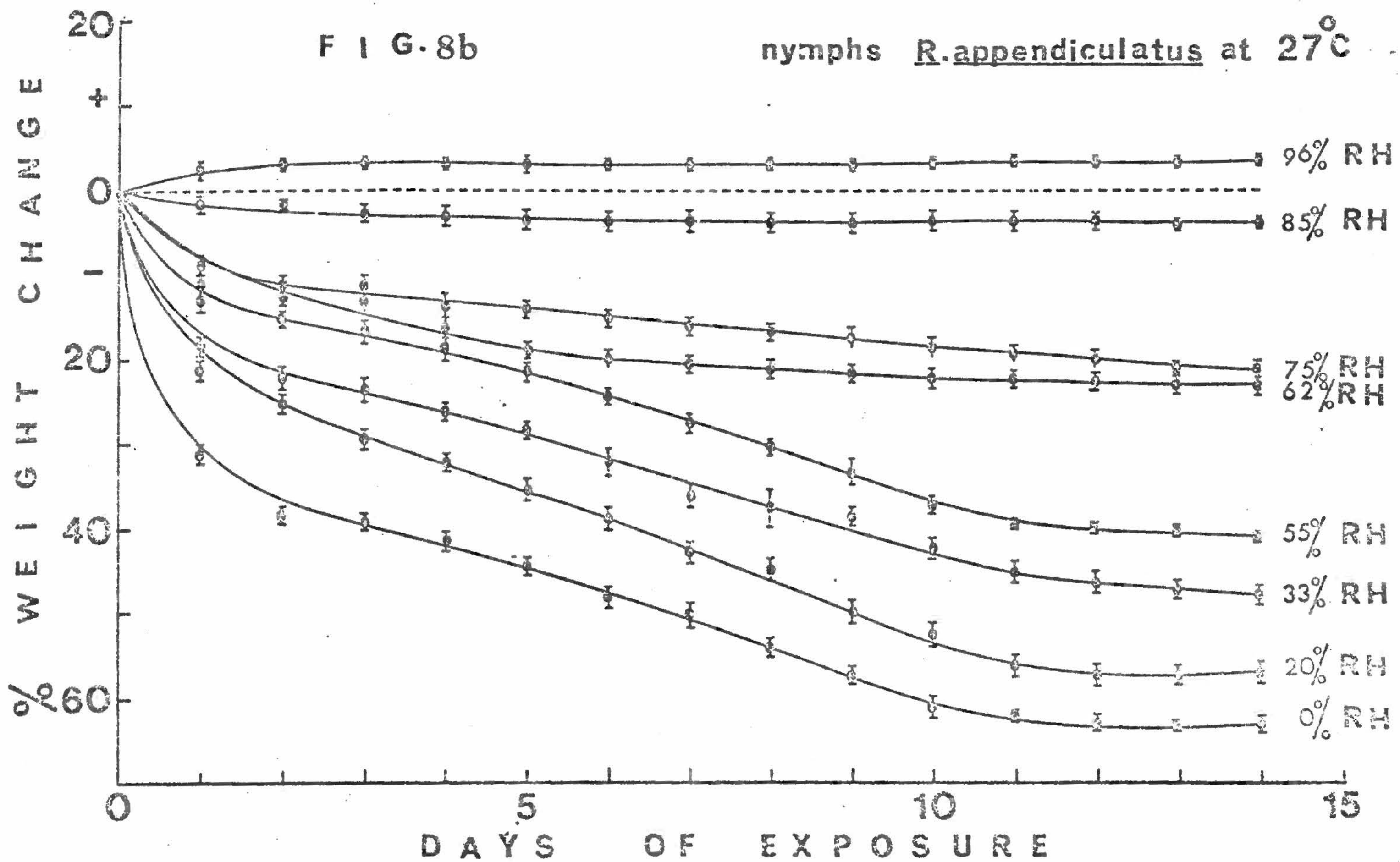

F I G.7c
male R. appendiculatus at 31°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

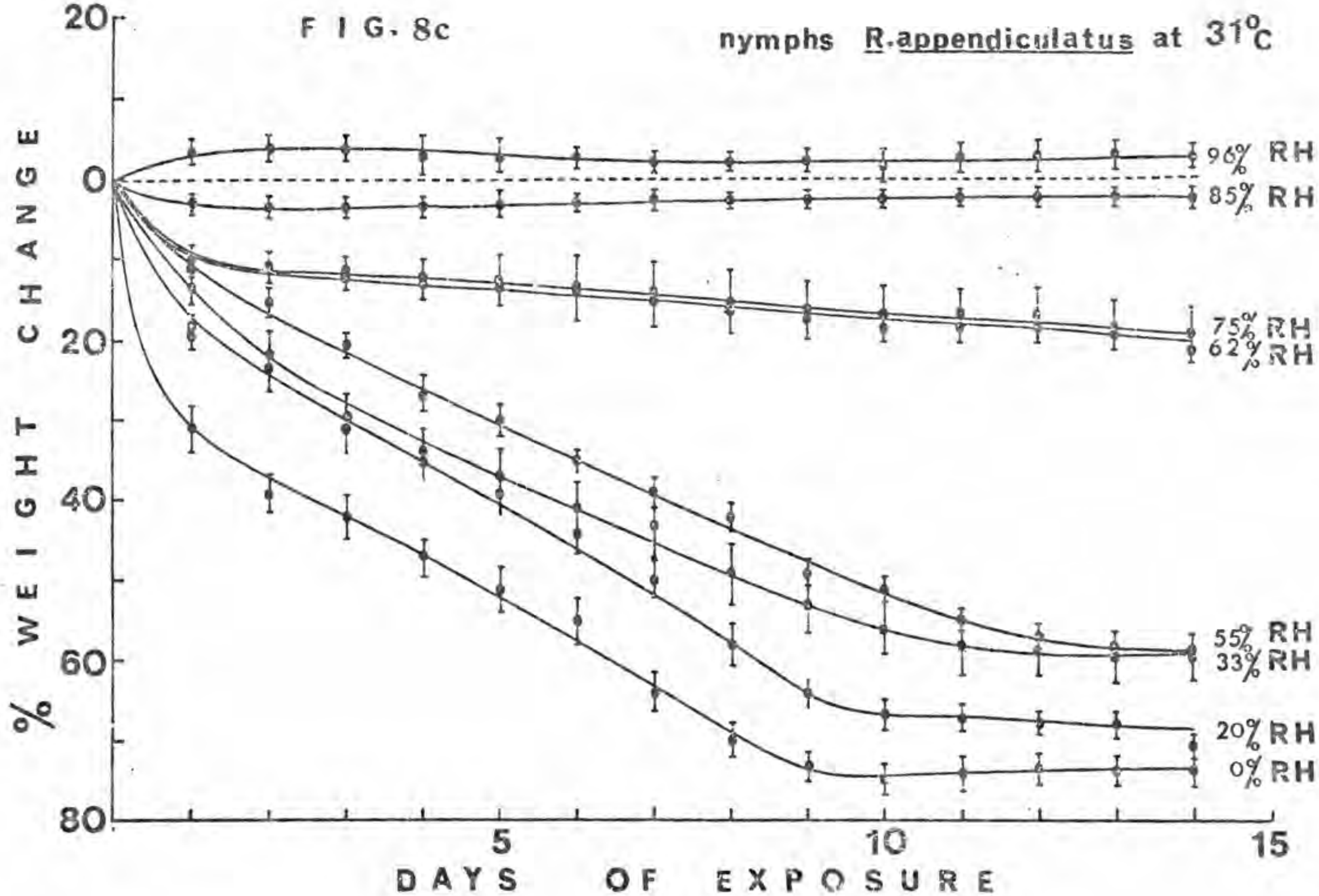

F I G. 7d
female R.appendiculatus at 31°C
% WEIGHT CHANGE
20
+
0
-
20
40
60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE

FIGURES 8a - 8c

Weight changes of nymphs of *R. appendiculatus* after exposure to 8 relative humidities (RHs) at 18°C, 27°C and 31°C respectively. The bars indicate ± S.E.


F I G. 8a
nymphs R.appendiculatus at 18°C
% WEIGHT CHANGE
DAYS OF EXPOSURE
20
0
20
40
60
80
0
5
10
15
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH


F I G. 8b
nymphs R.appendiculatus at 27°C
% WEIGHT CHANGE
20
+
0
-
20
40
%60
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
0
5
10
15
DAYS OF EXPOSURE


F I G. 8c
nymphs R.appendiculatus at 31°C
% WEIGHT CHANGE
20
0
20
40
60
80
96% RH
85% RH
75% RH
62% RH
55% RH
33% RH
20% RH
0% RH
5
10
15
DAYS OF EXPOSURE

pheric humidity (Figure 9a and 9b) at 23^{o}C, an approximate value of the CEH was obtained. Both species showed a minute initial loss in weight at 85% RH and then remained steady throughout the remainder of the period of observation. Neither low temperatures nor high temperatures affected this value.

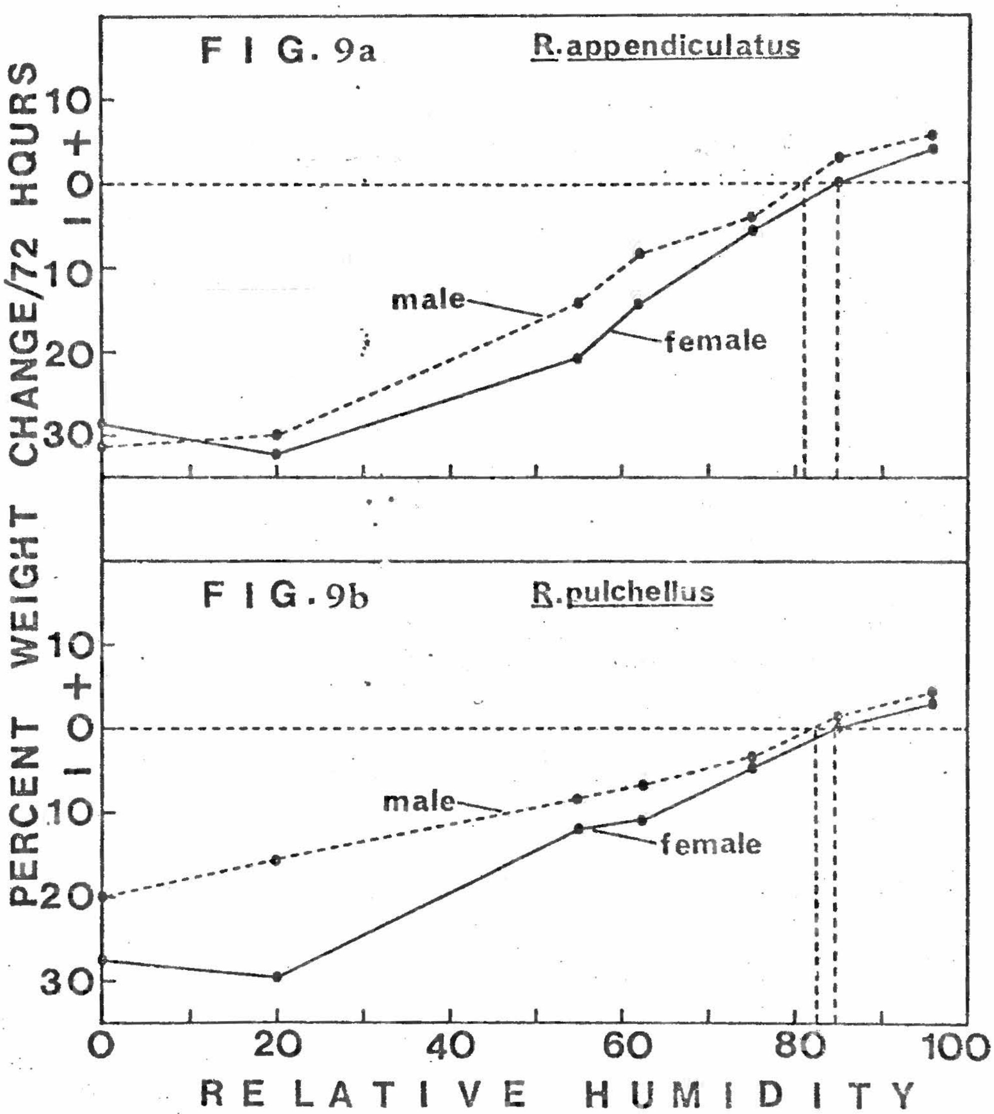
The ticks maintain their equilibrium weight by absorbing moisture from a saturated atmosphere and losing it to a subsaturated atmosphere when the need arises. Although the curves show little or no difference at the CEH value it is evident from the Table and Figures 9a and 9b that R.pulchellus achieve its equilibrium weight faster than R.appendiculatus. Similarly males of the two species also achieve this equilibrium faster than the females and their CEH is slightly below 85% RH.

Longevity was rapidly shortened at RHs below the CEH and this seem to correspond with water losses at 33%, 20% and 0% RHs, and therefore a limiting factor in their survival.

Mortality curves were drawn for each species for each humidity (Figures 10, 11, 12 & 13) from the data given in (Tables 21-24). The LD_{50} at 0% RH for female R. appendiculatus was 6.4 days and 6.8 days for female R. pulchellus and about 9.4 days for males of the two species. This value suggest that R.appendiculatus is more sensitive to water loss than R.pulchellus. However, no death occurred in either species at 85% and 96% RHs during the period of observation.

FIGURES 9a & 9b

Water loss: Determining the critical equilibrium humidity (CEH) for adult R.appendiculatus and R.pulchellus at 23^{o}C.


F I G. 9a
R. appendiculatus
male
female
F I G. 9b
R. pulchellus
male
female
PERCENT WEIGHT CHANGE/72 HOURS
10
+
0
-
10
20
30
0
20
40
60
80
100
RELATIVE HUMIDITY

FIGURES 10 & 11

Mortality curves for adult *R.appendiculatus* during exposure to different humidities at 23°C.

