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THE EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON SURVIVAL OF UNFED *HYALOMMA IMPELTATUM* (Acarina: Ixodidae)

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ABSTRACT

This work investigates survival of unfed *Hyalomma impeltatum* in which 8089 larvae, 3946 nymphs, 2058 males and 2304 females held at different combinations of temperature (21, 25, 29 and 34°C) and relative humidity (RH) (32, 52, 75 and 97%) levels. Survival was significantly improved with rise in RH and fall in temperature in all stages. The magnitude of the effect of RH and temperature on survival varied significantly between stages. Changes in RH and temperature had a stronger impact on survival in larvae than in nymphs and adults; and nymphs were the most tolerant to changes in temperature. Using 97% RH as a base-line level, the temperature-adjusted relative death rate (RDR) at 32% RH levels was 417.0 in larvae, 13.9 in nymphs and 8.1 in adults. The RH-adjusted RDR at 34°C relative to 21°C in these stages was 13.3, 4.6 and 7.3, respectively. Males fared significantly better than females, with age-, RH- and temperature-adjusted RDR for females relative to males being 1.7. The survival difference between males and females was largely post-median. No significant interaction was found between the effects on adult survival of (a) RH and temperature and (b) RH and sex. The difference in tolerance to RH and temperature changes were discussed in relation to differences in the cuticle properties and adaptability of the difference stages.

INTRODUCTION

In a previous study, the effect of four different temperatures on the developmental periods of all stages in the life cycle of a Qatari strain of *Hyalomma (Hyalomma) impeltatum* Schulze and Schlottke was investigated (Khalil and Hagras, 1988). That work was the first of a series of studies intended to investigate the physiological and behavioural responses of this species to abiotic factors confronted in the natural environment.

In this study, we report on survival of unfed larvae, nymphs and adults of this species held at different combinations of various levels of temperature and relative humidity (RH). Knowledge of the effect of the interaction between these two parameters on the different developmental stages should be of value in trying to assess the mechanisms of osmoregulation and other important patterns of the behaviour of this species.

MATERIALS AND METHODS

A *H. impeltatum* colony originating from engorged females collected from camels in Miazar area in Qatar was maintained in the laboratory at 28±1°C and 75% (RH). Rabbits, *Oryctologus cuniculus,* were used as hosts. Rearing methods were those of Berger *et al.* (1971).

Eggs laid by five females on days three and four after oviposition began were pooled and divided into four groups. These groups were held in incubators at 75% RH and 21±1, 25±1, 29±1 and 34±1°C, respectively. After hatching, larvae of each group were divided into five subgroups. Four of these subgroups were held in four desiccators containing saturated salt solutions to obtain a mean RH of about 32, 52, 75 and 97% (Winston and Bates, 1960), respectively, at each of the above temperatures, and were observed daily for mortality. Larvae of the fifth, subgroup were placed to feed on rabbits 14 days post-hatching. Engorged larvae were held at the same temperature at which they were maintained before feeding and at 75% RH, and were observed daily for moulting.

Nymphs emerging at each of the incubation temperatures were divided into five subgroups, four of which were held at the four RHs as described above, and observed daily for mortality. Nymphs of the fifth subgroup were placed to feed on rabbits seven days post-moulting. Engorged nymphs were held at the same temperature at which they were held before feeding and at 75% RH, and were observed daily for moulting.

Emerging adults were sexed and males and females were held separately. Adults of each sex emerging at each of the incubation temperatures, were divided into four subgroups which were held at the above four RHs, respectively, and were observed daily for mortality. Five replicates of each of the above larval, nymphal and adult subgroups were observed until all ticks died and the data were reported daily.

Product-limit estimates (Kaplan and Meier, 1958) were used for survival curves. For comparison purposes, death rate ratios were calculated under the assumption of a proportional hazards model for grouped survival data (Cox, 1972) and implemented via the computer package GLIM (Baker and Nelder, 1985).

RESULTS

Larvae:

A total of 8089 larvae were observed. The overall median survival time (MS, 50% survival) for these larvae was 13.7 days (95% confidence interval, CI = 13.1−14.6 days).

