

**Spektrale und absolute Empfindlichkeit,  
Sehfeld und Skototaxis der Zeckenarten  
*Hyalomma dromedarii* und *Amblyomma variegatum***

**Vergleichende sinnesphysiologische Untersuchungen  
am optischen System zweier Zeckenarten**

**Thèse présentée à la Faculté des Sciences de l'Université de Neuchâtel  
pour obtenir le grade de docteur ès sciences**

par  
**Martin Kaltenrieder**

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# IMPRIMATUR POUR LA THÈSE

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Hyalomma dromedarii und Amblyomma variegatum.....

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.....  
de Monsieur Martin Kaltenrieder.....

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UNIVERSITÉ DE NEUCHÂTEL

FACULTÉ DES SCIENCES

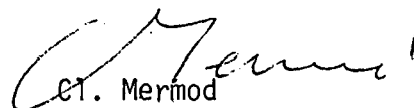
La Faculté des sciences de l'Université de Neuchâtel  
sur le rapport des membres du jury,

Messieurs P.A. Diehl, A. Aeschlimann,.....  
P. Guerin, E. Hess (Bâle) et R. Schwind.....  
(Regensburg).....

autorise l'impression de la présente thèse.

Neuchâtel, le .....8 novembre 1989.....

Le doyen :

  
C. Mermod

# Spectral sensitivity, absolute threshold, and visual field of two tick species, *Hyalomma dromedarii* and *Amblyomma variegatum*

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**Summary.** 1. The spectral sensitivity in the wavelength range of 340–750 nm was determined by both a behavioral approach based on spontaneous positive phototaxis and the electroretinogram (ERG).

2. Concerning phototaxis the camel tick, *Hyalomma dromedarii*, showed two sensitivity maxima, one in the UV range (ca. 380 nm) and another in the blue-green range (ca. 500 nm). At higher intensities the relative sensitivity was more pronounced in the UV and at lower intensities more pronounced in the blue-green (reverse Purkinje shift). In the tropical bont tick, *Amblyomma variegatum*, there was a single sensitivity maximum in the blue range (ca. 480 nm).

3. In the ERG there was a maximum in the blue range (ca. 470 nm) in both species and a weak secondary maximum in the UV in *Hyalomma*.

4. The absolute sensitivity was very high. The threshold irradiance of phototaxis was as low as  $5.2 \times 10^6$  photons  $\cdot$  s<sup>-1</sup>  $\cdot$  cm<sup>-2</sup> in *Hyalomma* and  $5.2 \times 10^8$  photons  $\cdot$  s<sup>-1</sup>  $\cdot$  cm<sup>-2</sup> in *Amblyomma*.

5. When the eyes of *Hyalomma* were covered, the threshold irradiance was still very low, namely  $5.2 \times 10^8$  photons  $\cdot$  s<sup>-1</sup>  $\cdot$  cm<sup>-2</sup>, indicating high absolute sensitivity of the extraretinal photoreceptors.

6. The visual field of the eyes was determined by ERG measurements. In both species the optical axis of each eye, i.e., the center of the visual field, was directed somewhat to the side and above the horizon. In *Hyalomma* this direction was 35° to the long axis of the animal and 30° above the horizon for natural body posture during walking. In *Amblyomma* the corresponding angles were 39° and 33°, respectively. The size of the field (at 50% sensitivity) in *Hyalomma* was relatively small,

namely 14° in the horizontal and 25° in the vertical direction, compared with that of *Amblyomma* with 43° and 49°, respectively.

7. This is the first demonstration in ticks of spectral and absolute sensitivity by the behavioral approach and of the visual field by ERG. The results suggest that tick eyes possess features of both spider eyes and insect ocelli.

## Introduction

The evidence that ticks can perceive light and respond to it is based on three types of observations. (1) The photoperiod influences activities and physiological processes such as host-seeking, feeding, disengagement, drop-off, egg-laying, development, and dormancy (review Belozero 1982). (2) Exposure of ticks to continuous or intermittent light induces nonoriented behavioral responses such as 'agitation' (El-Ziady 1958), 'questing' (McEnroe and McEnroe 1973), 'legraising', or 'hesitating' (Carroll and Pickens 1987). (3) Exposure of ticks to continuous light gives rise to negative or positive phototaxis (reviewed in Kaltenrieder, unpublished). The latter seems to be possible even in the absence of externally visible eyes, since several eyeless species display phototaxis. This points to the importance of extraretinal photoreceptors, the existence of which is proposed on the basis of structural and behavioral investigations (Binnington 1972; Panfilova 1976; Shoukrey and Sweatman 1984).