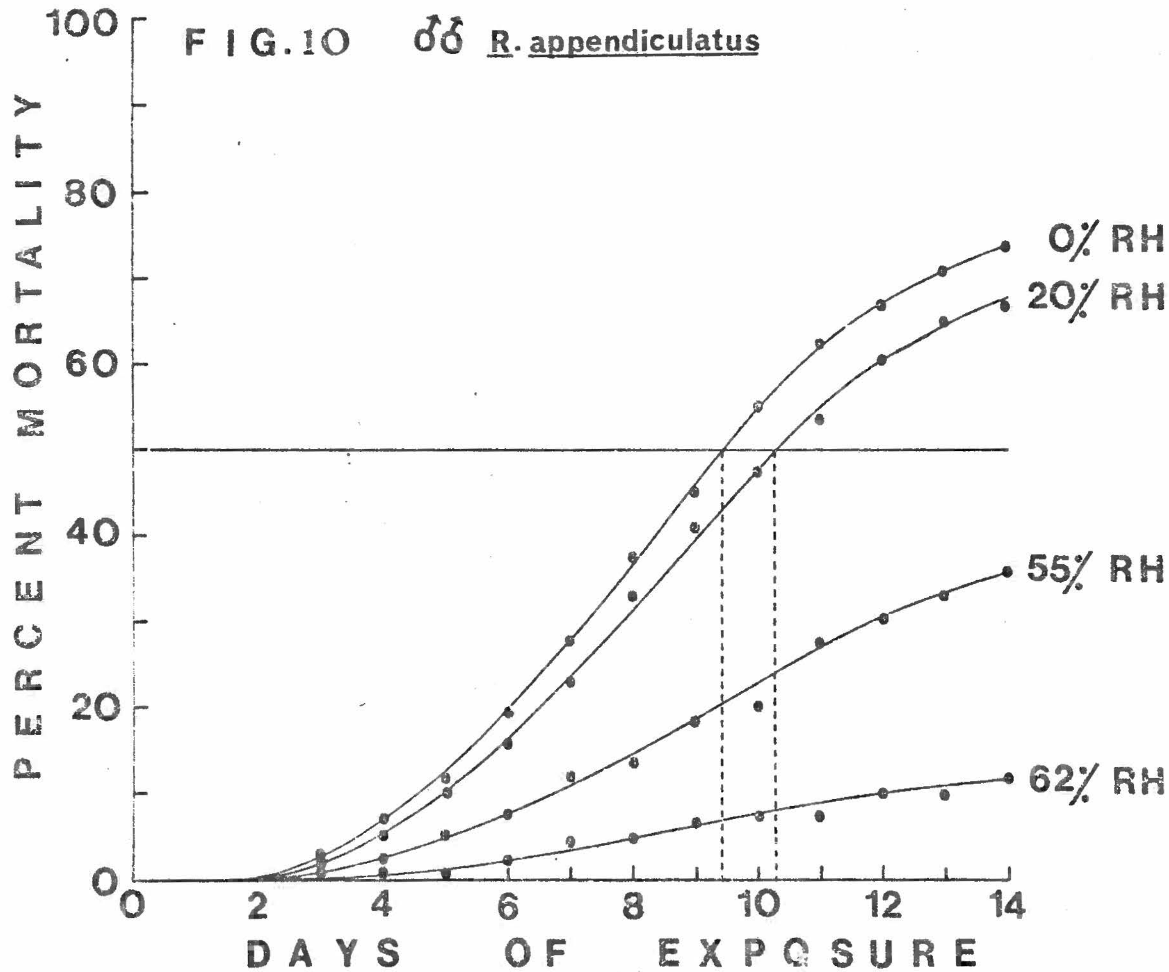
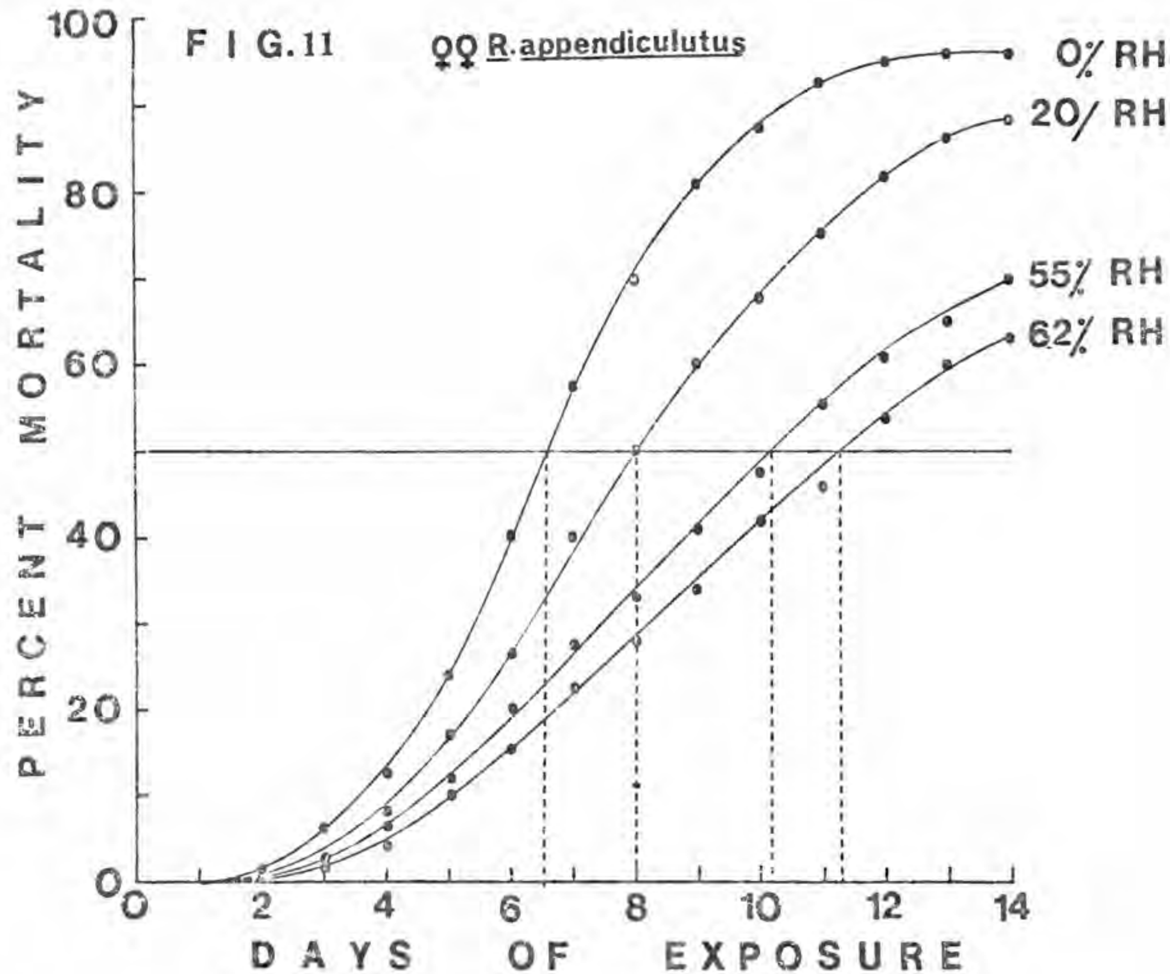
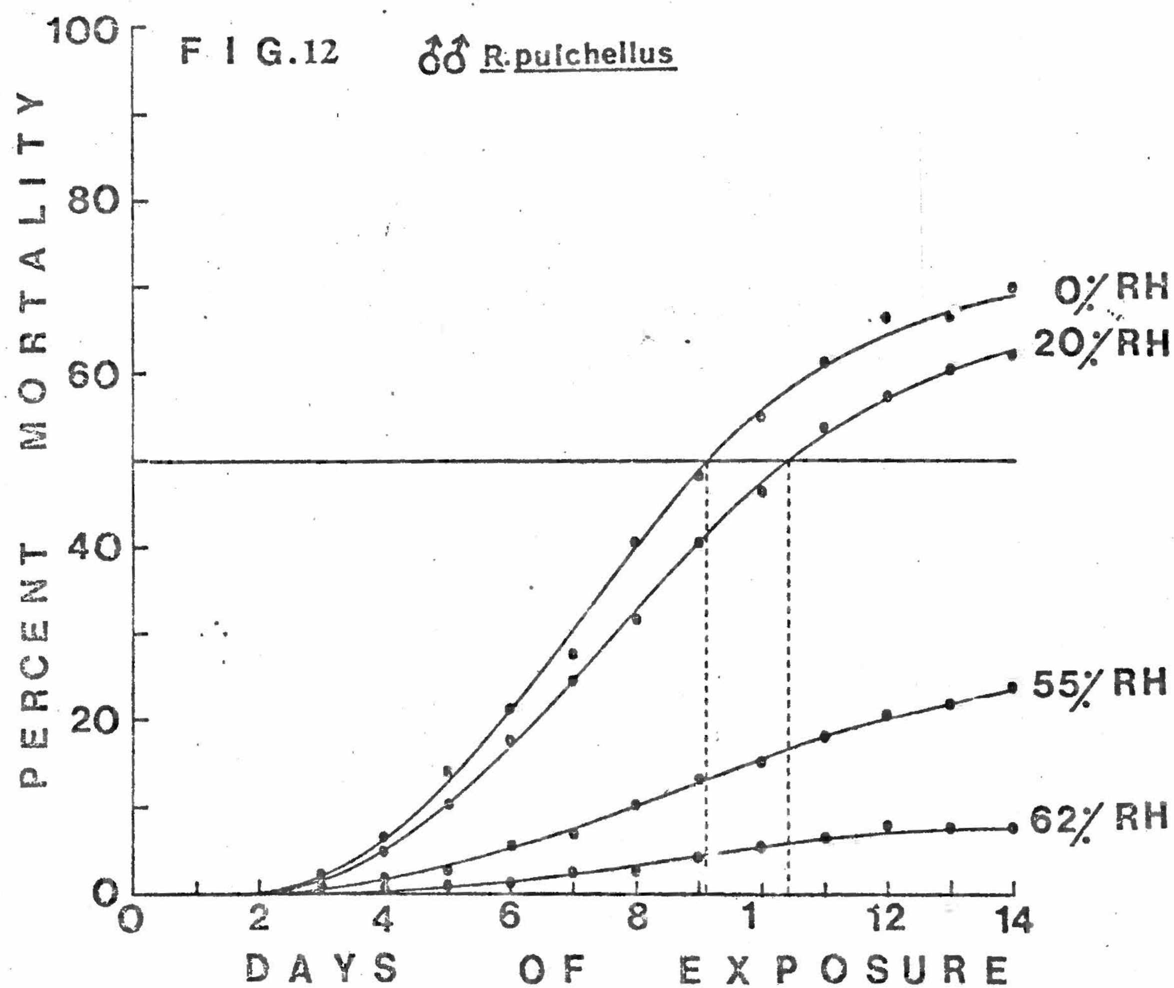


FIG.10 ♂♂ R. appendiculatus


F I G. 11
♀♀ R. appendiculutus
0% RH
20% RH
55% RH
62% RH
PERCENT MORTALITY
DAYS OF EXPOSURE
0
20
40
60
80
100
2
4
6
8
10
12
14

FIGURES 12 & 13

Mortality curves for adult R.pulchellus during exposure to different humidities at 23^{o}C.


F I G.12
♂♂ R. pulchellus
PERCENT MORTALITY
DAYS OF EXPOSURE
0% RH
20% RH
55% RH
62% RH
0
20
40
60
80
100
2
4
6
8
1
12
14

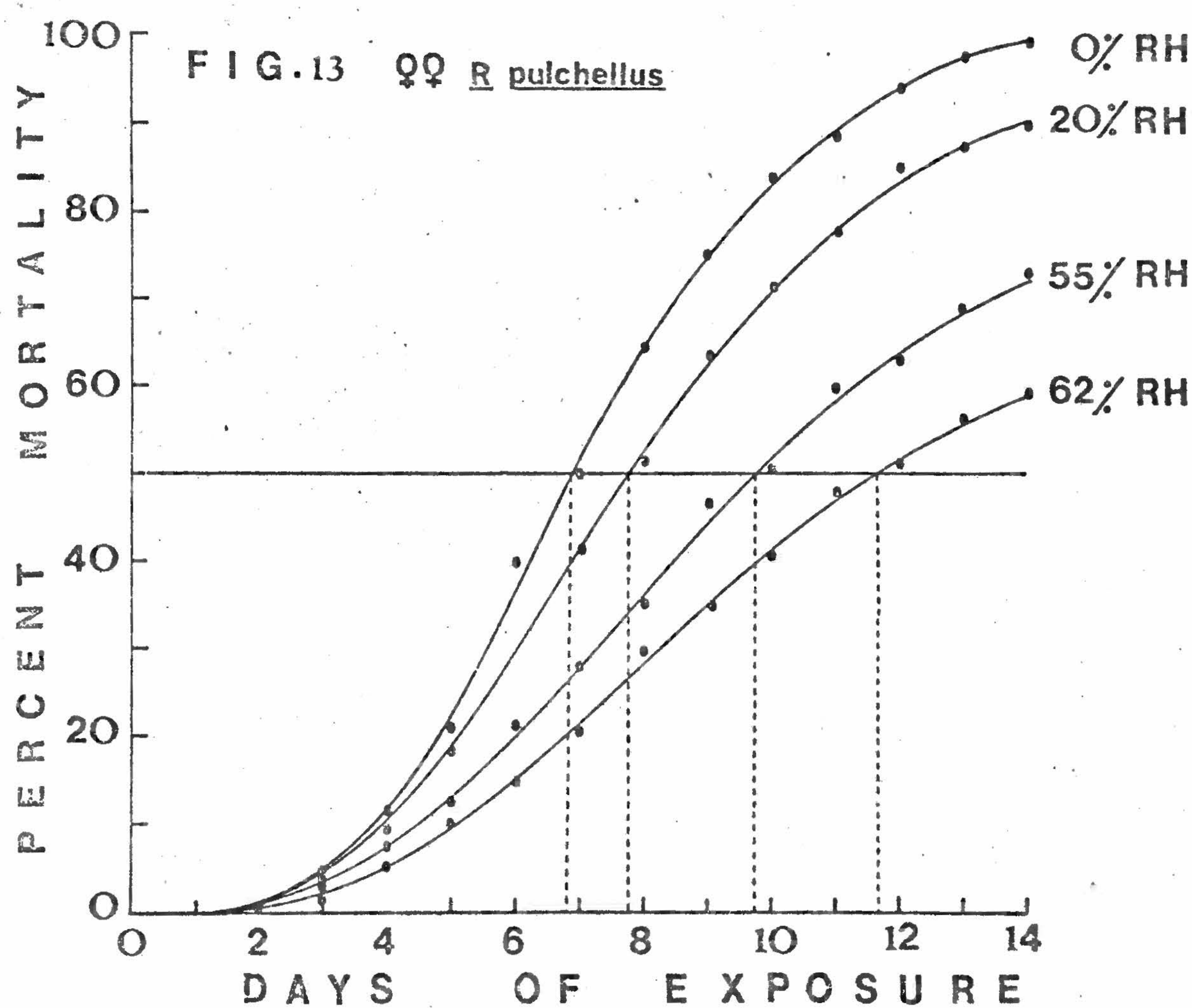


FIG. 13 ♀♀ R pulchellus

TABLE 21-22

Percent mortality according to number of days of exposure of 100 male and female R.appendiculatus respectively to different humidities at 23°C.

TABLE 21

% RH	DAYS OF EXPOSURE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0	0	0	2.8	7.1	11.5	19.0	27.5	37.5	45.0	55.1	62.6	67.0	70.8	74.0
20	0	0	2.2	5.0	10.2	15.7	22.6	32.7	40.6	47.5	53.4	60.6	65.0	67.3
55	0	0	0.5	2.5	5.0	7.5	10.6	13.5	18.0	20.2	27.5	30.1	33.0	35.5
62	0	0	0	0.8	0.8	2.8	4.0	4.8	6.5	7.5	7.6	10.0	10.1	12.0
75														
85														
96														

No mortality observed at 75%, 85% and 96% RHs.

TABLE 22

% RH	DAYS OF EXPOSURE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0	0	1.3	6.0	12.5	24.0	40.1	57.5	70.0	82.1	87.5	92.5	95.0	96.0	96.0
20	0	1.0	3.0	8.0	17.0	26.5	40.0	50.0	60.3	67.5	75.1	82.0	86.2	88.4
55	0	0	2.5	6.5	12.0	20.3	27.5	33.2	41.2	47.2	55.5	61.1	65.0	70.2
62	0	1.1	2.9	4.3	10.0	15.7	25.5	28.2	34.3	42.9	45.7	54.3	60.0	62.9
75	0	0	0	0	0	0	0	2.5	2.5	3.8	3.8	3.8	3.8	5.0
85														
96														

No mortality observed at 85% and 96% RHs.

TABLE 23-24

Percent mortality according to number of days of exposure of 100 male and female R.pulchellus respectively to different humidities at 23°C.

TABLE 23

% RH	DAYS OF EXPOSURE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0	0.4	1.0	2.0	6.6	14.0	21.3	27.5	40.5	48.0	55.0	61.4	66.5	66.8	70.0
20	0.0	0.5	1.7	4.7	10.0	17.8	29.4	31.5	40.5	46.7	53.9	57.8	60.5	62.0
55	0.0	0.0	0.6	1.7	3.0	5.5	6.7	10.0	13.0	15.1	18.0	20.5	21.5	23.6
62	0.0	0.0	0.0	0.5	0.6	1.0	2.4	2.5	4.0	5.0	6.5	7.5	7.3	7.4
75														
85														
96														

No mortality observed at 75%, 85% and 96% RHs.