The survival curves (Figs. 1 and 2) and the estimates of MS and relative death rates (RDR) given in Table 1 summarize the survival experience of unfed larvae according to the different levels of RH and temperature. Using 96% RH as a base-line, the RDR (adjusted for age and temperature) at 75%, 52% and 32% RH were 7.5, 301.0 and 417.0, respectively; all were highly significant and so was the trend of increased risk of death with reduction in humidity (x^2=89.1, df=1, P<.0001). The RDRs for larvae held at 25°C, were 2.8, 6.2 and 13.3, respectively; all were very significantly different from unity. The test for trend of increasing death risk with increase in temperature was also highly significant (x^2=58, df=1, P<0.0001). Table 2 gives a summary of the joint effect of temperature and RH on survival of the unfed larvae. The interaction between the effect of temperature and RH was highly significant (x^2=38.0, df=9, P<0.001).

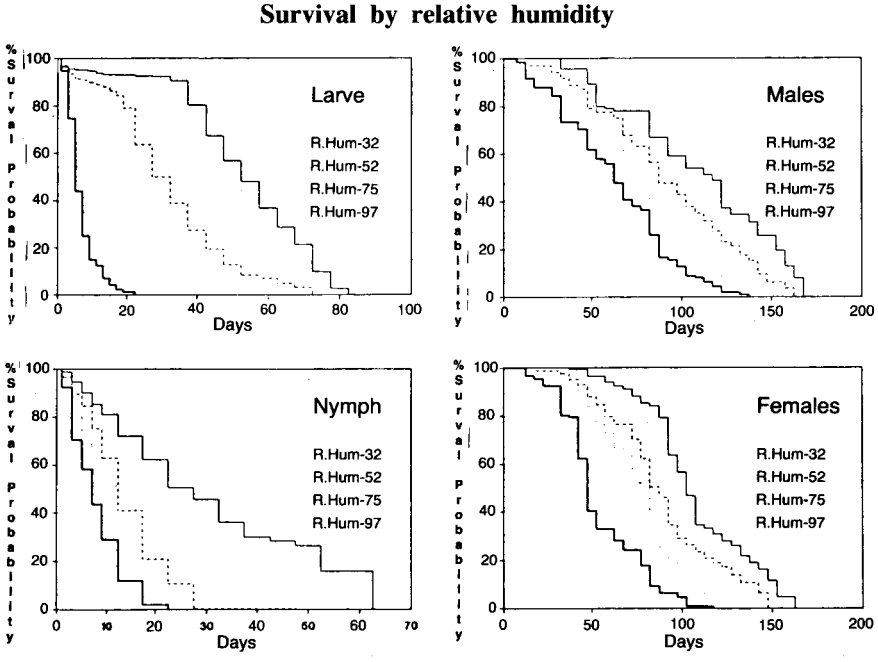

Fig. 1: Survival curves for *Hyalomma impeltatum* estimated according to different levels of relative humidity.

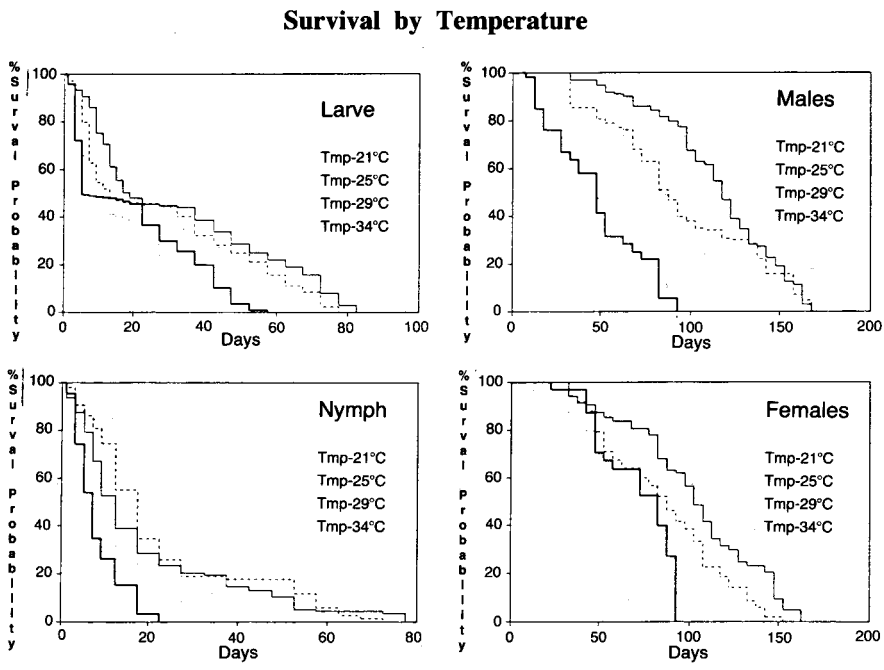

Fig. 2: Survival curves for *Hyalomma impeltatum* estimated according to different levels of temperature.