The behavioral response to different wavelengths of light has been investigated in several tick species (Hindle and Merriman 1912; Totze

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1933; Carroll and Pickens 1987; Koch et al. 1988). However, no attention was paid to the adjustment of the light intensities at the different wavelengths used in these experiments. Therefore, the different responses to the various light qualities could be caused by differences of the test light intensities. ERG measurements to determine the spectral response of tick eyes have only been done in *Hyalomma dromedarii* and *Dermacentor variabilis*, whose peak wavelengths are observed at 470 nm and 510 nm, respectively (Carroll and Pickens 1987). The optical axis of the eyes has so far only been measured in *Hyalomma asiaticum* (Leonovich 1986), and no data are as yet available regarding the width of the visual field in ticks.

Nevertheless, there is still little known on the visual system of ticks and therefore just as little on its possible involvement in host-seeking behavior. It is the aim of this study to compare fundamental properties of the visual system in two species which differ with respect to the morphology of their eyes and their host-seeking behavior. The camel tick, *Hyalomma dromedarii*, has single-lens eyes that protrude above the body surface and has been reported to hunt its host (e.g., Balashov 1968; Leonovich 1986). The tropical bont tick, *Amblyomma variegatum*, on the other hand, has comparatively flat single-lens eyes and is reported to ambush its host (F. Gigon, personal communication). Both species transmit important diseases to livestock such as heartwater, rickettsioses, theilerias, and viroses (Hoogstraal 1956; FAO 1984).

In this paper the spectral sensitivity of *Hyalomma dromedarii* and *Amblyomma variegatum* (Acari, Ixodidae) in the wavelength range of 340–750 nm over 5 and 3 log units of irradiance, respectively, was determined by both a behavioral approach based on spontaneous positive phototaxis towards a horizontal light beam and the ERG. We investigated the absolute threshold in phototaxis and the role of extraretinal photoreceptors. In addition we determined the size of the visual field by angular sensitivity measurement using electrophysiology. Some of the data have already been reported in an abstract (Kaltenrieder et al. 1988).

## Methods

### Animals

The camel tick, *Hyalomma dromedarii*, is widely distributed in eastern and northern Africa, in the Middle and Near Orient and on the Arabian peninsula, wherever dromedaries occur. Adults feed on dromedaries, cattle, horses, sheep, and goats, immatures on dromedaries, small burrowing mammals, and lizards (Hoogstraal 1956; Morel 1969).

The tropical bont tick, *Amblyomma variegatum*, is widely distributed in the tropics and subtropics south of the Sahara, in South Africa, the Madagascan archipelago, south-western Arabia, on the Cape Verde Islands and the West Indies (Hoogstraal 1956). The main hosts of all developmental stages are domestic animals, especially cattle, and game.

*Hyalomma dromedarii* Koch 1844 originating from Egypt (U.S. Naval Medical Research Unit No. 3; Cairo) and *Amblyomma variegatum* Fabricius 1794 from the Ivory Coast (Centre Suisse de Recherches Scientifiques, Adiopodoumé) were generously supplied by Ciba-Geigy Ltd, Animal Health (CRA, St. Aubin; Switzerland), where they were reared on tails of Simmental-Redholstein calves. We used unfed adults 2 to 10 months after nymphal drop-off.

### Behavioral experiments

**Keeping and preparation of animals.** Ticks (males and females separately) were put into glass tubes (40 mm, Ø 19 mm; 5 ticks per tube) with perforated plastic plugs at  $27 \pm 1^\circ\text{C}$  and  $85\% \pm 5\%$  r.h. and kept under nonrhythmic light conditions (Tungsten lamp, 80 lux; light and dark periods randomly lasting 40–100 min) for 1 to 4 weeks before an experiment. Under these conditions the ticks were most responsive in phototaxis (Kaltenrieder, unpublished). In some experiments the extraretinal photoreceptors situated along the rim of the scutum/alloscutum (Diehl et al., unpublished) were painted over with black paint (Herbol, Vollton- und Abtönfarbe; Herbol AG, Baar, Switzerland) and/or the eyes were covered with small pieces of aluminum foil whereby the paint was used as adhesive. In the control experiments the paint and/or the aluminum foils were applied medial to the photoreceptors.