TABLE 24

% RH	DAYS OF EXPOSURE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0	0.4	1.2	4.6	11.5	21.0	39.7	50.3	64.5	74.9	83.8	88.6	94.0	97.5	99.0
20	0.2	0.5	2.0	9.5	19.4	29.5	41.0	51.6	63.5	71.0	77.5	85.0	87.4	89.8
55	0.0	1.0	3.0	6.7	12.9	21.4	27.8	35.0	46.8	50.5	59.9	63.0	68.8	73.0
62	0.0	0.0	1.7	5.0	10.1	15.2	20.6	29.7	35.0	40.5	48.0	51.5	56.0	59.0
75														
85														
96														

No mortality observed at 75%, 85% and 96% RHs.

III.3: Investigation of the site of water vapour uptake

The patterns of water vapour uptake for both males and females of the two species are given in Tables 25-28 and are plotted in Figures 13a-13d. A three way analysis of variance was used to compare the results at 4, 8 and 12 days of exposure (Tables 29-37). It is evident from the curves that the water vapour uptake in all cases proceeded regularly at about the same rate for each site studied. Ticks with the whole body covered established an equilibrium with the atmosphere after day one of exposure indicating that the wax used was satisfactory for preventing the passage of water vapour. The results also show that the ticks with an average water loss of about 27-31% of their original weight when transferred to the high RH took up water vapour gradually over several days of exposure until an equilibrium was reached. The amount of water vapour uptake under each treatment was, in descending order:

(a) untreated controls
(b) dorsal surface covered
(c) spiracles, blocked
(d) ventral surface covered
(e) mouthparts covered

The analysis of variance (Tabel 35-37) showed that the treatments species —— sex interactions are highly significant but there is no significant difference with the other interactions. However, the sex/species difference was only significant on day 4 and totally insignificant on day 8 and 12. The ANOVA results show a highly significant difference in rate of water vapour uptake between sexes and species, with females absorbing water faster than males and R.pulchellus faster than R.appendiculatus. The rate of water vapour absorption decreased after about day 8 and was virtually complete by day 12. Examination of the different treatments (Table 29-34) shows that by day 12 blocking of the dorsal surface or the anus produced only slight and not significant impairment of water vapour uptake, whereas blocking the spiracles or mouthparts did so. Furthermore, the effect of blocking the mouthparts was significantly greater than blocking the spiracles. Blocking the ventral surface gave a just significantly greater effect than blocking the anus alone. The results obtained for ventral surface covered, reflect a summation of possibly the anus, spiracles and some unsclerotized parts of the ventral surface. Similarly when the dorsal surface was covered, there was a decrease in the rate of water vapour uptake as compared to the control suggesting that the dorsal surface does play a role in the water vapour absorption process and that it is not completely impermeable. Throughout the experimental observation, there were no deaths recorded but a moriband situation was seen after day 12 for the ticks with their ventral surface, anus and spiracles covered; probably the beginning of asphyxiation. It therefore appears from this study, that the mouthparts are the most important single site of water vapour uptake followed by the spiracles (i.e. the tracheal system)

TABLE 25-26

Mean weight gains of male and female *R.appendiculatus* respectively (expressed as percentage of the initial weight), during exposure to 96% RH and 27^{o}C with various sites of the body covered with paraffin wax (M.P. 44-45^{o}C). Each reading is the mean of five individuals.

TABLE 25

SITE COVERED	MALES					
	DAYS OF EXPOSURE					
	1	2	3	4	5	6
UNTREATED CONTROLS	8.87	11.06	13.59	17.98	20.19	23.48
± SE	0.45	0.46	0.44	0.74	0.74	0.69
DORSAL SURFACE	9.26	11.13	12.92	15.54	18.36	21.48
± SE	0.45	0.76	0.63	0.87	0.84	0.86
SPIRACLES	4.35	6.04	8.20	10.25	12.09	13.97
± SE	0.73	0.66	0.33	0.37	0.50	0.52
ANUS	8.47	12.23	13.71	15.90	17.86	20.37
± SE	0.67	1.11	1.23	0.85	1.13	1.26
VENTRAL SURFACE	2.75	4.11	5.97	8.82	10.47	12.75
± SE	0.10	0.34	0.29	0.40	0.48	0.20
MOUTHPARTS	3.12	4.42	6.05	8.02	9.98	11.72
± SE	0.29	0.45	0.33	0.29	0.36	0.35
WHOLE BODY	0.75	0.83	0.87	0.97	0.98	0.99
± SE	0.09	0.05	0.06	0.02	0.02	0.03

TABLE 25 cont.

SITE COVERED	MALES					
	DAYS OF EXPOSURE					
	7	8	9	10	11	12
UNTREATED CONTROLS	27.35	30.63	32.47	32.85	32.93	32.95
± SE	0.60	0.48	0.84	0.77	0.74	0.73
DORSAL SURFACE	22.73	24.75	27.86	29.01	29.28	29.31
± SE	1.10	0.87	0.53	0.57	0.75	0.79
SPIRACLES	15.86	18.19	20.32	21.36	21.76	21.77
± SE	0.74	0.83	1.06	0.68	0.53	0.53
ANUS	21.61	24.22	25.63	27.89	28.71	28.89
± SE	1.27	1.67	2.03	2.03	2.03	2.00
VENTRAL SURFACE	14.51	16.08	18.98	20.23	20.61	20.70
± SE	0.92	0.82	0.81	0.74	0.57	0.55
MOUTHPARTS	13.76	15.79	17.29	18.52	19.38	19.63
± SE	0.36	0.83	0.71	0.98	0.92	0.92
WHOLE BODY	1.00	1.00	1.00	1.01	0.99	1.00
± SE	0.03	0.05	0.05	0.05	0.04	0.04

TABLE 26

SITE COVERED	FEMALES					
	DAYS OF EXPOSURE					
	1	2	3	4	5	6
UNTREATED CONTROLS	9.85	13.32	16.93	20.34	23.51	26.72
± SE	0.41	0.43	1.02	1.17	1.31	1.29
DORSAL SURFACE	9.53	12.12	14.89	17.89	20.41	22.82
± SE	0.29	0.43	0.35	0.60	0.25	0.46
SPIRACLES	7.86	9.83	13.04	15.81	16.71	19.18
± SE	1.04	0.94	0.95	0.92	0.67	1.20
ANUS	8.84	12.02	14.32	17.01	21.16	24.07
± SE	0.81	0.99	0.65	0.56	0.89	0.65
VENTRAL SURFACE	7.07	9.55	12.15	14.15	16.45	18.22
± SE	0.57	0.93	0.88	1.07	1.13	0.76
MOUTHPARTS	8.70	10.58	12.31	14.61	15.61	17.34
± SE	0.91	0.83	0.37	0.43	0.31	0.63
WHOLE BODY	0.97	0.82	1.54	1.31	1.31	1.15
± SE	0.34	0.49	0.54	0.53	0.54	0.58

TABLE 26 cont.

SITE COVERED	FEMALES					
	DAYS OF EXPOSURE					
	7	8	9	10	11	12
UNTREATED CONTROLS	29.86	32.44	34.24	35.83	36.81	36.80
± SE	1.18	1.32	1.39	1.28	1.27	1.27
DORSAL SURFACE	25.69	28.14	30.72	32.35	34.09	34.20
± SE	0.49	0.58	0.31	0.77	1.38	1.42
SPIRACLES	20.94	20.95	24.50	25.20	25.35	25.53
± SE	1.10	1.11	0.53	0.79	0.81	0.81
ANUS	27.36	28.81	29.86	30.72	30.95	31.18
± SE	0.36	0.38	0.33	0.52	0.63	0.62
VENTRAL SURFACE	20.05	22.27	23.22	23.40	23.45	23.58
± SE	0.78	0.61	0.46	0.49	0.51	0.44
MOUTHPARTS	19.07	19.64	20.63	21.49	21.60	21.59
± SE	0.44	0.45	0.65	0.97	1.19	1.29
WHOLE BODY	0.95	0.63	0.70	0.85	0.83	0.88
± SE	0.61	0.58	0.65	0.60	0.53	0.52

TABLE 27-28

Mean weight gain of male and female *R.pulchellus* respectively (expressed as percentage of the initial weight), during exposure to 96% RH and 27°C with various site of the body covered with paraffin wax (M.P. 44-45°C). Each reading is the mean of five individuals.

SITE COVERED	MALES					
	DAYS OF EXPOSURE					
	1	2	3	4	5	6
UNTREATED CONTROLS	9.41	15.02	21.13	23.24	26.25	29.08
± SE	1.07	1.50	2.79	3.26	3.90	4.05
DORSAL SURFACE	8.32	13.61	21.19	23.07	26.43	28.22
± SE	0.31	0.87	0.25	0.11	0.18	0.07
SPIRACLES	7.61	12.27	17.49	21.35	20.93	18.90
± SE	1.81	1.45	1.98	1.95	2.58	1.70
ANUS	12.79	15.30	19.16	22.83	25.27	26.94
± SE	1.66	0.73	1.60	2.43	3.98	4.81
VENTRAL SURFACE	4.88	12.56	15.43	17.00	18.92	20.87
± SE	1.07	0.47	1.38	1.27	1.26	1.01
MOUTHPARTS	7.43	12.14	15.66	15.66	17.58	19.40
± SE	1.04	2.31	3.04	3.04	3.94	3.10
WHOLE BODY	0.64	1.39	1.95	2.61	3.22	3.43
± SE	0.13	0.54	0.74	0.82	0.67	0.78

SITE COVERED	MALES					
	DAYS OF EXPOSURE					
	7	8	9	10	11	12
UNTREATED CONTROLS	33.44	32.31	32.02	32.99	31.92	32.91
± SE	2.48	4.45	5.33	5.25	4.13	4.44
DORSAL SURFACE	30.32	30.52	31.61	31.59	31.64	33.37
± SE	0.69	0.31	0.04	0.09	0.04	0.16
SPIRACLES	20.76	22.22	25.91	28.20	29.28	26.00
± SE	1.56	1.44	2.15	2.93	3.88	3.43
ANUS	27.68	27.56	28.98	30.03	31.61	32.69
± SE	4.76	4.67	4.53	5.65	4.63	5.08
VENTRAL SURFACE	22.18	24.14	25.58	26.58	26.80	27.13
± SE	0.45	1.18	1.05	0.87	0.78	0.87
MOUTHPARTS	19.39	21.20	21.94	22.14	22.24	21.56
± SE	3.04	3.37	3.54	3.37	3.27	2.73
WHOLE BODY	3.31	3.93		3.50	3.35	3.36
± SE	0.73	0.50	0.69	0.65	0.81	0.69

SITE COVERED	FEMALES					
	DAYS OF EXPOSURE					
	1	2	3	4	5	6
UNTREATED CONTROLS	9.84	16.04	20.52	24.65	31.24	33.22
± SE	2.59	3.72	4.80	5.10	5.50	4.99
DORSAL SURFACE	9.23	14.51	20.22	25.11	28.64	28.26
± SE	2.25	2.83	3.15	2.56	2.65	2.84
SPIRACLES	4.50	12.35	15.78	20.07	20.89	24.09
± SE	1.12	4.82	4.96	4.68	4.56	4.33
ANUS	7.44	12.15	15.62	20.36	22.42	25.52
± SE	1.95	1.59	1.23	1.85	2.42	2.07
VENTRAL SURFACE	6.91	10.00	14.26	16.20	20.02	21.36
± SE	1.67	2.71	3.69	3.44	3.42	3.68
MOUTHPARTS	3.36	6.59	10.96	14.96	17.83	19.87
± SE	0.98	1.96	1.69	1.89	1.67	1.40
WHOLE BODY	3.18	4.11	4.87	6.69	6.60	6.37
± SE	0.98	1.08	1.05	1.79	1.77	1.30

TABLE 28 cont.

SITE COVERED	FEMALES					
	DAYS OF EXPOSURE					
	7	8	9	10	11	12
UNTREATED CONTROLS	36.68	38.47	40.01	40.20	41.63	41.71
± SE	3.75	3.83	3.93	3.72	3.47	3.45
DORSAL SURFACE	30.63	32.72	33.43	34.52	34.00	35.46
± SE	2.52	2.60	2.47	2.45	3.45	2.94
SPIRACLES	28.02	29.19	30.72	32.97	34.10	35.86
± SE	3.98	3.86	3.24	2.75	2.48	2.29
ANUS	28.16	31.04	33.45	34.37	35.14	35.91
± SE	1.80	2.07	2.17	2.21	2.13	2.23
VENTRAL SURFACE	23.87	25.10	27.88	28.09	30.35	31.57
± SE	3.89	4.02	3.66	3.78	3.35	3.27
MOUTHPARTS	22.01	24.42	25.01	25.44	26.43	25.40
± SE	1.18	1.57	1.87	1.52	1.54	2.18
WHOLE BODY	6.33	6.17	6.08	6.01	5.83	5.99
± SE	1.45	1.46	1.63	1.76	1.73	1.87

TABLE 29-34

Three-way analysis of variance with replications, data for percentage weight gain days 4, 8 and 12 for *R. appendiculatus* and *R. pulchellus*. Different sites of the tick body covered with paraffin wax (M.P. 44-45°C) to show possible site of water vapour uptake.