Nymphs:

A total of 3946 nymphs were observed. The overall MS was 10.5 days (95% CI=10.1-10.9 days). The ratio of the overall rate (adjusted for age, RH and temperature) of nymphs, relative to larvae, was 1.4 (95 CI=1.1-1.7, P = <0.005).

Table 1 gives estimates of the MS and RDR for nymphs at the different RHs and temperaturs. The corresponding survival curves are shown in Figures 1 and 2. The age-temperature-adjusted death rates increased significantly (4.2, 9.4 and 13.9-folds) as the RH decreased from 97% to 75%, 52% and 32%, respectively. The test of significance for this trend was x^2=38.1, df=, P<0.001.

No significant difference occurred between the age-RH-adjusted death rates of 21°C and 25°C, while the increase in death risk at 29°C, relative to 21°C, was marginally significant (RDR=1.9, P = <0.04). At 34°C, the death rate increased 4.6-folds and this was highly significant (P<0.001). However, the general trend of increased death risk with increase in temperature was highly significant (x^2=25.8, df=1, P<0.0001).

The interaction between the effects of temperature and RH was very significant

Table 1

Median survival (MS)* and relative death rates of larval and nymphal *Hyalomma impeltatum* held at different levels of relative humidity and temperature.

Factors and levels	Larvae				Nymphs			
	No	MS	RDR	95%CI+	No	MS	RDR	95%CI
Relative humidity++								
97%ǂ	2028	53.9	1.0	—	967	25.5	1.0	—
75%	2005	30.0	7.5b[II]	5.4-10.4	946	12.9	4.2b	2.6-6.3
52%	1951	6.4	301.3b	167.2-542.7	1027	8.1	9.4b	5.6-15.7
32%	2105	5.6	417.0b	228.3-761.5	1006	7.1	13.9b	8.2-23.6
Temperature π								
21°Cǂ	1997	18.3	1.0	—	856	10.9	1.0	—
25°C	1910	13.0	2.8b	2.1-3.7	958	16.2	0.8	0.5-1.2
29°C	2113	7.9	6.2b	4.5-8.4	1070	11.3	1.9a	1.2-2.8
34°C	2069	6.0	13.3b	9.4-18.8	1062	6.4	4.6b	3.0-7.2

* In days
\+ Confidence intervals
++ Rates are adjusted for age and temperature
ǂ Baseline groups
II a = P<0.05; b = P< 0.001
π Rates are adjusted for age and relative humidity

(x^2=25.0, df=9, P = <0.003). The joint effect of these two factors on survival of unfed nymphs is given in Table 3.

Adults:

A total of 4362 adults (2058 males and 2304 females) were observed. The overall MS was 83.7 days (95% CI=82.6-84.8 days) for males and 82.5 days (95% CI=81.3-83.8 days) for females. The survival difference between the two sexes was significant with age-, RH- and temperature-adjusted RDR for females relative to males, being 1.7 (95% CI=1.2-2.3, P=<0.003).

Using 97% RH and 21°C as base-line levels for RH and temperature, respectively, the age-sex-temperature adjusted RDRs for adults at 75%, 52% and 32% RH were 1.7, 3.2 and 8.1, respectively, and the age-sex-RH adjusted RDRs at 25°C, 29°C and 34°C were 2.0, 4.5 and 7.3, respectively. All these relative rates were significantly different from unity (Table 4). Survival curves at different levels of RH and temperature are given in Figures 1 and 2.

Table 2

Maximum (MxS)* and median survival (MS)*, relative death rate (RDR)+ and 95% confidence intervals (CI) for RDR of larval *Hyalomma impeltatum* held at various combinations of different levels of relative humidity (RH) and temperature.