**Light stimulus.** The light of a halogen lamp (reflector lamp, No. 6426, 6 V/15 W; Philips) passed through a heat-absorption filter (KG 1; Schott), a set of neutral density filters (Balzers) for intensity adjustment in steps of 1.0 or 0.5 log units covering a range of 5 log units and a set of 11 narrow band interference filters for the generation of monochromatic light with  $\lambda_{\text{max}}$  ranging from 344 to 748 nm. Finally the light passed through a scattering filter of 38 mm diameter (tracing paper No. 139; Aerni-Leuch AG, Liebfeld, Switzerland), which was positioned at the periphery of the arena. The surface temperatures of the scattering filter were measured with a temperature radiometer (KT 15; Heimann GmbH, Wiesbaden, Germany). The lamp and the filters were surrounded with styrofoam. Absolute irradiance at each wavelength was determined by (1) measuring the spectral irradiance of the unfiltered (except heat-absorption and scattering filter) white light in the center of the arena and (2) convolution of the spectral transmittances of interference and neutral density filters with the spectral irradiance curve. The spectral irradiances of monochromatic stimuli were adjusted to equal energy ( $\pm 0.05$  log units) by neutral density filters. Maximal monochromatic irradiance in the center of the arena was  $2.0 \times 10^{-8} \text{ W} \cdot \text{cm}^{-2}$  for 521 nm, which corresponds to  $5.2 \times 10^{10} \text{ photons} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$ .

**Arena and experimental setup** (Fig. 1a, b). Experiments were conducted in a dark room at  $27 \pm 1^\circ\text{C}$  and  $55\% \pm 5\%$  r.h. The white arena (Ø 204 cm) was provided with markings (Fig. 1b) and surrounded with a black cotton cloth rising 55 cm above the arena surface (Fig. 1a). In the experiments with *Amblyomma*, which is extremely thermosensitive, a plastified aluminum foil was fitted to the outer side of the cotton cloth, and the arena was covered with a styrofoam plate (thickness 5 cm, Ø 230 cm) 58 cm above the surface. The plate had a circular opening of Ø 125 cm in the center for the infrared observation

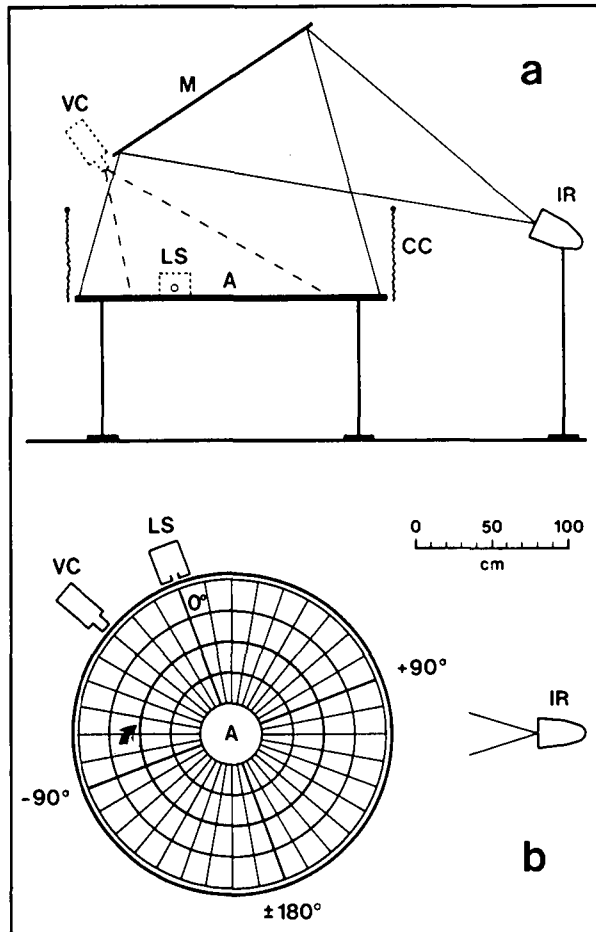


Fig. 1 a, b. Setup for measurement of phototaxis, side-view (a) and top-view (b). A, arena; CC, cotton cloth (not shown in b); LS, light stimulus; VC, videocamera; IR, infrared light which is deflected by mirror (M). Arrow points at the 60-cm circle

light (see below: Recording). The light stimulus was presented at a distance of 106 cm from the center of the arena and at 4.9 cm above its surface through a hole in the cloth (Fig. 1 a, b). For a tick at the starting point in the center of the arena this spot was situated between  $1.6^\circ$  and  $3.7^\circ$  above the horizon.