TABLE 29

Sums over both species

Sexes	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
Male	329.29	21.81	313.38	244.48	286.64	236.53	205.97	1638.10
Female	392.56	34.37	348.48	306.96	334.97	275.76	234.95	1928.05
Total	721.85	56.18	661.86	551.44	621.61	512.29	440.92	3566.15
Mean	36.09	2.81	33.09	27.57	31.08	25.61	22.05	

33.28 30.28 5.52 3.51 5.47 3.56

3.00

8.52 5.52

5.01 9.03

14.04

LSD
(P=0.05)
=5.48

Sums over both sexes

Species	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
R.pul-chellus	373.09	46.74	344.29	314.95	342.98	290.86	234.82	1947.73
R.appendi-culatus	348.76	9.44	317.57	236.49	278.63	221.43	206.10	1618.42

TABLE 30

		Male	Female	Total
Sums of all the treatments	*R. pulchellus*	888.07 (25.37)	1059.66 (30.27)	1947.73
	R. appendiculatus	750.03 (21.43)	868.81 (24.81)	1618.42
	Total	1638.10	1928.05	3566.15

TABLE 31

Sums over both species	Sexes	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
	Male	222.64	20.94	193.05	157.96	193.69	129.10	118.43	1035.81
	Female	224.93	40.02	215.01	179.41	186.85	151.78	147.88	1145.88
	Total	447.57	60.96	408.06	337.37	380.54	280.88	266.31	2181.69
	Mean	22.38	3.05	20.40	16.86	19.02	14.04	13.32	

Sums over both sexes	Species	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
	R.pulchellus	255.95	49.56	240.89	207.10	215.96	166.03	153.14	1288.63
	R.appendiculatus	191.62	11.40	167.17	130.27	164.58	114.85	113.17	893.06

TABLE 32

		Male	Female	Total
Sums over all treatments	<u>R.pulchellus</u>	648.40 (18.53)	640.23 (18.29)	1286.63
	<u>R.appendi-culatus</u>	387.41 (11.07	505.65 (14.45)	893.06
	Total	1035.81	1145.88	2181.69

TABLE 33

Sums over both species

Sexes	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
Male	285.89	24.65	276.33	211.66	258.89	191.51	184.96	1433.89
Female	354.57	34.04	304.29	250.71	299.24	236.84	220.28	1699.97
Total	640.46	58.69	580.62	462.37	558.13	428.35	405.24	3133.86
Mean	33.03	2.93	29.03	23.12	24.79	21.42	20.26	

Sums over both sexes

Species	Control	Whole body	Dorsal	Spiracles	Anus	Ventral	Mouthparts	Total
R. pulchellus	325.09	50.52	316.17	266.65	293.00	236.60	228.08	1716.11
R. appendiculatus	315.37	8.17	264.45	195.72	265.13	191.75	177.16	1417.75

TABLE 34

		Male	Female	Total
Sums over all treatments	*R. pulchellus*	780.54 (21.83)	935.57 (26.73	1716.11
	R. appendiculatus	653.35 (18.67)	764.40 (21.84)	1417.75
	Total	1433.89	1699.97	3133.86

TABLE 35-37

Summary table for three-way analysis of variance; of results on site of water uptake days 4, 8 and 12 for adult *R. appendiculatus* and *R. pulchellus*

TABLE 35

Source	df	SS	MS	F	P
Treatment	6	4951.22	852.20	62.90	***
Sex	1	86.54	86.54	6.60	*
Species	1	1117.68	1117.68	85.19	***
Treatment x Sex	6	50.47	8.41	0.64	NS
Treatment x Species	6	71.77	11.96	0.91	NS
Sex x Species	1	114.14	114.14	8.70	**
Treat. x Sex x Species	6	108.62	18.10	1.38	NS
Residual	112	1469.95	13.12	-	

df	5%	1%	0.1%
(1,112)	3.93	6.88	11.46
(6,112)	2.19	2.98	4.08

Studentized range $q_{7,112} = 4.25$

* Significant at 5% level

** Significant at 1% level

*** Significant at 0.1% level

LSD (P = 0.05) between treatment means (based on studentized range) = $\sqrt{\frac{13.12}{20}} \times 4.25 = 3.44$

TABLE 36

Source	df	SS	MS	F	P
Treatment	6	11037.01	1839.50	96.76	***
Sex	1	505.70	505.70	26.60	***
Species	1	635.85	635.85	31.87	***
Treatment x Sex	6	96.41	16.07	0.85	NS
Treatment x Species	6	112.91	18.82	0.99	NS
Sex x Species	1	13.82	13.82	0.73	NS
Treat. x Sex x Species	6	146.84	24.47	1.29	NS
Residual	112	2129.36	19.01	-	

df	5%	1%	0.1%
(1,112)	3.93	6.88	11.46
(6,112)	2.19	2.98	4.08

Studentized range $q_{7,112} = 4.25$

LSD (P = 0.05) between treatment means (based on studentized range) = $\sqrt{\frac{19.01}{20}} \times 4.25 = 4.14$

TABLE 37

Source	df	SS	MS	F	P
Treatment	6	14642.18	2440.36	73.26	***
Sex	1	600.50	600.50	18.03	***
Species	1	774.60	774.60	23.25	***
Treatment x Sex	6	100.06	16.68	0.50	NS
Treatment x Species	6	157.37	26.23	0.79	NS
Sex x Species	1	20.25	20.25	0.61	NS
Treat. x Sex x Species	6	83.91	13.99	0.42	NS
Residual	112	3730.96	33.31	-	

df	5%	1%	0.1%
(1,112)	3.93	6.88	11.46
(6,112)	2.19	2.98	4.08

Studentized range $q_{7,112} = 4.25$

LSD (P = 0.05) between treatment means (based on studentized range) = $\sqrt{\frac{33.31}{20}} \times 4.25 = 5.48$

with some general absorption throughout the body surfaces particularly the rest of the ventral surface.

III.4: Investigations of cuticular permeability in adults

The effects of temperature have been observed on cuticular water loss of Rhipicephalus appendiculatus and R.pulchellus when exposed to dry moving air.

The results obtained on the rate of water loss from males and females of the two species are given in Tables (38-41) and are plotted in Figures 14 and 15. The curves were transformed to linearity by means of the transformation: $\log_{10}\left\{W^{\frac{1}{3}}/SI^{\frac{1}{2}}\right\}$ where W = Weight change in mg and SI is the scutal index (Obenchain 1976). The advantage of this method is that comparisons between ticks of different body sizes can be made and there is due allowance for the fact that the ratio of the evaporating surface to the moisture-containing volume of an organism increases as the body size decreases.

It was necessary to measure the evaporating surface per unit area of the cuticle because the irregularities and convolutions of the alloscutum are hard to assess. Hence measuring the scutal indices is a useful step in understanding water loss in ixodid ticks.

Since the ticks were of the same age group, the cuticular age effect was minimised. It is reasonable to assume that newly moulted ticks will lose greater

TABLE 38 - 39

The effect of temperature on cuticular perm4ability on live and dead adult R. appendiculatus. Cuticular water loss expressed as $\log_{10}$ (W 1/3 /SI½).

TABLE 38

TEMPERATURE °C	MALE *R. APPENDICULATUS*	
	LIVE $\log(W^{\frac{1}{3}}/SI^{\frac{1}{2}})$. ±SE	DEAD $\log(W^{\frac{1}{3}}/SI^{\frac{1}{2}})$. ±SE
10	− 1.238 ± 0.011	− 1.158 ± 0.004
20	− 1.210 ± 0.012	− 1.141 ± 0.003
30	− 1.172 ± 0.022	− 1.108 ± 0.006
40	− 1.136 ± 0.014	− 1.059 ± 0.004
50	− 1.112 ± 0.011	− 1.036 ± 0.004
60	− 1.050 ± 0.006	− 1.003 ± 0.003
70	− 1.022 ± 0.017	− 0.965 ± 0.002

TABLE 39

	FEMALE *R. APPENDICULATUS*	
	LIVE $LOG(W\frac{1}{3}/SI\frac{1}{2}).\pm SE$	DEAD $LOG(W\frac{1}{3}/SI\frac{1}{2}).\pm SE$
10	- 0.963 ± 0.009	- 0.945 ± 0.004
20	- 0.937 ± 0.009	- 0.916 ± 0.005
30	- 0.903 ± 0.002	- 0.844 ± 0.009
40	- 0.889 ± 0.005	- 0.823 ± 0.002
50	- 0.824 ± 0.006	- 0.750 ± 0.010
60	- 0.812 ± 0.009	- 0.712 ± 0.030
70	- 0.746 ± 0.016	- 0.682 ± 0.004

TABLE 40 - 41

The effect of temperature on cuticular permeability on live and dead adult *R. pulchellus* Cuticular water loss expressed as $\log_{10}$ (W 1/3 /SI½)

TABLE 40

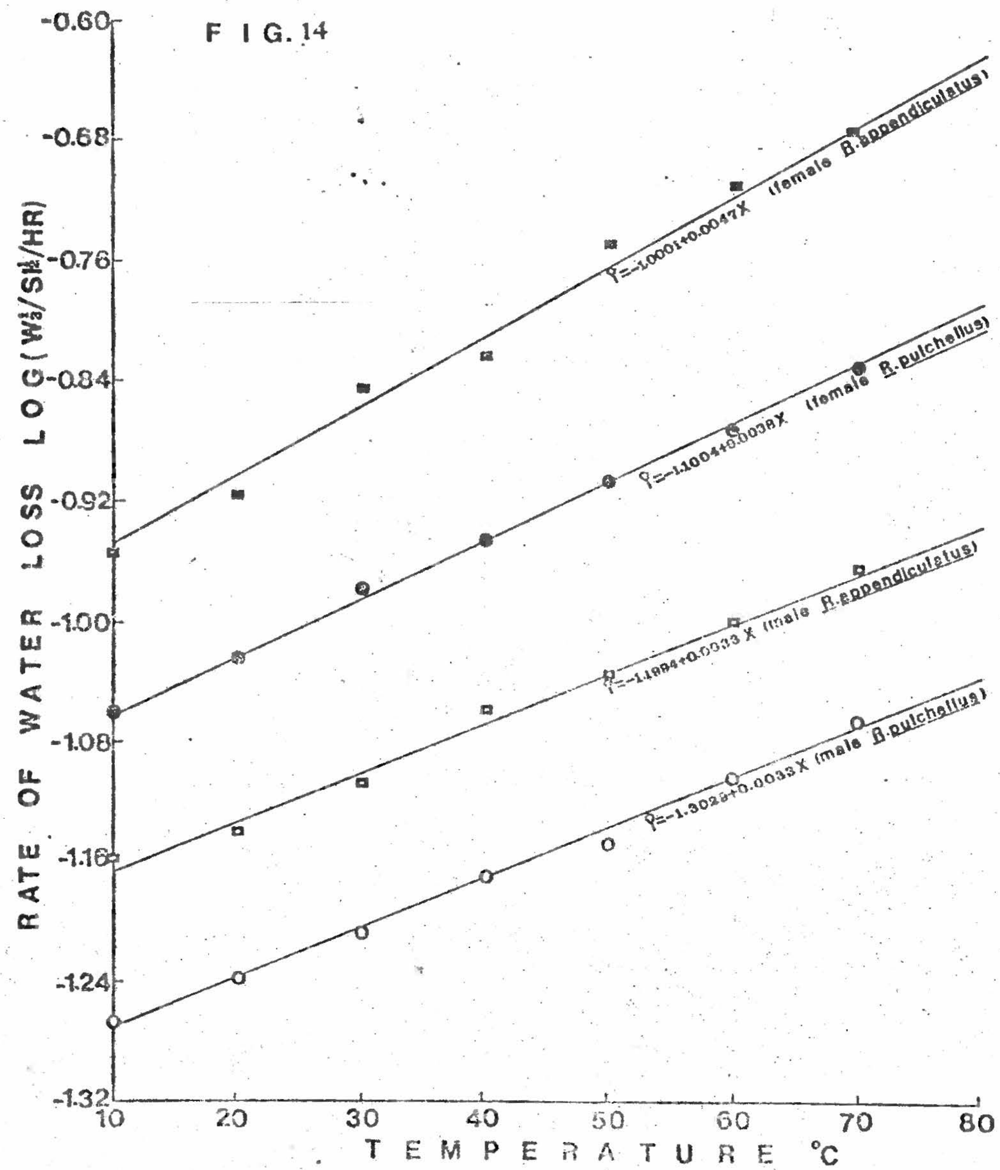
TEMPERATURE °C	MALE R. PULCHELLUS	
	LIVE $LOG(W\frac{1}{3}/SI\frac{1}{2}) \pm SE$	DEAD $LOG(W\frac{1}{3}/SI\frac{1}{2}) \pm SE$
10	- 1.296 ± 0.029	- 1.266 ± 0.008
20	- 1.258 ± 0.010	- 1.238 ± 0.007
30	- 1.269 ± 0.016	- 1.208 ± 0.016
40	-.1.197 ± 0.019	- 1.166 ± 0.011
50	- 1.159 ± 0.015	- 1.148 ± 01014
60	- 1.099 ± 0.011	- 1.104 ± 0.05
70	- 1.072 ± 0.016	- 1.067 ± 0.013

TABLE 41

TEMPERATURE °C	FEMALE R. PULCHELLUS	
	LIVE $LOG(W^{\frac{1}{3}}/SI^{\frac{1}{2}}).\pm SE$	DEAD $LOG(W^{\frac{1}{3}}/SI^{\frac{1}{2}}).\pm SE$
10	- 1.183 ± 0.024	- 1.066 ± 0.002
20	- 1.120 ± 0.014	- 1.024 ± 0.007
30	- 1.086 ± 0.009	- 0.979 ± 0.004
40	- 1.032 ± 0.028	- 0.945 ± 0.011
50	- 0.938 ± 0.012	- 0.907 ± 0.006
60	- 0.874 ± 0.014	- 0.874 ± 0.003
70	- 0.829 ± 0.006	- 0.832 ± 0.006

FIGURE 14

The effect of temperature on the rate of cuticular water loss of unfed, ammonia-killed adult *R.appendiculatus* and *R.pulchellus*. Rate of water loss expressed as $\log_{10}(W^{\frac{1}{3}}/SI$
Points on the graph represent mean values of five replicat

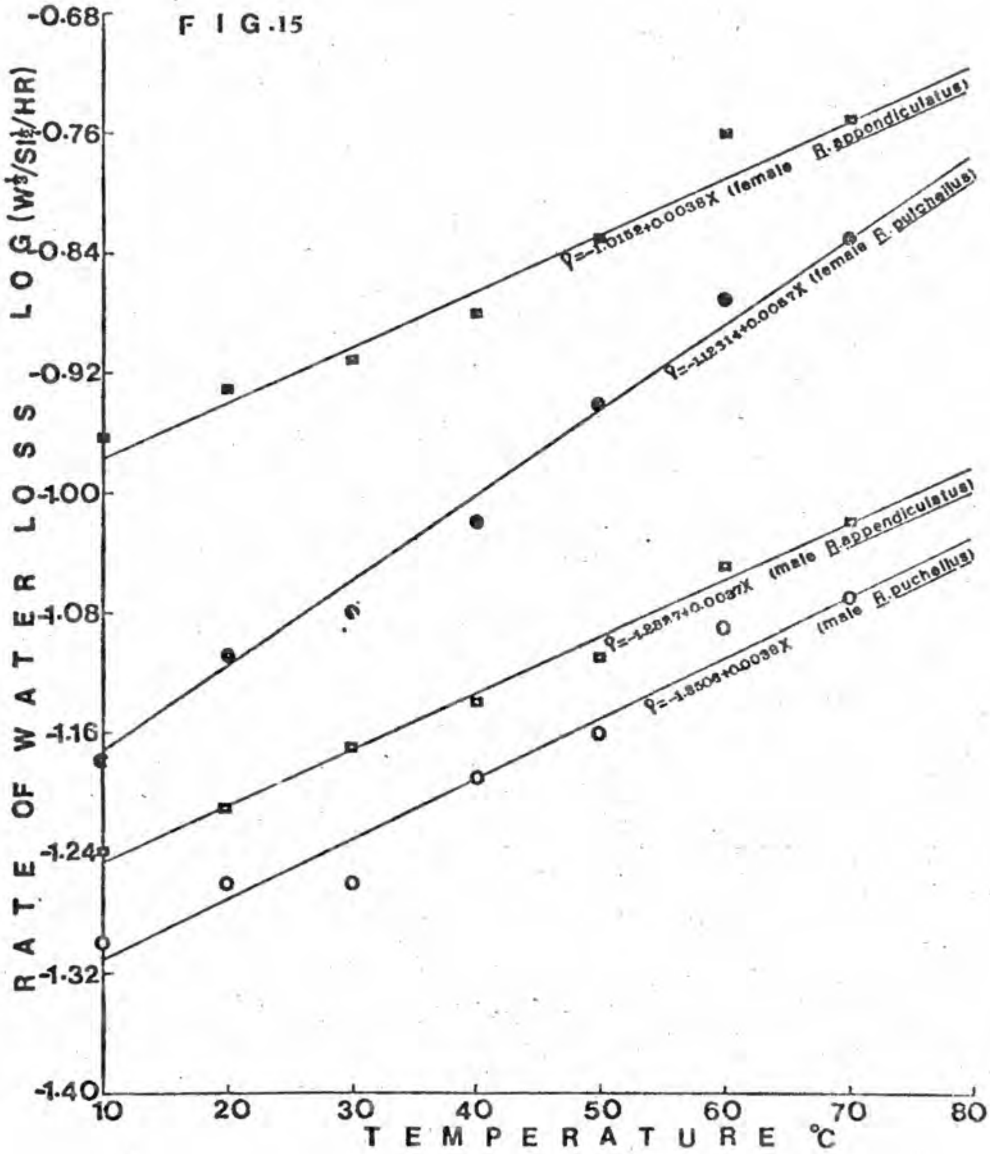


F I G. 14
RATE OF WATER LOSS LOG (W⅔/S⅔/HR)
-0.60
-0.68
-0.76
-0.84
-0.92
-1.00
-1.08
-1.16
-1.24
-1.32
10
20
30
40
50
60
70
80
T E M P E R A T U R E °C
Ŷ=-1.0001+0.0047X (female R. appendiculatus)
Ŷ=-1.1004+0.0038X (female R. pulchellus)
Ŷ=-1.1994+0.0033 X (male R. appendiculatus)
Ŷ=-1.3028+0.0033X (male R. pulchellus)

FIGURE 15

The effect of temperature on the rate of cuticular water loss of unfed, live adult *R.appendiculatus* and *R.pulchellus*. Rate of water loss expressed as $\log_{10}(W^{\frac{1}{3}}/SI^{\frac{1}{2}})$. Points on the graph represent mean values of five replicates.