RH	Values estimated	Temperature			
		21°C	25°C	29°C	34°C
97%					
	No	468	480	495	285
	MxS	79	75	72	55
	MS	70.9	63.5	52.9	43.0
	RDR	1.0 ++	1.8a§	4.2b	11.4b
	CI	—	1.0-3.2	2.3-7.8	5.9-22.0
75%					
	No	492	470	533	510
	MxS	72	58	36	33
	MS	48.2	37.6	21.1	23.9
	RDR	4.0b	16.9b	128.9b	116.1b
	CI	2.2-7.3	8.5-33.5	59.3-280.3	52.3-257.5
52%					
	No	511	450	510	480
	MxS	20	18	16	5
	MS	10.7	8.4	6.1	4.2
	RDR	563.7a	968.3b	2818.5b	5636.9b
	CI	238.0-1108.0	395.4-1618.0	834.3-4509.5	4622.3-8455.4
32%					
	No	526	510	575	494
	MxS	20	9	8	4
	MS	12.1	6.0	5.3	3.7
	RDR	533.8b	1601.4b	3202.7b	5337.9b
	CI	225.9-1006.2	951.9-1868.3	2135.2-4270.3	4470.3-8006.9

* In days
\+ Adjusted for age
++ Baseline group
§ a = P <0.05; b = P < 0.001

The trend of improved survival with higher levels of RH was extremely significant (x^2=46.3, df=1, P<0.0001) as was the trend of improved survival with lower temperatures (x^2=44.6, df=1, P<0.0001).

Table 3

Maximum (MxS)* and median survival (MS)*, relative death rate (RDR)+ and 95% confidence intervals (CI) for RDR of nymphal *Hyalomma impeltatum* held at various combinations of different levels of relative humidity (RH) and temperature.

RH	Values estimated	Temperature			
		21°C	25°C	29°C	34°C
97%					
	No	197	224	275	271
	MxS	78	69	35	20
	MS	47.6	54.7	25.0	12.3
	RDR	1.0 ++	1.0	8.7a∮	39.3a
	CI	—	0.4-2.5	3.0-25.3	12.4-124.6
75%					
	No	230	245	225	246
	MxS	28	27	24	20
	MS	11.0	19.8	15.2	8.4
	RDR	28.4a	16.9a	29.2a	60.2a
	CI	9.5-85.2	5.4-52.9	9.0-94.5	18.7-194.2
53%					
	No	204	247	282	294
	MxS	21	20	13	11
	MS	8.7	13.8	9.1	6.1
	RDR	51.8a	35.9a	79.1a	151.7a
	CI	5.7-170.5	1.2-115.0	24.6-254.6	46.9-491.2
32%					
	No	225	242	288	251
	MxS	20	17	12	8
	MS	8.3	11.9	7.4	3.5
	RDR	56.9a	47.6a	105.3a	338.3a
	CI	17.5-184.9	14.7-154.4	32.7-338.8	101.3-1120.4

* In days
\+ Adjusted for age
++ Baseline group
∮ a = $P < 0.001$

In the adult stage, the interaction between the effects of temperature and humidity was not statistically significant ($x^2=12.4$, df=9, $P>0.15$), and neither was the interaction between sex and RH ($x^2=1.3$, df=3, $P>0.7$). However, the effect of

Table 4

Median survival (MS)* and relative death rate (RDR) of adult *Hyalomma impeltatum* estimated according to relative humidity (RH) and temperature.

Factor and levels	Males				Females				All adults		
	No	MS	RDR+	95%CI	No	MS	RDR+	95%CI	No	RDR++	95%CI
RH											
97%ϕ	503	117.7	1.0	—	567	103.4	1.0	—	1070	1.0	—
75%	512	88.7	1.7a II	1.1-2.7	580	85.4	2.0b	1.3-3.1	1092	1.7c	1.3-2.4
52%	523	81.4	2.9c	1.8-4.6	584	80.9	4.1c	2.6-6.5	1107	3.2c	2.3-4.4
32%	531	63.7	5.5c	3.4-8.9	573	47.8	13.0c	7.8-21.5	1104	8.1c	5.7-11.5
Temperature											
21°Cϕ	521	118.0	1.0	—	574	104.0	1.0	—	1095	1.0	—
25°C	524	86.1	1.8a	1.1-2.7	616	86.8	2.4c	1.5-3.6	1140	2.0c	1.5-2.7
29°C	522	84.4	3.7c	2.3-6.1	568	66.9	6.4c	3.9-10.3	1090	4.5c	3.2-6.4
34°C	491	47.4	11.7c	6.9-19.9	546	81.0	6.6c	4.0-11.0	1037	7.3c	5.1-10.5

* In days

\+ Adjusted for age and temperature; or age and RH as appropriate

\++ Adjusted for age, sex and temperature; or age, sex and RH as appropriate

ϕ Baseline groups

II a : $P < 0.05$; b = $P < 0.01$; c = $P < 0.001$

Table 5

Maximum (MxS)* and median survival (MS)* for adult *Hyalomma impeltatum* at various combinations of different levels of relative humidity (RH) and temperature.