**Recording** (Fig. 1 a). The walking paths of the ticks were recorded from above by an infrared-sensitive videocamera equipped with a wide-angle lens which allowed viewing of the surface within the 60-cm circle. Videosignals were stored by a recorder and displayed on a black and white monitor. Infrared illumination from above was provided by a tungsten lamp, equipped with an infrared cut-on filter ( $\lambda_H$ : 880 nm; Siemens AG, Zürich, Switzerland).

**Testing procedures.** Ticks were adapted to dim white light (tungsten lamp,  $<0.2$  lux) for at least 15 min. To activate the ticks they were then exposed to a temperature of  $31^\circ \pm 1^\circ \text{C}$  for 3 min, gently shaken several times in their glass tube, and after removal of the plug the experimenter blew on them for 3 s. The ticks were then introduced into the center of the arena which at this moment was illuminated with dim white light (tungsten

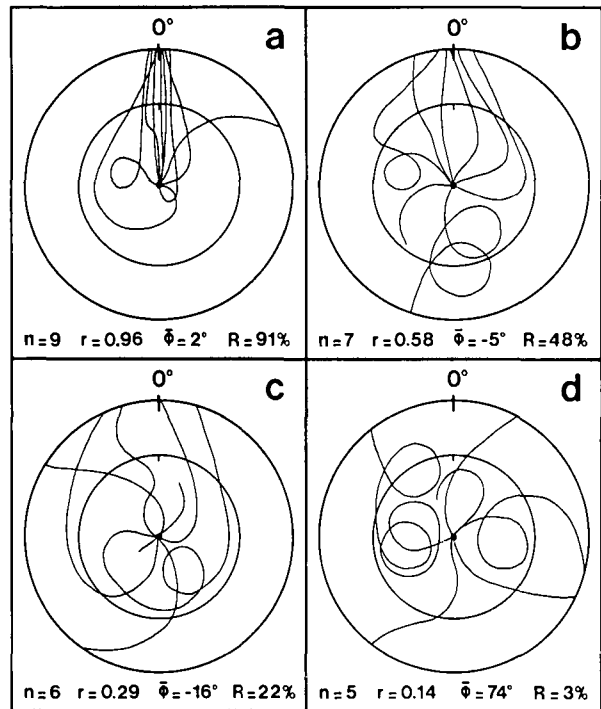


Fig. 2 a-d. Typical walking paths in phototaxis and corresponding parameters of the response of a sample of 10 ticks each (*Hyalomma*): a High stimulus irradiance (e.g., log rel I = 0). b Medium stimulus irradiance (e.g., log rel I = -2). c Low stimulus irradiance (e.g., log rel I = -4). d Extremely low stimulus irradiance (e.g., log rel I = -5) or control. Outer circle = 100-cm circle; inner circle = 60-cm circle; stimulus in  $0^\circ$ -direction

lamp, 6 lux). *Hyalomma* were introduced in the opened upright glass tube, while *Amblyomma* were poured out of the tube. Then the dim white light was turned off, and the stimulus light together with the infrared observation light was switched on. The experimenter retreated behind a curtain 2 m from the arena. The ticks were exposed to the test light stimulus for 150 s. After 10 test runs the arena surface was cleaned with ethanol 70%.

**Evaluation of data.** The angular values where the ticks for the first time crossed the 60-cm circle were registered. The circle was graduated from  $0^\circ$  to  $\pm 180^\circ$ , the  $0^\circ$ -direction pointing to the centre of the test light (Fig. 1 b). The formula which gave linear  $R$ -log I functions was developed to quantify the phototactic response. The response of *Hyalomma* was defined as:

$$\text{Response } R = \sqrt{n/N} \cdot r \cdot \cos \bar{\Phi} \cdot 100\%$$

where  $n$  is the number of ticks crossing the 60-cm circle,  $N$  the total number of ticks introduced in the arena,  $r$  the mean vector length (measure of concentration), and  $\bar{\Phi}$  the mean angle (measure of direction) of the sample (see Batschelet 1981). Negative response values (obtained if  $\bar{\Phi} > |90^\circ|$ ) were defined as 0%. Typical walking paths at high, medium, low, and extremely low stimulus irradiance and the corresponding parameters of the response are shown in Fig. 2: With decreasing irradiance (1) the number  $n$  decreased, (2) the mean vector length  $r$  also decreased, and (3) the mean angle  $\bar{\Phi}$  became more and more different from zero. All this together led to a decrease of the response  $R$ . Spectral efficiency measurements were obtained

with equal energy stimuli adjusted to equal photon stimulation using the corresponding  $R$ -log  $I$  functions. Sensitivities were calculated from the efficiency measurements and the corresponding  $R$ -log  $I$  functions for the different wavelengths.