FIG.15


-0.68
-0.76
-0.84
-0.92
-1.00
-1.08
-1.16
-1.24
-1.32
-1.40
RATE OF WATER LOSS LOG (W⅓/SI½/HR)
Ŷ=-1.0152+0.0038X (female R. appendiculatus)
Ŷ=-1.12314+0.0087X (female R. pulchellus)
(male R. appendiculatus)
Ŷ=-1.8506+0.0038X (male R. puchellus)
10
20
30
40
50
60
70
80
TEMPERATURE °C

quantity of water than older ones. It was also necessary that the apparatus provided an atmosphere of constant saturation deficit and temperature, because the evaporating surface of the tick must be under the same conditions as the space above it. This was achieved by employing a stream of moving air. Short exposures were used in order to obtain a series of readings without unduly affecting the water content of the ticks.

As defined earlier, permeability is the rate of diffusion through a unit area for a unit of the transporting agence. There must therefore be an activity gradient along the whole path through which the water moves that is strictly analogous to an electrical potential gradient.

In the transformed state the results showed that the rate of water loss was temperature dependent and an exponential curve was obtained. Above 45°C the rate of water loss gradually increased. It is possible (Beament, 1945 ; Wigglesworth, 1945; Lees, 1946) to extrapolate from the changes in the curve the temperature at which the cuticular wax layer can be assumed to have melted, but this was not attempted in the present case.

When the rates of water loss of live ticks and freshly dead ticks are compared (Figures 14 and 15) it can be seen that the later lose water more rapidly.

From the results of an analysis of covariance (Table 42-43) it can also be seen that dead ticks lose water more rapidly than live ones, R.appendiculatus more quickly than R.pulchellus and females lose more than males. It seems therefore that the cuticle of R.appendiculatus is more permeable in general than that of R.pulchellus. The difference between the sexes is explicable on the grounds that the entire dorsal surface of the males is covered with the heavily sclerotised scutum, less permeable than the back of the unfed female which is only partly protected by the small conscutum.

III.5: Rate of lipid depletion

The data on lipid depletion for both sex of both species during exposure for 10 days at 0% RH and 27°C are given in Table 44 and 45, and compared in Figure 16 and 17.

Due to shortage of time and inadequate facilities the conclusions drawn from these results must be regarded as tentantive. There is also little published information concerning ixodid lipid metabolism. The females initially contained slightly, but significantly more lipids than the males, i.e. 2.57% for R.pulchellus females and 2.63% for R.appendiculatus females compared with 2.4% and 2.3% for the males respectively.

TABLE 42-43

Covariance analysis for comparing regression lines - The effect of temperature on cuticular permeability on both live and dead _R.appendiculatus_ and _R.pulchellus_.

TABLE 42

	Source	df	$\sum x^2$	$\sum xy$	$\sum y^2$	Regression coefficient	Deviations from regression df	SS	MS
Single regression	Male R.pulchellus	34	140	4.6220	0.1714	0.0330	33	0.0188	0.0005700
	Female R.pulchellus	34	140	5.3800	0.2123	0.0384	33	0.0056	0.0001697
	Male R.appendiculatus	34	140	4.6360	0.1568	0.0331	33	0.0033	0.0001000
	Female R.appendiculatus	34	140	6.5940	0.3195	0.0458	33	0.0089	0.0002697
	TOTALS	136	560	21.2320	0.8600	0.0379	132	0.03658	0.0002771
	Pooled Slope						135	0.0550	0.0004074
	Difference between slopes						3	0.01842	0.00614

Comparison of slopes : $F = \frac{0.00614}{0.0002771} = 22.158$ (df = 3,132) ***

Since the slopes are significantly different, further test was necessary.

TABLE 42 cont.

$$t = \text{variance of regression coefficient} = \frac{\text{M.S. deviation from regression}}{x^2}; \text{ all at } (df = 3,132)$$

t-test for female *R.appendiculatus* vs female *R.pulchellus*

$$t = \frac{0.0384 - 0.0458}{\sqrt{^2/140\ (0.0002771)}} = 3.7193\ ***$$

t-test for female *R.appendiculatus* vs male *R.appendiculatus*

$$t = \frac{0.0331 - 0.0458}{\sqrt{^2/140\ (0.0002771)}} = 6.3831\ ***$$

t-test for female *R.pulchellus* vs male *R.pulchellus*

$$t = \frac{0.0330 - 0.0384}{\sqrt{^2/140\ (0.0002771)}} = 2.7141\ ***$$

t-test for male *R.appendiculatus* vs male *R.pulchellus*

$$t = \frac{0.0330 - 0.0331}{\sqrt{^2/140\ (0.0002771)}} = 0.0503\ \text{NS}$$

TABLE 43

	Source	df	$\sum x^2$	$\sum xy$	$\sum y^2$	Regression coefficient	Deviations from regression df	SS	MS
Single regression	Male R.pulchellus	34	140	5.5700	0.5700	0.0369	33	0.0496	0.001485
	Female R.pulchellus	34	140	8.0500	0.5100	0.0380	33	0.0471	0.001427
	Male R.appendiculatus	34	140	5.1700	0.1464	0.0369	33	0.0445	0.001348
	Female R.appendiculatus	34	140	5.3000	0.2195	0.0572	33	0.0189	0.000573
	TOTALS	136	560	24.0900	1.4459	0.04302	132	0.1595	0.001208
	Pooled Slope						135	0.4096	0.003034
	Difference between slopes						3	0.2501	0.08337

Comparison of slopes: $F = \frac{0.08337}{0.001208} = 69.01$ ***

Since the slopes are significantly different, further test was necessary.

TABLE 43 cont.

t = variance of regression coefficient = $\frac{\text{M.S. Deviation from regression}}{x^2}$, all at (df = 3,132)

t-test for female *R.appendiculatus* vs female *R.pulchellus*

$$t = \frac{0.0380 - 0.0572}{\sqrt{2/140\ (0.001208)}} = 4.6218\ ***$$

t-test for female *R.appendiculatus* vs male *R.appendiculatus*

$$t = \frac{0.0369 - 0.0572}{\sqrt{2/140\ (0.001208)}} = 4.8866\ ***$$

t-test for female *R.pulchellus* vs male *R.pulchellus*

$$t = \frac{0.0369 - 0.0380}{\sqrt{2/140\ (0.001208)}} = 0.2648\ \text{NS}$$

t-test for male *R.appendiculatus* vs Male *R.pulchellus*

$$t = \frac{0.0369 - 0.0369}{\sqrt{2/140\ (0.001208)}} = 0.0000\ \text{NS}$$

TABLE 44

Mean lipid content of male and female *R.appendiculatus* (expressed as a percentage of the initial dry weight) during exposure to 0% RH and 27°C.

TABLE 44

Days of exposure		Male		Female	
		(mg) lipid per tick	Mean lipid content as % dry weight	(mg) lipid per tick	Mean lipid content as % dry weight
0	0	0.3503	2.38	0.4136	2.63
	± SE	0.0129	0.04	0.0188	0.09
1	1	0.3972	2.21	0.3842	2.43
	± SE	0.0560	0.01	0.0095	0.07
2	2	0.3332	2.06	0.2591	1.68
	± SE	0.0138	0.06	0.0029	0.04
3	3	0.3278	1.72	0.2460	1.64
	± SE	0.0122	0.02	0.0037	0.0191
4	4	0.2766	1.62	0.2460	1.51
	± SE	0.0079	0.02	0.0071	0.04
5	5	0.2645	1.51	0.2175	1.46
	± SE	0.0171	0.15	0.0044	0.02

TABLE 44 cont.

Days of exposure			Male		Female	
			(mg) lipid per tick	Mean lipid content as % dry weight	(mg) lipid per tick	Mean lipid content as % dry weight
6	6		0.2616	1.35	0.2355	1.30
		± SE	0.0128	0.02	0.0192	0.01
7	7		0.2224	1.30	0.1644	1.07
		± SE	0.0059	0.02	0.0019	0.01
8	8		0.1959	1.24	0.1990	0.95
		± SE	0.0061	0.02	0.0058	0.06
9	9		0.1996	1.19	0.1647	1.06
		± SE	0.0069	0.01	0.0043	0.01
10	10		0.1898	1.15	0.2219	0.92
		± SE	0.0072	0.01	0.0033	0.02

TABLE 45

Mean lipid content of male and female R.pulchellus (expressed as a percentage of the initial dry weight) during exposure to 0% RH and 27°C.

TABLE 45

	Male			Female	
Days of exposure		(mg) lipid per tick	Mean lipid content as % dry weight	(mg) lipid per tick	Mean lipid content as % dry weight
0 0		0.3884	2.46	4.4093	2.57
	± SE	0.0223	0.11	0.0151	0.10
1 1		0.3496	2.37	0.3804	2.35
	± SE	0.0287	0.24	0.0163	0.10
2 2		0.3371	1.95	0.3635	2.28
	± SE	0.0063	0.01	0.0136	0.08
3 3		0.2591	1.67	0.3466	2.18
	± SE	0.0196	0.10	0.0125	0.05
4 4		0.2414	1.57	0.2517	1.60
	± SE	0.0079	0.05	0.0201	0.11
5 5		0.2336	1.55	0.2122	1.37
	± SE	0.0113	0.08	0.0064	0.03

TABLE 45 cont.

Days of exposure		Male (mg) lipid per tick	Male Mean lipid content as % dry weight	Female (mg) lipid per tick	Female Mean lipid content as % dry weight
6 6		0.2371	1.48	0.2046	1.27
	± SE	0.0116	0.08	0.0037	0.03
7 7		0.2183	1.36	0.1891	1.19
	± SE	0.0042	0.04	0.0045	0.04
8 8		0.2204	1.33	0.1687	1.08
	± SE	0.0087	0.03	0.0039	0.02
9 9		0.2102	1.33	0.1659	1.06
	± SE	0.0018	0.02	0.0030	0.01
10 10		0.1912	1.25	0.1654	1.03
	± SE	0.0061	0.04	0.0023	0.02

FIGURE 16

Mean lipid content of male and female R.appendiculatus (expressed as % of the initial dry weight). Each point on the graph represents a mean value of five replicates.

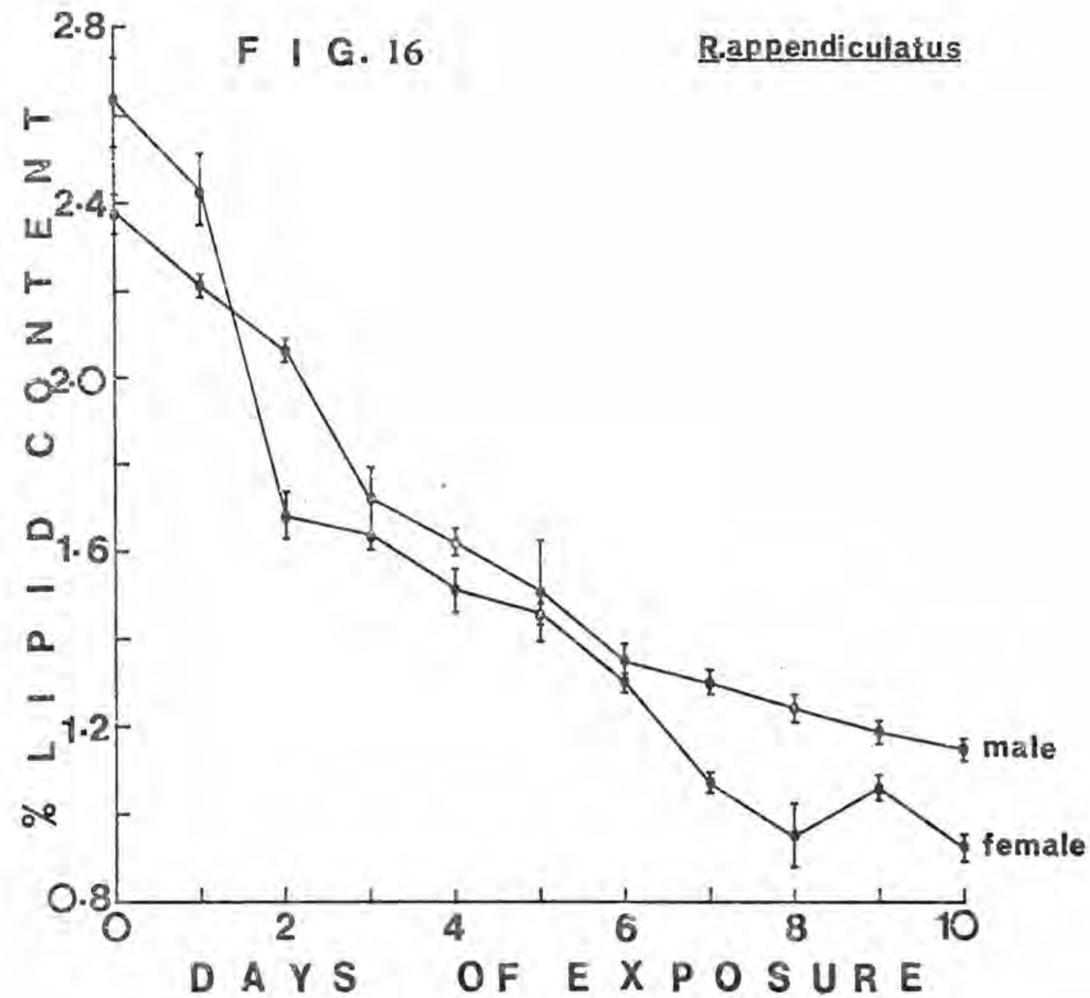
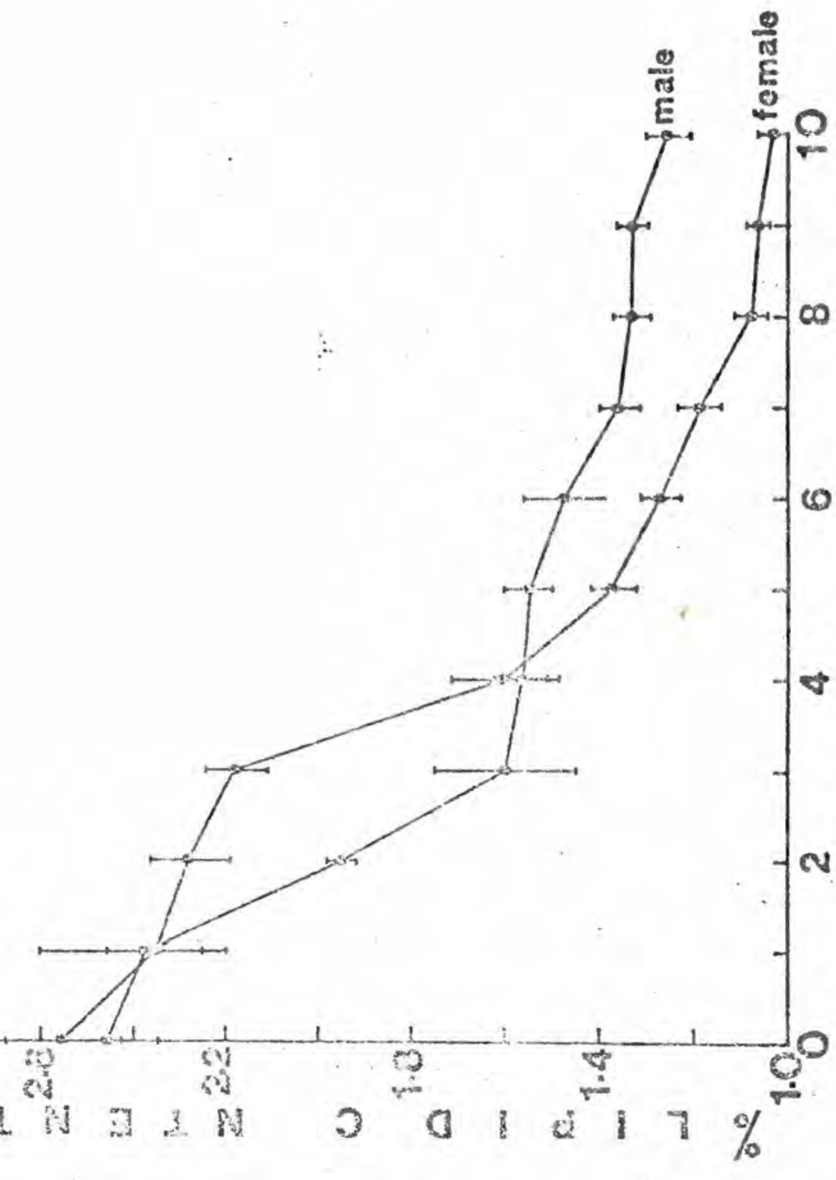

F I G. 16
R.appendiculatus
% L I P I D C O N T E N T
2·8
2·4
2·0
1·6
1·2
0·8
0
2
4
6
8
10
D A Y S OF E X P O S U R E
male
female

FIGURE 17

Mean lipid content of male and female of R.pulchellus (expressed as % of the initial dry weight). Each point on the graph represents a mean value of five replicates.