RH	Values estimated	Temperature							
		Males				Females			
		21°C	25°C	29°C	34°C	21°C	25°C	29°C	34°C
97%									
	No	135	138	130	126	144	171	132	126
	MxS	164	164	122	91	160	150	117	91
	MS	151.4	143.4	112.3	53.1	147.5	109.7	97.0	91.0
75%									
	No	156	116	117	125	164	138	142	140
	MxS	160	161	120	80	146	143	102	91
	MX	126.9	101.3	88.7	47.3	126.3	95.8	75.5	83.6
52%									
	No	105	144	143	120	132	152	156	140
	MxS	162	135	109	79	123	113	88	84
	MS	117.3	84.7	78.3	37.9	97.2	85.5	64.2	82.4
32%									
	No	125	126	132	120	134	155	138	140
	MxS	137	121	89	79	116	88	81	47
	MS	97.5	72.1	62.5	26.1	79.0	50.1	45.3	44.4

* In days

temperature on survival of males was significantly greater than that on females (x^2=25.1, df=3, P<0.0.001). The data on maximal and median survival in both sexes are given in Table 5.

DISCUSSION

The data of the present study clearly demonstrated that both RH and temperature have an extremely significant impact on survival of all unfed stages of *H. impeltatum*, with the effect of RH being stronger than that of temperature. Within the ranges of RH (32–97%) and temperature (21–34°C) used in this study, survival was improved significantly with elevation in RH and reduction in temperature. Similar observations on the effect of RH and temperature on survival were reported for *H. asiaticum* Schulze and Schlottke (Balashov, 1968), *H. lusitanicum* Koch (Ouhelli and Pandey, 1984), *Rhipicephalus evertsi evertsi* Neumann (Hamel and Gothe, 1974) and *R. sanguineus* (Latreille) (Koch and Tuck, 1986). Improvement of survival with elevation in RH at a constant temperature was also reported for *H. (H.) dromedarii* Koch (Hafez *et al.* 1970).

The qualitative effect of RH on *H. impeltatum* survival was uniform between stages, between the sexes in the adult stage and between the various levels of temperature within each stage. The same uniformity in the qualitative effect applies to temperature. Thus, there was no evidence from the present data of a qualitative interaction between the effects of temperature, RH and stage on death risk (i.e. the effect of one of these factors does not change direction between the levels of the other factor). However, the magnitudes of the effects of RH and temperature on *H. impeltatum* survival varied significantly between stages, i.e. a qualitative interaction between RH, temperature and stage on death risk is evident.

Although larvae exhibited a longer life span than nymphs, the impact of changes in RH on survival was stronger in the larval stage where we estimate, on the average, an 8% reduction in mortality with every 1% increase in RH as compared to about 3% reduction in mortality in the nymphal as well as in the adult stages. *H. impeltatum* larval stage also seem to be the most vulnerable to changes in temperature with an estimated 22% average rise in death rate with every 1 degree rise in temperature, as compared with a rise in death rate of 14% and 17% for nymphs and adults, respectively. The lower tolerance of larval *H. impeltatum* to low RH and high temperature may be attributed to the higher permeability of their delicate integument to water vapour as compared to that of the successive developmental stages (reviewed by Hackmann, 1982). In the natural habitat, larval *H. impeltatum* remains throughout their development in the burrows of their rodent hosts (Hoogstrall, 1956) at a relatively high and nearly constant RH and moderate temperature (Yunker and Guirgis, 1969). At RH below their critical

equilibrium activity [(RH% in the air at which no gain or loss of water occurs (Wharton and Devine, 1968) and below which active water absorption cannot occur (Knulle and Devine, 1972)], larval *H. impeltatum* probably lose water faster than nymphs and adults which results in a stronger reduction in larval survival with reduction in RH. Survival of larval *Amblyomma americanum* (L.) (Lancaster and McMillan, 1955) and *H. dromedarii* (Hafez *et al.*, 1970) was also greatly reduced with reduction in RH, with a significant increase in weight loss rate, owing to water loss, in the latter species.