For *Amblyomma* in principle the same formula was used, but because a slight bias in the 135° direction was observed in the control experiments (see Results: Controls), a correction was applied: The mean vector of the sample was separated into a 0°- and in a 135°-element, and the 0°-element was considered as the mean vector. The phototactic response of *Amblyomma* thus was defined as: Response  $R = \sqrt{n/N} \cdot r \cdot (\sin \bar{\Phi} + \cos \bar{\Phi}) \cdot 100\%$ . In *Amblyomma* the adjustment of the spectral efficiency measurements to equal photon stimulation and the calculation of the sensitivities were based on a single averaged  $R$ -log  $I$  function.

**Statistics.** In order to evaluate whether a sample of ticks was oriented in the direction of the stimulus, the  $V$  test was used, and for comparing the orientation of two samples (home strength), a nonparametric test for dispersion was used (Batschelet 1981). Other tests which were applied are referred to in the Results section.

#### Electrophysiology

In principle, the same setup and procedures of stimulation and evaluation as described in detail by Labhart (1980) were used. Here, only relevant differences will be mentioned. The duration of the stimulus was 100 ms, and the interstimulus interval was 10 s or 15 s. The diameter of the stimulus was 11.4° for spectral sensitivity and 1.9° for angular sensitivity measurements. In the latter, steps of 5° or 10° were used. Maximal monochromatic irradiance at the eye surface was  $3.2 \times 10^{15}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ . These relatively high irradiances were necessary to record a reasonable, low noise signal in these animals. Spectral and angular sensitivity functions were calculated from the respective efficiency functions (obtained with equal photon stimuli) using  $R$ -log  $I$  functions as calibrations.

**Keeping, preparation, and recording.** The ticks were kept at L/D=14/10 h, 22° ± 1 °C and 85% ± 5% r.h. The experiments were done by using a conventional setup for electrophysiological recording consisting of a high impedance, low noise amplifier, a storage oscilloscope (bandwidth set 1–100 Hz) and a high frequency chart recorder (50 Hz bandwidth). The electrodes consisted of mechanically sharpened, noninsulated steel needles. The ticks were mounted on a holder with dental wax, the rostrum, scutum (and alloscutum), and the legs were fixed rigidly, and the whole animal was oriented according to its normal walking posture (previously determined by photographs and video films of freely walking ticks). This posture was characterized by a positive pitch of the long axis of 15° in *Hyalomma* and 13° in *Amblyomma*. The eye was centered with respect to the perimeter system and the recording electrode was carefully pushed into the rim of the lens or just beside the lens. The reference electrode was placed in the scutum or alloscutum close to the eye.

## Results

### Controls

Since ticks are extremely thermosensitive we first tested whether warming up of the setup during an experiment had an influence on the orientation

of the ticks. (1) A sample of 100 ticks of each species was tested with the light beam interrupted by a piece of black cardboard inserted after the scattering filter. The temperature of the cardboard rose from 27 °C at the beginning of the experiment to 30 °C at the end of 20 test runs, but neither *Hyalomma* and *Amblyomma* was oriented in the direction of the stimulus ( $P > 0.10$ ) or in any other direction ( $P > 0.10$ ; Rayleigh test and Rao's spacing test, Batschelet 1981). (2) A sample of 100 ticks of each species was tested after the stimulus was switched on for 150 s just before a test run. In this case the temperature of the scattering filter at the beginning of a test run was maximally 31 °C, but again *Hyalomma* and *Amblyomma* were not oriented in the direction of stimulus ( $P > 0.10$ ) or in any other direction ( $P > 0.10$  in *Hyalomma* and  $P > 0.05$  in *Amblyomma*). In addition, the response of the ticks to infrared light of the same quality and irradiance as used for the observation light was tested: Neither *Hyalomma* and *Amblyomma* was oriented in the direction of the infrared test light ( $P > 0.10$ ).

However, when the results of three control series (= 300 ticks) were combined, *Amblyomma* significantly clustered around the 135° direction ( $P < 0.05$ ) in all three types of controls. The influence of this phenomenon of unknown origin on the mean response vector was eliminated by special treatment of the data (see Methods: Evaluation of data).