FIG.17

R. pulchellus



In all cases, the reduction in lipid content was most rapid during days 2-4, after which the males had a consistantly higher lipid content than the females. All ticks continued to lose lipids steadily, presumably as a result of oxidation which would have yielded energy plus some molecular water which could have gone towards reducing the moisture deficit. Females of *R.appendiculatus* showed a loss of more than one third of their lipid content between days 1 and 2, whereas a similar decrease did not occur in *R.pulchellus* until two days later.

III.6: Water and dry weight changes during dehydration

The water content of the ticks after exposure to 0% RH and 27^{o}C was calculated separately for exposures of 0 to 10 days and expressed as a percentage of the initial weight, for males and females of *R.pulchellus* and *R. appendiculatus*. The results are given in Table 46-49. Water content was plotted against days of exposure Figures 18a-19b.

The initial water content in all cases ranged from 48.7% - 54.3%. The dry weight was 45% - 48% for males and females of *R.appendiculatus* and 42% - 43% for males and females of *R.pulchellus*. There was little change in water content at 96% RH in all cases as it can be seen in Tables 46-49.

Desiccation at 0% RH caused continuous water loss. Males and females of *R.appendiculatus* had lost about 33% and 40% respectively of their initial water content and

TABLE 46

Water content, dry weight (expressed as percentage of the initial live weight) and ratio of water mass to dry weight of male *R. appendiculatus* during exposure to 0% RH and 27°C.

TABLE 46

TREATMENT	Initial live weight (mg)	Weight (mg) after exposure	Dry weight (mg)	Water (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 0 Mean	2.895	2.795	1.236	1.559	53.84	1.26
± SE	0.036	0.043	0.025	0.043	1.27	0.05
Day 1 Mean	3.073	2.908	1.249	1.658	53.96	1.32
± SE	0.077	0.058	0.013	0.049	0.68	0.03
Day 2 Mean	2.999	2.844	1.239	1.605	53.49	1.29
± SE	0.098	0.079	0.038	0.067	1.24	0.06
Day 3 Mean	3.211	3.028	1.314	1.714	53.26	1.29
± SE	0.126	0.150	0.053	0.099	1.61	0.03
Day 4 Mean	3.079	2.813	1.257	1.556	50.76	1.23
± SE	0.150	0.065	0.027	0.046	1.43	0.03
Day 5 Mean	2.942	2.64	1.249	1.378	47.44	1.12
± SE	0.099	0.022	0.029	0.047	1.77	0.05

TABLE 46 cont.

TREATMENT	Initial live weight (mg)	Weight (mg) after exposure	Dry weight (mg)	Water (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 6 Mean	2.785	2.423	1.132	1.291	45.68	1.12
± SE	0.075	0.069	0.018	0.064	1.62	0.06
Day 7 Mean	3.075	2.511	1.199	1.312	42.99	1.09
± SE	0.159	0.092	0.045	0.050	1.41	0.02
Day 8 Mean	3.357	2.849	1.442	1.408	41.82	0.96
± SE	0.094	0.174	0.065	0.123	3.39	0.07
Day 9 Mean	3.233	2.639	1.199	1.439	42.54	1.21
± SE	0.079	0.080	0.064	0.021	0.50	0.06
Day 10 Mean	3.337	2.628	1.225	1.403	42.22	1.15
± SE	0.163	0.081	0.043	0.049	1.13	0.04

TABLE 47

Water content, dry weight (expressed as percentage of the initial live weight) and ratio of water mass to dry weight of female R.appendiculatus during exposure to 0% RH and 27°C.

TABLE 47

TREATMENT	Initial live weight (mg)	Weight (mg) after exposure	Dry weight (mg)	Water (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 0 Mean	3.561	3.421	1.605	1.816	51.10	1.13
± SE	0.079	0.075	0.034	0.049	0.76	0.03
Day 1 Mean	3.329	3.147	1.474	1.671	50.97	1.13
± SE	0.076	0.102	0.038	0.072	1.33	0.04
Day 2 Mean	3.174	2.980	1.359	1.612	50.56	1.17
± SE	0.067	0.075	0.017	0.070	1.25	0.05
Day 3 Mean	3.568	3.349	1.581	1.768	49.52	1.12
± SE	0.082	0.071	0.017	0.057	0.63	0.03
Day 4 Mean	3.454	3.204	1.517	1.687	48.92	1.12
± SE	0.059	0.053	0.052	0.031	1.35	1.05
Day 5 Mean	3.464	3.053	1.468	1.585	45.56	1.07
± SE	0.117	0.136	0.033	0.105	1.66	0.05

TABLE 47 cont.

TREATMENT	Initial live weight (mg)	Weight (mg) after exposure	Dry weight (mg)	Water (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 6 Mean	3.520	3.094	1.489	1.605	45.48	1.07
± SE	0.099	0.116	0.034	0.089	1.38	0.05
Day 7 Mean	3.134	2.789	1.377	1.412	45.08	1.03
± SE	0.143	0.110	0.061	0.066	0.83	0.04
Day 8 Mean	3.458	3.059	1.511	1.556	44.82	1.03
± SE	0.086	0.074	0.051	0.027	0.53	0.02
Day 9 Mean	3.200	2.624	1.310	1.314	41.31	1.00
± SE	0.194	0.123	0.067	0.063	1.06	0.03
Day 10 Mean	2.986	2.451	1.230	1.219	40.41	0.99
± SE	0.010	0.010	0.012	0.016	0.72	0.02

TABLE 48

Water content, dry weight (expressed as percentage of the initial live weight) and ratio of water mass to dry weight of male *R.pulchellus* during exposure to 0% RH and 27^{o}C.

TABLE 48

TREATMENT	Initial live weight (mg)	Weight (mg)	Dry weight (mg)	Actual water mass (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 0 Mean	2.850	2.777	1.389	1.328	48.70	1.10
± SE	0.105	0.101	0.047	0.047	0.54	0.02
Day 1 Mean	3.014	2.834	1.382	1.382	48.17	1.05
± SE	0.107	0.104	0.064	0.064	0.48	0.02
Day 2 Mean	3.069	2.780	1.401	1.401	47.96	1.05
± SE	0.082	0.048		0.032	0.97	0.02
Day 3 Mean	0.095	2.881	2.881	1.467	45.89	0.96
± SE	0.078	0.123	0.123	0.056	1.68	0.03
Day 4 Mean	2.799	2.620	2.620	1.290	45.86	0.99
± SE	0.034	0.041	0.041	0.019	1.96	0.06
Day 5 Mean	2.815	2.533	2.533	1.345	42.86	0.91
± SE	0.033	0.035	0.035	0.061	2.31	0.08

TABLE 48 cont.

TREATMENT	Initial live weight (mg)	Weight (mg)	Dry weight (mg)	Actual water mass (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 6 Mean	2.800	2.469	2.469	1.308	41.18	0.88
± SE	0.023	0.013	0.013	0.014	0.55	0.02
Day 7 Mean	2.712	2.340	2.340	1.293	38.81	0.82
± SE	0.024	0.019	0.019	0.020	1.04	0.04
Day 8 Mean	2.928	2.543	2.543	1.374	39.91	0.85
± SE	0.015	0.007	0.007	0.018	0.61	0.03
Day 9 Mean	2.769	2.293	2.293	1.259	37.33	0.82
± SE	0.045	0.022	0.022	0.024	0.84	0.02
Day 10 Mean	2.943	2.343	2.343	1.298	35.01	0.76
± SE	0.024	0.016	0.016	0.022	0.81	0.04

TABLE 49

Water content, dry weight (expressed as percentage of the initial live weight) and ratio of water mass to dry weight of female *R.pulchellus* during exposure to 0% RH and 27^{o}C.

TABLE 49

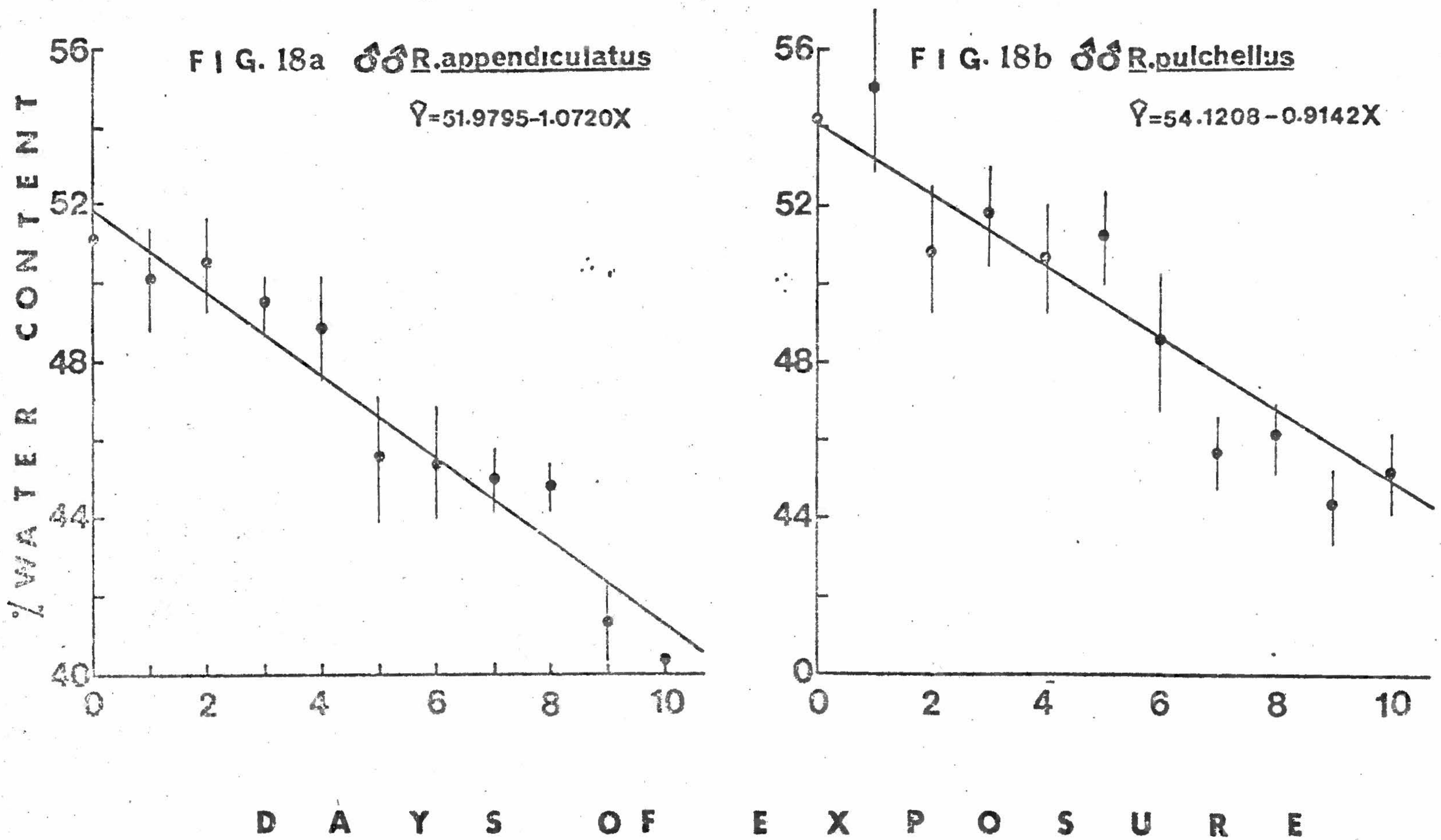
TREATMENT	Initial live weight (mg)	Weight (mg)	Dry weight (mg)	Actual water mass (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 0 Mean	3.684	3.546	1.545	2.002	54.33	1.28
± SE	0.153	0.144	0.059	0.092	1.10	0.03
Day 1 Mean	4.185	3.732	1.595	2.137	51.04	1.34
± SE	0.099	0.135	0.050	0.129	2.16	0.10
Day 2 Mean	4.008	3.564	1.529	2.035	50.88	1.34
± SE	0.243	0.228	0.108	0.121	1.49	0.02
Day 3 Mean	4.068	3.666	1.561	2.108	51.83	1.35
± SE	0.519	0.168	0.085	0.083	1.18	0.03
Day 4 Mean	3.867	3.375	1.464	1.908	49.62	1.25
± SE	0.159	0.048	0.032	0.022	1.90	0.07
Day 5 Mean	4.143	3.681	1.598	2.084	50.32	1.31
± SE	0.087	0.090	0.039	0.054	1.21	0.02

TABLE 49 cont.

TREATMENT	Initial live weight (mg)	Weight (mg)	Dry weight (mg)	Actual water mass (mg)	Water content (%)	Ratio Water mass / Dry weight
Day 6 Mean	3.963	3.567	1.648	1.919	48.58	1.17
± SE	0.204	0.114	0.084	0.044	1.68	0.05
Day 7 Mean	3.981	3.354	1.530	1.834	45.72	1.19
± SE	0.138	0.078	0.024	0.069	0.85	0.04
Day 8 Mean	4.245	3.567	1.608	1.958	46.11	1.22
± SE	0.159	0.144	0.065	0.081	0.90	0.02
Day 9 Mean	4.158	3.441	1.604	1.838	44.30	1.14
± SE	0.159	0.204	0.084	0.124	0.93	0.02
Day 10 Mean	3.987	3.552	1.626	1.925	45.32	1.11
± SE	0.237	0.114	0.079	0.051	0.94	0.06

FIGURES 18a - 18b

Water content for males of R.appendiculatus and R.pulchellus expressed as percentage of the initial live weight during exposure to 0% RH and 27°C.