In *H. impeltatum,* nymphs exhibited the lowest elevation of death risk with the increase in temperature. This phenomenon may be associated with the facultative two- or three-host character of this species (Osman, 1979; Khalil and Hagras, 1988). Engorged larvae often remain attached to the mammalian host until moulting, and emerging nymphs spend their pre-feeding period on the host (Osman, 1979) at a temperature close to the latter's body temperature. Thus, unfed nymphs are probably adapted to tolerate relatively high temperatures.

In the pre-adult *H. impeltatum* stages, the magnitude of the effect of RH on survival varied significantly between the different levels of temperature. However, no such RH-temperature interaction was observed in the adult stage. Adult ticks have a great ability to tolerate desiccating conditions. In several tick species, adults were reported to produce a hygroscopic salivary secretion, rich in sodium and potassium, which appears to be responsible for extracting water vapour from the air (McMullen *et al.*, 1976; Rudolph and Knulle, 1974, 1978; Knulle and Rudolph, 1982). Excretion of this hygroscopic fluid also enables the adult ticks to maintain the osmalirity of their body (cells and haemolymph) at a non-harmful level (Shih *et al.* 1973) and, meanwhile, functions as a storage excretion of valuable ions (Needham and Teel, 1986) which become re-imbibed as the RH is increased (Rudolph and Knulle, 1974). Absorption of the imbibed fluid then occurs either in the gut and/or through the salivary glands (reviewed by Knulle and Rudolph, 1982). Such mechanism of osmoregulation-rehydration, which has been observed in adults but not in immature stages, probably contributes to the greater ability of the adults to survive for lengthy periods at low RHs.

Among other factors that may contribute to the prolonged survival of adult ixodids under desiccating conditions is the lower permeability of their cuticle to water (Lees, 1946). The difference in the cuticular permeability is probably associated with the qualitative and quantitative variation in the composition of the water-proofing epicuticular lipids (Gai and Jiang, 1983). Such variation, probably, results in a different critical equilibrium activity for each stage, as reported to occur in several ixodid species (Lees, 1946; also reviewed by Needham and Teel, 1986).

In the present study, elevation in temperature resulted in a shorter survival of all *H. impeltatum* stages. As the temperature is raised within a physiologically tolerable

range, the tick metabolic rate is increased, as expressed by elevation in the respiratory coefficient (Maklygin and Alekseev, 1960), and the nutritional reserve is exhausted in a shorter time. Elevation of temperature also enhances the rate of transpiration (Arlian and Veselica, 1979) which becomes detrimental when the ambient RH is much below the critical equilibrium activity; a greater rate of loss of tick body weight, owing to a faster loss of water vapour with the decrease in RH and leading to a shorter survival, has been reported for several ixodid species (reviewed by Needham and Teel, 1986).

In *H. impeltatum* adult stage, the median survival time for males (83.7 days) is only slightly greater than that for females (82.5). However, the death rate for females (after taking the effects of age, temperature and RH in account) is 70% higher than that of males, which suggests that females tend to fare worse than males particularly during the post-median survival times. Hafez *et al.* (1970) reported that female *H. dromedarii* also survive for shorter periods than males at RHs below their critical equilibrium activity. However, lack of a statistical analysis of their data makes accurate comparison of female and male survival in *H. impeltatum* with that in *H. dromedarii* impossible. The shorter post-median survival of female *H. impeltatum* may be associated with a greater effect of aging on females than on males. As the tick ages, the integument may become less effective as a barrier to water loss owing to the lower ability of the tick to replenish the water-proofing lipids. The active water vapour uptake mechanism would then have to operate either more frequently or for longer periods, causing a greater depletion of the energy reserves (Needham and Teel, 1986). The epicutice of unfed female ixodids is highly folded while the male epicuticle is not (Balashov, 1968; also reviewed by Hackmann, 1982). This structural difference between the sexes results in a greater surface area containing the water-proofing lipids in females which places a greater burden on the female than the male as it ages.

In this study, temperature changes in the upper range (34^{0}C) had a significantly stronger effect on survival in male than in female *H. impeltatum*. However, RH appeared to affect both sexes equally throughout its range (32-97%). The difference in the temperature effect between the sexes may reflect differences in the physiological and metabolic activities between the sexes and requires investigation.