### Spectral sensitivity in *Hyalomma*

For quantifying the positive phototaxis we measured the spectral efficiency functions (Fig. 3), plotted the  $R$ -log  $I$  functions (Fig. 4), and from these calculated the spectral sensitivity functions (Fig. 5a). Although the shape of the sensitivity functions changed with stimulus irradiance, two maxima could be distinguished. At maximal irradiance (log rel  $I = 0$ ) there was a maximum in the UV range (ca. 380 nm). With decreasing irradiance, this maximum disappeared, and a second maximum in the blue-green range (ca. 500 nm) appeared (Fig. 5a). Thus, at high irradiances the relative sensitivity was more pronounced in the UV (UV: blue-green ratio 20:1) and at low irradiances more pronounced in the blue-green (UV: blue-green ratio 1:5). This phenomenon, called reverse Purkinje shift, was also expressed by the crossing of the UV  $R$ -log  $I$  functions with the blue/green functions (Fig. 4). The slopes did not differ significantly ( $P > 0.05$ ; comparison of regression coefficients, Sachs 1984), although a trend was clearly

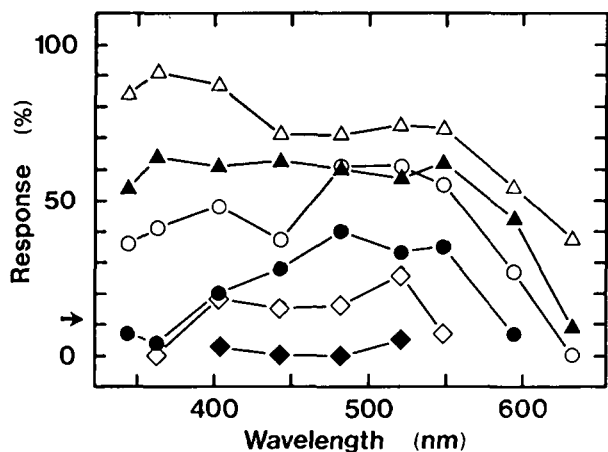


Fig. 3. Spectral efficiency functions of *Hyalomma* in phototaxis.  $\Delta$  log rel  $I=0$  (maximal irradiance =  $5.2 \times 10^{10}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ ),  $\blacktriangle$  log rel  $I=-1$ ,  $\circ$  log rel  $I=-2$ ,  $\bullet$  log rel  $I=-3$ ,  $\diamond$  log rel  $I=-4$ ,  $\blacklozenge$  log rel  $I=-5$ . Each symbol represents the response obtained with 100 ticks. Arrow: threshold response of orientation ( $P=0.05$ )

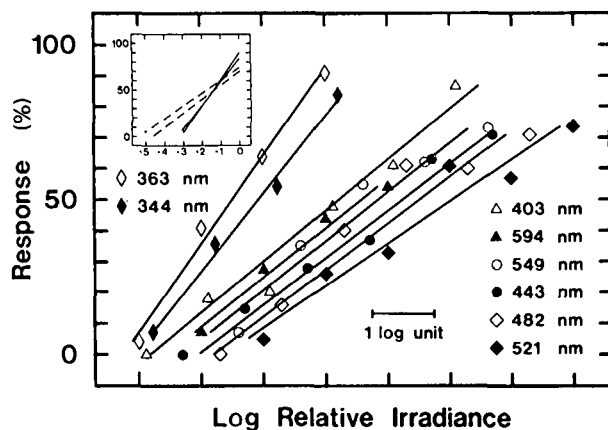


Fig. 4.  $R$ -log  $I$  functions of *Hyalomma* in phototaxis, based on data from Fig. 3 and calculated by linear regression analysis (all correlation coefficients  $r \geq 0.96$ ). For the sake of clarity  $R$ -log  $I$  functions in the main figure are arranged in order of decreasing slopes and taken apart. Each symbol represents the response obtained with 100 ticks. In the inset, UV  $R$ -log  $I$  functions at  $\lambda_{\max}$  344 nm and 363 nm (solid lines) and blue/green  $R$ -log  $I$  functions at  $\lambda_{\max}$  482 nm and 521 nm (dashed lines) are plotted without displacement. Units and data same as in the main figure

visible. In the efficiency measurements no response ( $P > 0.10$ ) was obtained by red light of  $\lambda_{\max}$  704 nm (response = 2%) and 748 nm (response = 0%) at maximal irradiance. At none of the wavelengths tested was a significant difference ( $P > 0.05$ ) in the response between males and females seen.