F I G. 18a ♂♂ R.appendiculatus
Ŷ=51.9795-1.0720X
F I G. 18b ♂♂ R.pulchellus
Ŷ=54.1208-0.9142X
% WATER CONTENT
56
52
48
44
40
0
2
4
6
8
10
D A Y S OF E X P O S U R E

FIGURES 18c - 18d

Water content of females of *R.appendiculatus* and *R.pulchellus* expressed as percentage of the initial live weight during exposure to 0% RH and 27^{o}C.

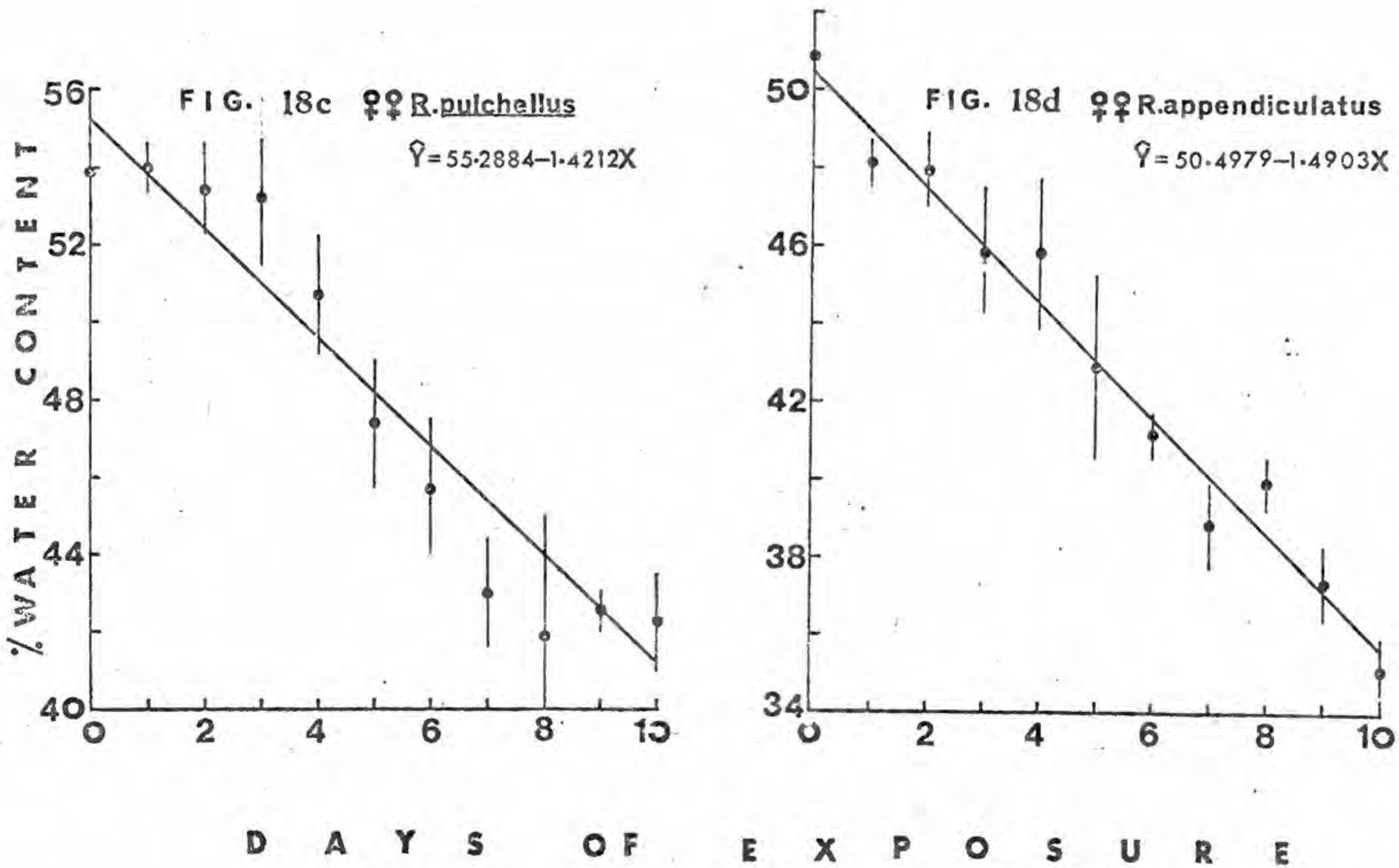


FIG. 18c ♀♀ R.pulchellus
Ŷ=55·2884–1·4212X
FIG. 18d ♀♀ R.appendiculatus
Ŷ=50·4979–1·4903X
% WATER CONTENT
56
52
48
44
40
50
46
42
38
34
0
2
4
6
8
10
DAYS OF EXPOSURE

R.pulchellus had lost about 42% and 45% respectively by day 10.

Both water and dry weight content seem to have decreased continuously during exposure although the rate of dry weight depletion seems to be much lower since an exact plateau is not obvious. Only in female R.pulchellus is anything like a constant trend shown Figures 18a and 18d. In each case, female R.appendiculatus had the greatest proportion of dry weight.

It was interesting to note that the LD_{50} for females was 6.7 days and 9.5 days for males. These values correspond to those reported in the earlier excercise. R.pulchellus showed longer survival than R.appendiculatus. It was also noted that in all cases, marked changes in total weight occurred after the 3rd day of exposure. A careful study of the Tables and the plotted Figures, (ignoring the regression lines) will reveal that there was an initial resistance to desiccation and this was better demonstrated in R.pulchellus than R.appendiculatus; although males of the two species reveal this even better. These results might indicate a degree of water retention and regulation but this homeostatic mechanism soon breaks down when the constraint continues longer.

Covariance analysis for comparing the regression lines Tables 50-51 for the rates of water loss for the two species during the period of exposure was highly

TABLE 50

Covariance analysis for comparing regression lines - percent water content of adult *R.appendiculatus* and *R.pulchellus* during exposure to 0% RH and 27°C.

TABLE 50

	Source	df	x^2	xy	y^2	Regression coefficient	Deviations from regression df	SS	MS
Single regression	Male R.pulchellus	54	550	-502.87	1064.88	-0.9143	53	605.10	11.42
	Female R.pulchellus	54	550	-781.65	1826.93	-1.4212	53	715.38	13.50
	Male R.appendiculatus	54	550	-589.62	952.29	-1.0720	53	320.19	6.04
	Female R.appendiculatus	54	550	-819.69	1589.74	-1.4903	53	368.12	6.95
	TOTALS	216	2200	-2693.83	5433.84	TOTAL	212	2008.79	9.48
	Pooled slope					-1.2245	215	2135.33	9.93
	Difference between slopes						3	126.54	42.18

Comparison of slopes : $F = \frac{42.18}{9.48} = 4.45$ (df = 3,212) ***

Since the slopes are significantly different, further test was necessary

TABLE 50 cont.

Variance of reg. coeff. = $\frac{\text{M.S deviation from reg.}}{x^2}$ = t = $\frac{-1.4903 + 1.0720}{\sqrt{\frac{6.95}{550} + \frac{6.04}{550}}}$ = 108.49 (df = 53+53 =106) ***

e.g. Male R.appendiculatus vs Female R.appendiculatus

Variance of reg. coeff. = $\frac{\text{M.S. deviation from reg.}}{x^2}$ = t = $\frac{-1.4903 + 1.4212}{\sqrt{\frac{6.95}{550} + \frac{13.50}{550}}}$

e.g. Femalr R.appendiculatus vs Female R.pulchellus

= 78.30 (df = 53 + 53 = 106) ***

TABLE 51

Covariance analysis for comparing regression lines - ratio water mass to dry weight of adult *R.appendiculatus* and *R.pulchellus* during exposure to 0% RH and 27°C.

TABLE 51

	Source	df	x^2	xy	y^2	Regression coefficient	Deviations from regression df	SS	MS
Single regression	Male R.pulchellus	54	550	-12.07	0.9170	-0.0219	53	0.6521	0.0123
	Female R.pulchellus	54	550	-12.90	1.1643	-0.0235	53	0.8617	0.0163
	Male R.appendiculatus	54	550	-9.41	0.5206	-0.0171	53	0.3596	0.0068
	Female R.appendiculatus	54	550	-17.98	0.9480	-0.0327	53	0.3603	0.0068
	TOTALS	216	2200	-52.36	3.5499	TOTAL	212	2.2337	0.1054
	Pooled slope					-0.0238	215	2.3037	0.1071
	Difference between slopes						3	0.0700	0.0233

Comparison of slopes : $F = \frac{0.0233}{0.1054} = 0.2210$ (df = 3,212) NS

$$t = \frac{-0.0171 + 0.0327}{\sqrt{\frac{0.0068}{550} + \frac{0.0068}{550}}} = 0.0037$$ (df = 53 + 53 = 106) NS

significant. From these Tables the coefficients of regression show that R.appendiculatus lose water more rapidly than R.pulchellus but R.appendiculatus show a more regular trend than R.pulchellus. The females show a more regular rate of water loss than the males.

The plotted curves of the ratio of water mass to dry weight contents for the two species can be compared in Figures 19a and 19b. Despite the large differences in total body weights, a constant value was not observed. This is supported by the fitted regression lines which show a very good linear relationship with the days of exposure. However, covariance analysis for comparing the fitted regression lines showed no signficant difference in either sex or species. Since there was no constancy obtained and the regression lines were not significantly different from each other the results suggest that the two species have a poorly developed mechanism for converting food reserves into metabolic water.

Work on Amblyomma americanum has shown such a pattern varying with the degree of hydration (Shih et al. 1973). In unfed A.americanum little dry weight reserve was converted into metabolic water to replace water lost via transpiration during exposure to 0% RH (Sauer and Hair, 1971) and my findings are in agreement with their observations.

FIGURE 19a

Ratio of water mass to dry weight of males of *R.appendiculatus* and *R.pulchellus* during exposure to 0% RH and 27^{o}C.

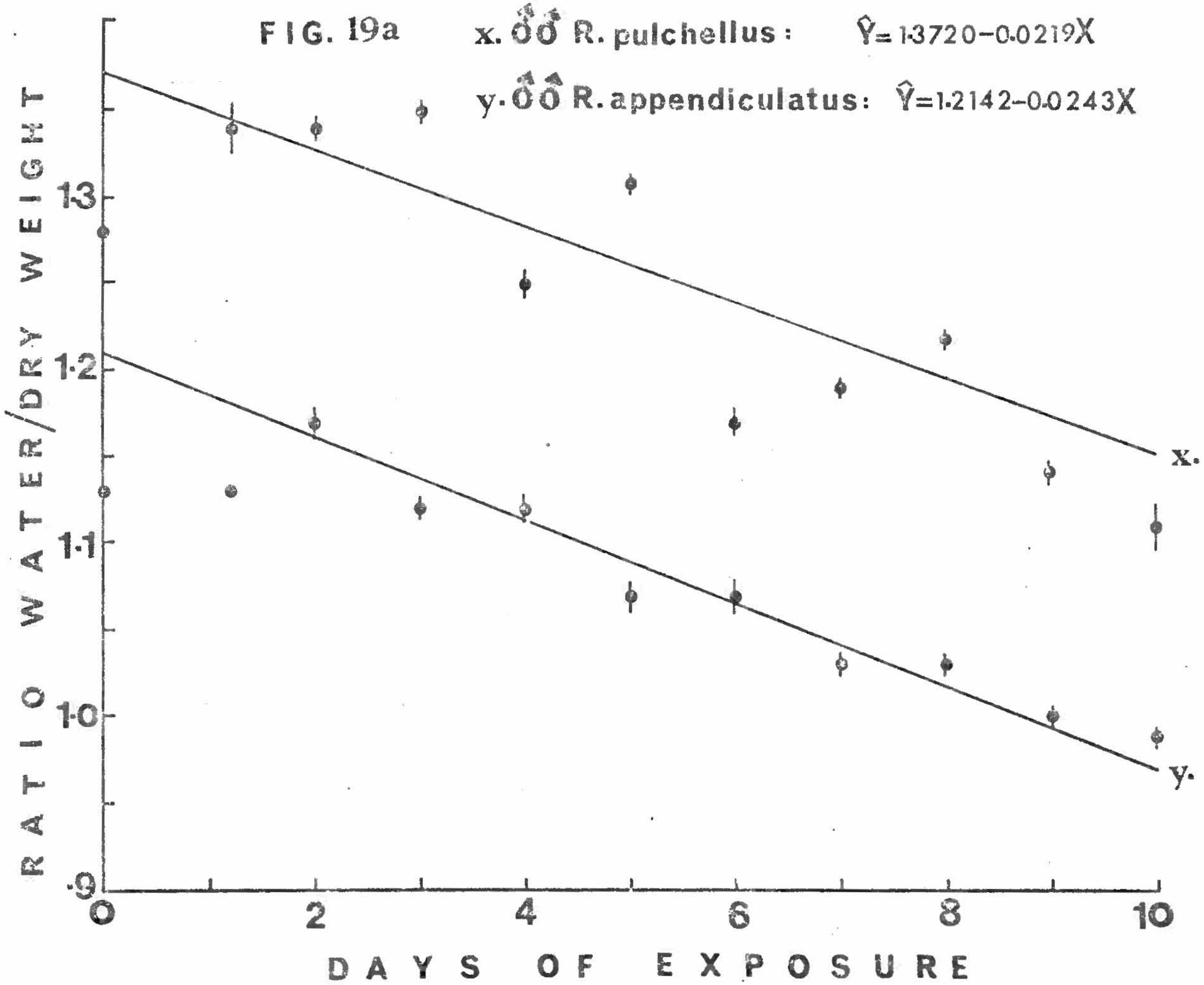
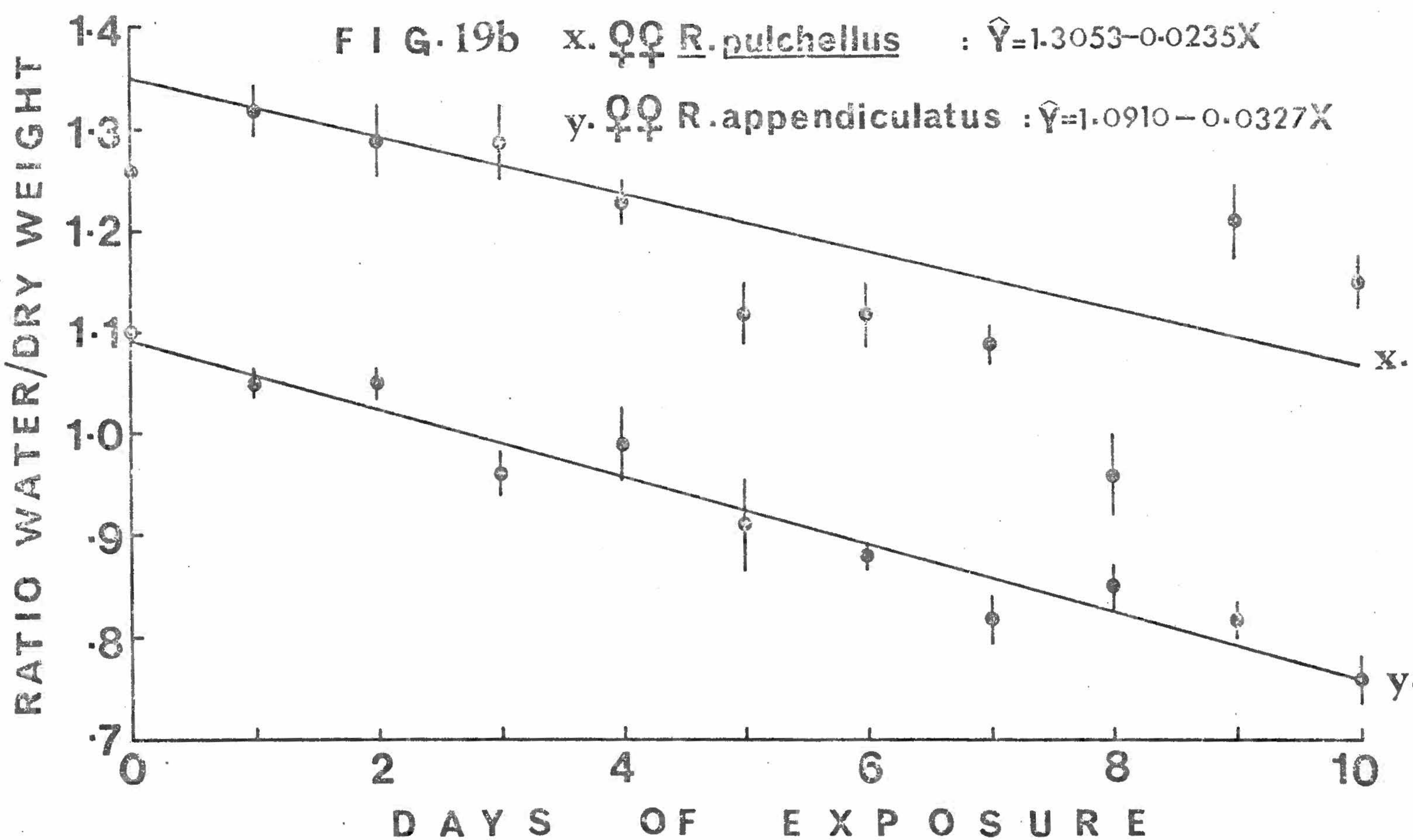

x. ♂♂ R. pulchellus : Ŷ= 1·3720–0·0219X
y. ♂♂ R. appendiculatus : Ŷ=1·2142–0·0243X
RATIO WATER/DRY WEIGHT
1·3
1·2
1·1
1·0
·9
0
2
4
6
8
10
x.
y.
DAYS OF EXPOSURE