From this investigation, it is possible to explain certain biological, ecological and behavioural characteristics of *H. impeltatum*. Natural hosts of larval and nymphal *H. impeltatum* are small burrowing mammals, hares and rarely lizards (Hoogstraal, 1956) but adults venture forth in search of larger hosts, which are camels in Qatar. Unfed larvae and nymphs appear to require burrows for shelter as they cannot withstand desiccation for lengthy periods. However, adults are probably provided with more efficient mechanisms for maintaining water balance and osmoregulation

to tolerate considerable desciccation; adults are often seen rushing across the desert toward moving camels or humans.

The periodic questing-hiding behaviour of *H. impeltatum*, as well as many other adult ixodids, may reflect a water balance regulatory mechanism (Balashov, 1968). Awaiting passing hosts on the soil surface or in the upper parts of burrows with RHs below their critical equilibrium activity and at relatively high temperatures (diurnal temperature in Qatar is around 40°C for about 5 months per year), inevitably results in water loss by transpiration. Decrease in the body water content to a certain level within the tick changes its behaviour and it moves into more humid places at a relatively lower temperature, such as ground cracks or burrows. In these locations, active water uptake restores the body water content to the normal level. Then, the tick moves up to drier, warmer habitats with more chance for finding a host.

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أثر الحرارة والرطوبة النسبية على طول عمر الأفراد الجائعة من هيولوما إمبلتاتام (القراديات : القراد الجامد)

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شملت الدراسة ٨٠٨٩ يرقة ٣٩٤٦ حورية و ٢٠٥٨ ذكراً و ٢٣٠٤ أنثى من القراد هيالوما إمبلتاتام ، وتم في هذا البحث دراسة طول عمر الأفراد الجائعة من هذه الأطوار عندما تعيش تحت تأثير ارتباطات مختلفة من درجات حرارة (٢١ ، ٢٥ ، ٢٩ ، ٣٤°م) ورطوبة نسبية (٣٢ ، ٥٢ ، ٧٥ ، ٩٧ ٪) متباينة . وقد زاد طول العمر لمدد ذات دلالة عالية في جميع الأطوار كلما ارتفع معدل الرطوبة النسبية وانخفضت درجة الحرارة ، ولكن اختلف مدى تأثير معدل الرطوبة النسبية ودرجة الحرارة باختلاف الطور . فقد كان التغير في معدل الرطوبة النسبية ودرجة الحرارة ذا أثر أكبر على اليرقات منه على الحوريات والطور البالغ ، وكانت الحوريات أكثر الأطوار تحملاً للتغيرات في درجة الحرارة . وعند احتساب طول العمر عند مستوى ٩٧٪ من الرطوبة النسبية أساساً لحساب معدل النفوق وجد أن معدل النفوق النسبي ـ المعدل تبعاً لدرجة الحرارة ـ عند مستوى ٣٢٪ من الرطوبة النسبية هو ٤١٧ لليرقات و ١٣,٩ للحوريات و ٨,١ للطور البالغ . وعند احتساب طول العمر عند مستوى ٢١°م أساساً لحساب معدل النفوق وجد أن معدل النفوق النسبي ـ المعدل تبعاً لمستوى الرطوبة النسبية ـ عند درجة حرارة ٣٤°م هو ١٣,٣ لليرقات و ٤,٦ للحوريات و ٧,٣ للطور البالغ . وقد كان تحمل الذكور للتغيرات في درجة الحرارة والرطوبة أكثر منه في الإناث . فقد وجد أن معدل النفوق النسبي ـ المعدل تبعاً للعمر ومستوى الرطوبة النسبية ودرجة الحرارة ـ هو ١,٧ للإناث بالنسبة للذكور ، مع ملاحظة أن الفرق في طول العمر كاد أن يكون قاصراً على فترة ما بعد العمر الوسطى . كذلك لم يلاحظ تفاعل ذو دلالة بين تأثير مستوى الرطوبة النسبية وكلا من درجة الحرارة أو الجنس في الطور البالغ . وفي البحث تمت مناقشة أسباب الاختلاف في قدرة الأطوار المختلفة على تحمل التغيرات في درجات الحرارة ومستوى الرطوبة النسبية وعلاقته بصفات الجليد والتأقلم للظروف البيئية المختلفة .