The spectral sensitivity in the ERG (Fig. 5b) revealed only one peak in the blue range (ca. 470 nm), although a slight sensitivity increase in the UV could be seen.

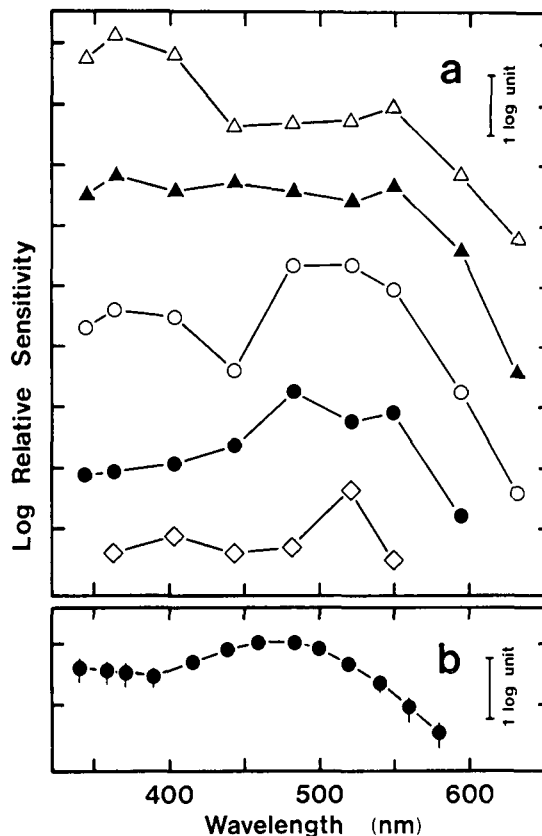


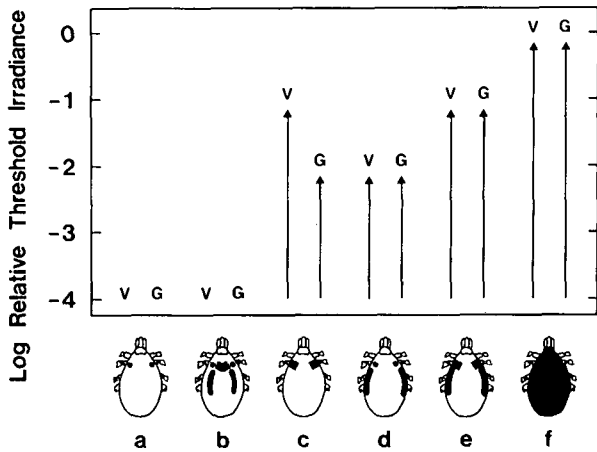
Fig. 5. a Spectral sensitivity functions of *Hyalomma* in phototaxis, based on data from Figs. 3 and 4:  $\Delta$  log rel  $I=0$  (maximal irradiance =  $5.2 \times 10^{10}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ ),  $\blacktriangle$  log rel  $I=-1$ ,  $\circ$  log rel  $I=-2$ ,  $\bullet$  log rel  $I=-3$ ,  $\diamond$  log rel  $I=-4$ . For the sensitivities at  $\lambda_{\max}$  632 nm the  $R$ -log  $I$  function of  $\lambda_{\max}$  594 nm was used. Each symbol represents the response obtained with 100 ticks. b Spectral sensitivity function of the eye of *Hyalomma* in ERG. Irradiance of the monochromatic stimuli was  $3.2 \times 10^{15}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ . Bars:  $\pm$ SD ( $n=4$ , total runs = 15)