FIG. 19a

FIGURE 19b

Ratio of water mass to dry weight of females of *R. appendiculatus* and *R. pulchellus* during exposure to 0% RH and 27°C.


F I G·19b
x. ♀♀ R. pulchellus : Ŷ=1·3053–0·0235X
y. ♀♀ R. appendiculatus : Ŷ=1·0910–0·0327X
RATIO WATER/DRY WEIGHT
1·4
1·3
1·2
1·1
1·0
·9
·8
·7
0
2
4
6
8
10
x.
y.
DAYS OF EXPOSURE

CHAPTER IV

DISCUSSION AND CONCLUSION

III.1:2: The effect of different humidities on water loss and CEH

It is evident from the results obtained during this study Figures 4a-7d that female *R.appendiculatus* lose water to the atmosphere more readily than female *R.pulchellus* under the same conditions, but the males of the two species lose water at almost the same rate. These findings suggest why female *R.pulchellus* is able to withstand more adverse conditions of weather than female *R.appendiculatus*.

The results also suggest that the rate of water loss from the ticks is humidity dependent. In any case, we cannot over-rule the fact that at low RHs there is some form of control mechanism which seem to operate by minimizing the degree of water loss but probably not as efficient.

In general the rate of water loss also increases with temperature Table 2-20. The CEH for both species lies at approximately 85% RH, but this should be further investigated as it may be influenced by the age of the tick (Lees, 1946, 1964). Since the ticks used in this study were laboratory bred and therefore of uniform size and of known age (3-5 weeks old), the value given above certainly applies in this particular case. This finding supports that of Sauer and Hair (1971) that the CEH for *Amblyomma americanum* females lies at approximately 85% RH and is slightly less for males.

The concept of repeated gain and loss of body water is an important one in understanding the behaviour of ticks in the field since it leads to problems of osmotic regulation in the ticks. Any gain on loss of water will only alter the relative concentration of solutes without providing a corresponding means of regulating the absolute concentration of solutes in the tick's body.

Wilkinson (1953) showed that Boophilus microplus larvae, in this case the only unfed stage of the tick found off the host, can imbibe free water from dew or other sources. However, at all humidities below the CEH although the mechanism for the regulation of water loss exists, it is not sufficient to compensate fully for the rate of loss of water experienced below the CEH, so there is a progressing loss of water as RH decreases.

Although the mechanism for the regulation of water loss is unknown, Edney (1957) and Beament (1961) have suggested that it may be the same as that which produces active uptake of atmospheric water at high humidities in some arthropods.

Lees (1946) showed that there was a restriction of water loss by some form of active mechanism. This process seen only in a few insects and in several ixodid and argasid ticks probably involves the epidermal cells.

He also showed that the nymphs of Ixodes ricinus were able to replenish body moisture by absorbing water vapour from the atmosphere.

Tenebrio larvae under confined conditions bring the surrounding air to about 90% RH whether the animals were initially exposed to humidities above or below this level; but the atmosphere becomes nearly saturated when the animals die (Kalmus, 1936). The early work of Buxton (1930) on the uptake of atmospheric moisture by the mealworm Tenebrio molitor was subsequently confirmed by Mellanby (1932), Browning (1954) and Edney (1957). All agreed that at humidities at or above 88% RH, starved mealworm larvae gain weight by increasing their body water content. Mellanby believed that equilibrium between the animal and atmospheric moisture was established at 88% RH over a wide biological range of temperatures.

It can therefore be concluded that the ticks water pump can direct water into the haemolymph from air of humidities down to a level which will be species - specific but probably the pump has no purchase when working against humidities substantially below the CEH. Alternatively it can be visualized as a pump of fixed capacity but the rate of outward flow of water vapour the ticks experience varies with the atmospheric humidity, resulting in losses of body moisture below the CEH and gains above the CEH.

Thus the daily alternation of low and high humidities, which allows the ticks frequent opportunities to replace water losses, can probably be better exploited by R.pulchellus than R.appendiculatus. This is why R. pulchellus is able to withstand long rainless periods in the field and it survives a little longer than R.appendiculatus at continuous low RH in the laboratory.

In the field, the ticks climb the vegetation and wait to be picked by a passing host. Meanwhile the mean RH experienced by the ticks is usually below the CEH and moisture is lost by then. When the loss amount to 50% and 60% of the hydrated body weight (R.J. Tatchell and A. O. Mongi unpublished observation on R.appendiculatus in the field at Dar es Salaam) the ticks descend the vegetation to the generally higher humidities found on or near the soil surface amongst the bases of the stems. The dehydrated ticks stay near the ground for several days and start their next journey up the vegetation when the water balance is fully replenished and possibly even beyond the CEH.

In the case of R.pulchellus which lives in the drier parts of the country probably the same process takes place, but together with its high resistance to water loss during the day, and its lower CEH value it can absorb sufficient water vapour during the night, or dew in the early morning to compensate for losses during the day.

To date, no work has been carried out on the rate of oxygen consumption at different temperatures:

(i) under conditions at which water is being lost

(ii) at equilibrium humidity

(iii) when water is being gained to replenish previous losses.

Such studies should lead to a better understanding of the mechanisms by which ticks regain water from humid air.

I speculate that there exists some form of regulatory mechanism in R.pulchellus as yet unknown to us. The internal environments of the ticks in terms of haemolymph volume and osmotic pressure or different energy metabolism turnovers are possible explanations for the varied ecological differences of the two species.

III.3: Investigation of the site of water vapour uptake

Some of the results obtained in these experiments not only confirm those of Knülle (1974), but reveal more information on some other parameters which were not thoroughly examined before. The replacement of body moisture could have been either by absorbing water vapour through the integument or, possibly, from metabolic sources.

The existence of a mechanism for water vapour uptake by dehydrated ticks when exposed to a high RH is definite but the mode of operation is still not clear. Although the mouthparts seem to be the principal site for water absorption, I suggest that there are other mechanisms involved at other sites as well as demonstrated by Knülle (1974) and Knülle and Devine (1972) on Hyalomma anatolicum, Hyalomma schulzei and on Amblyomma americanum.

If a "water pump" exists it could be either a function of the epidermal cells (as reported earlier) or the involvement of the salivary glands (Dr. F. Obenchain pers. comm.). Beament (1964) and Locke (1966) have suggested that the epicuticular lipids are also involved in such a mechanism.

Noble-Nesbitt (1970) confirmed that the anus is a site of water uptake in the insect Thermobia domestica. This could be misleading as he did not check many sites on the insects' body for the actual site of water uptake and the role of the general integument of this insect in active uptake of water vapour is still subject to re-appraisal. Knülle (1962; 1965) demonstrated that water uptake in the grain mite Acarus siro, which has no tracheal system, takes place over the entire integument. In the present case various sites were observed and from the general shape of the water vapour uptake curves it can be concluded that the mouthparts are the most important site of water vapour uptake.

III.4: Investigations of cuticular permeability in adults

A substantial body of evidence now exists in support of the idea that the rate of evaporation from insects depends:

(i) on the permeability to water of the transpiring membrane

(ii) on the temperature of the transpiring surface which will affect the rate of diffusion of molecules of water

(iii) on the activity gradient between the insect and the general atmosphere which is itself a function of temperature.

Thus the data obtained for rates of water loss from the ticks into dry air at various temperatures was temperature dependent and this varied upon the permeability of the species cuticle. Holdgate and Seal (1956) concluded that cuticular permeability changes exponentially with temperature. The movement of water vapour and certain other gases by active diffusion through some organic membranes is also temperature dependant (Barner, 1939; Doty, Aiken and Hermann 1944). Although no histological studies were made of the cuticle to confirm the presence of epicuticular waxes, their presence in argasid and in other ixodids was demonstrated by Lees (1946). It is certain therefore that they also occur in ticks of the genus Rhipicephalus.

The increased rate of water loss from the ticks at temperatures above 50°C was certainly as a result of changes in the epicuticle, either expansion of the micropores (if at all they exist), or disorientation of a wax layer. It is also probable that the structure of the alloscutum of the unfed female, which is highly folded cuticle and therefore provides a large surface for evaporation contributes to the higher rate of water loss compared with the male which has very much less such folded cuticle.

The generally higher rate of cuticular water loss in both species at higher temperatures could be accounted for in part by increased respiration, and hence metabolic activity, or due to changes in the basic rate of evaporation from the cuticular surface. However these suggestions need to be investigated by measuring the effect of temperature on the rate of respiration when the spiracles are unblocked and also under blocked contitions.

We have also seen that R.pulchellus is more successful than R.appendiculatus in the drier parts of the country, probably by having a relatively more impermeable integument and thus reducing the rate of water loss. However, reducing the rate of water loss will also reduce the cooling effect that such evaporation would give the tick, but R.pulchellus seems able to withstand this also.

The waterproofing mechanism in the majority of species that have been investigated shows the presence of a wax layer, formed during the process of cuticle deposition.

Wigglesworth (1947, 1948) demonstrated that a substantial amount of wax appears on the surface of the polyphenol layer (i.e. the quinone tanned surface of the cuticulin), where it may itself be subsequently overlaid by a layer of cement. Similar evidence of a lipid layer was recorded for ticks by Lees (1947), though the method of formation of this layer is said to be different from that in insects such as Diptera. Beament and Lees (1948) found that wax was deposited on the outer surface of the eggs of ticks by means of Gene's organ whereas the eggshells of cockroaches are not themselves waterproof (Wigglesworth and Beament, 1950). The female cockroach is known to transfer grease from the body to the surface of ootheca by wiping it with her legs.

Beament (1958) put forward the idea of the presence of protein molecules on the outer surface of the tick. Although he could not show whether these molecules are directly involved in the restriction of permeability to water, he suggested, however, their involvement in the lowering of the rate of evaporation from the tick.

Killing the ticks not only altered the activity level of the internal water but also the permeability of the membranes themselves. Since there is no concrete evidence of the mechanism controlling the passage of water from the tick, we should expect greater losses when the barriers operating when the tick is alive cease doing so.

Although there is no recent biological study of the integument of arthropods other than insects and since they have received very little attention it is reasonable to suggest that the degree of waterproofing and physical properties of the cuticle of the two species vary considerably and their specific correspondence in laboratory and in the field are also very different.

III.5: Lipid depletion

The lipid content of newly moulted, fully hydrated ticks ranged from 2.2% - 2.7%, with significant differences between sex and species (Table 44 and 45,) the females containing more lipids than the males ; however, these figures are very low compared with the 25% lipid content recorded for female *Glossina morsitans* (Bursell, 1959).

Whilst lipids are essential components of membranes and have a predominant role in controlling embryogenesis, and morphogenesis (Clayton, 1964; Fast, 1964; Gilby, 1965; Gilbert, 1967), in the present situation it is most likely that they are fulfilling their other major role as metabolic reserves. The ticks' lipid content decreased during starvation and dehydration Figures 16 and 17, though there were some differences with sex and species. It must be concluded, therefore, that the lipids were being metabolised, but the energy production was not measured.

Since fats yield an approximately equivalent weight of water on oxidation, the amounts of water produced in this case, even if it was fully retained by the ticks, would be of negligible importance in replacing actual water losses which were at least ten times as great. However, the production of metabolic water at RHs close to CEH, could be considered of significant importance in off setting the amount of water loss to the environment; but under extreme desiccating conditions, this kind of physiological process becomes less important in the whole process of water regulation

Tatchell (1964) demonstrated histochemically that the major lipid fraction of the blood meal is utilised by the 12th day after feeding in female Argas persicus and concluded that the lipid remaining after the initial phase of digestion was insignificant when compared to the massive undigested haemoglobin. Thus the presence of small amounts of lipids found in the unfed adults of R.appendiculatus and R.pulchellus is not surprising although Lees (1948, 1964) found that the principal reserve in Ixodes ricinus was lipid; but this may not hold true for all ixodids.

In Ornithodoros concanensis exposed to 64% and 96% RHs there was no reduction in lipid content Cook (1973). One cannot refute these findings but 64% RH is close to 70% RH, the CEH for this particular species Cook (1972); and it would be difficult to detect such small changes in lipid content, as might occur. If however, the ticks had been exposed to 0% RH, the results might have been different.

The decrease in lipid content signifies, therefore, the utilisation of this substrate at low RH and represents the most significant aspect of this investigation; that the two species have stores of lipids and the differences between them are very small. These results give only part of the picture of the ticks energy resources since other types of food reserves such as glycogen, could as well be incorporated in the system. As we have seen earlier, R.pulchellus is tolerant of more arid conditions than R.appendiculatus and appears to have slightly more fat reserves, and to use them more rapidly when dehydrated. The work above shows that ticks survival is as well determined by a complex interrelationship of water and metabolite conservation.

III.6: Water and dry weight changes during dehydration

The relatively constant water content observed for the first three days of experiment Tables (46-49) indicates a water retention mechanism in which the total water remains unchanged initially and then decreases suddenly when the presupposed mechanism breaks down.

Since the water loss under the above conditions was so great and the amount of metabolic water if at all produced difficult to detect then the observed fluctuaon oxidation to provide enough water to contribute significantly to replacing water losses.

Cuticular permeability in both live and dead ticks at different rates of desiccation showed a curvilinear relationship to temperature. Females showed significantly greater water losses than males of the same species. Between species, *R.pulchellus* females consistently showed a significantly lower rate of water loss than *R.appendiculatus* females.

These findings help in explaining the distribution of the two species in nature, where *R.pulchellus* shows a preference for markedly arid habitats compared to *R. appendiculatus*.

CHAPTER V

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