#### Absolute threshold in *Hyalomma*

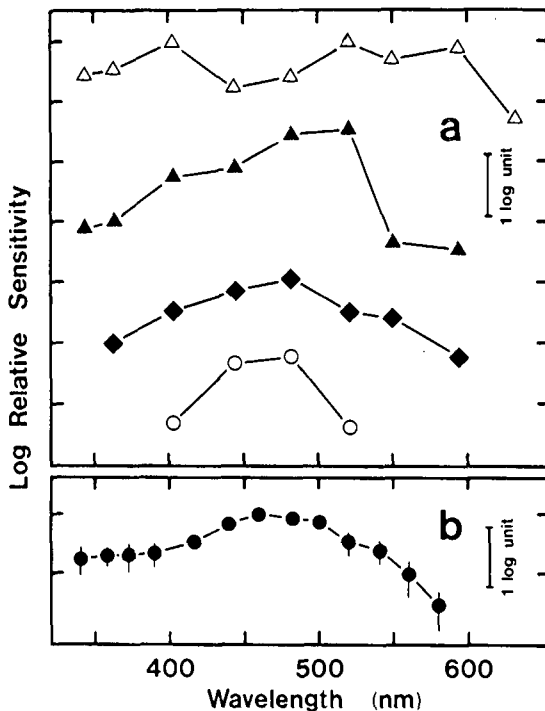
The lowest irradiance that elicited a significant ( $P < 0.05$ ) response in phototaxis (threshold irradiance) was  $5.2 \times 10^6$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  (log rel  $I = -4$ ) for  $\lambda_{\max}$  403–521 nm (Fig. 3).

#### Occlusion of photoreceptors in *Hyalomma*

In order to investigate the relative importance of eyes and extraretinal photoreceptors in phototaxis occlusion experiments were carried out (Fig. 6a–c). The results show that the threshold irradiance of violet ( $\lambda_{\max}$  403 nm) and green light ( $\lambda_{\max}$  521 nm) was higher in ticks with covered eyes (Fig. 6c) and/or with extraretinal photoreceptors painted over (Fig. 6d and e) than in intact or control ticks (Fig. 6a and b). When also the dorsal surface and whole rim of scutum/alloscutum were painted over (Fig. 6f) the threshold irradiance was even higher.



**Fig. 6a-f.** Threshold irradiances of ticks with occluded photoreceptors: **a** Intact ticks. **b** Control ticks with aluminum foil and paint applied medial to the eyes and extraretinal photoreceptors, respectively. **c** Ticks with eyes covered. **d** Ticks with extraretinal photoreceptors painted over. **e** Ticks with both eyes and extraretinal photoreceptors occluded. **f** Ticks with eyes, extraretinal photoreceptors, dorsal surface, and whole rim of scutum/alloscutum occluded. *V* = violet light of  $\lambda_{\max}$  403 nm; *G* = green light of  $\lambda_{\max}$  521 nm. The position of *V* and *G* represents respective threshold irradiance level. Arrows: a shift of the threshold irradiance with respect to intact and control ticks. Each threshold irradiance was determined with 50 ticks



**Fig. 7.** **a** Spectral sensitivity functions of *Amblyomma* in photo-taxis, based on a single averaged *R-log I* function:  $\Delta$  log rel *I* = 0 (maximal irradiance =  $5.2 \times 10^{10}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ ),  $\blacktriangle$  log rel *I* = -1,  $\blacklozenge$  log rel *I* = -1.5,  $\circ$  log rel *I* = -2. Each symbol represents the response obtained with 100 ticks. **b** Spectral sensitivity function of the eye of *Amblyomma* in ERG. Irradiance of the monochromatic stimuli was  $3.2 \times 10^{15}$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$ . Bars:  $\pm$  SD (*n* = 3, total runs = 10)

It is interesting to note that when only the eyes were covered (Fig. 6c) the threshold irradiance of violet light was higher than that of green light, whereas when only the extraretinal photoreceptors were painted over (Fig. 6d) the threshold irradiance of both light qualities was the same. None of the two photoreceptor systems alone (Fig. 6c and d) was as sensitive as both together (Fig. 6a). In all control experiments with aluminum foil and/or paint applied medial to the photoreceptors (as for example in Fig. 6b) the same threshold irradiance as in the experiments with intact ticks was observed.

#### *Spectral sensitivity in Amblyomma*

The spectral sensitivity function at maximal irradiance (log rel *I* = 0) showed no distinct maximum. At lower irradiances there was only one maximum in the blue range (ca. 480 nm) (Fig. 7a). Because the threshold irradiance of *Amblyomma* was 2 log units higher than in *Hyalomma* (see below), useful *R-log I* functions could only be obtained at 403–521 nm. Therefore, the spectral sensitivity is based on a single averaged *R-log I* function. In the efficiency measurements no response ( $P > 0.10$ ) was obtained by red light of  $\lambda_{\max}$  704 nm (response = 1%) and 748 nm (response = 0%) at maximal irradiance. At none of the wavelengths tested was a significant difference ( $P > 0.05$ ) in the response between males and females seen.

The spectral sensitivity in the ERG (Fig. 7b) revealed only one peak in the blue range (ca. 470 nm).

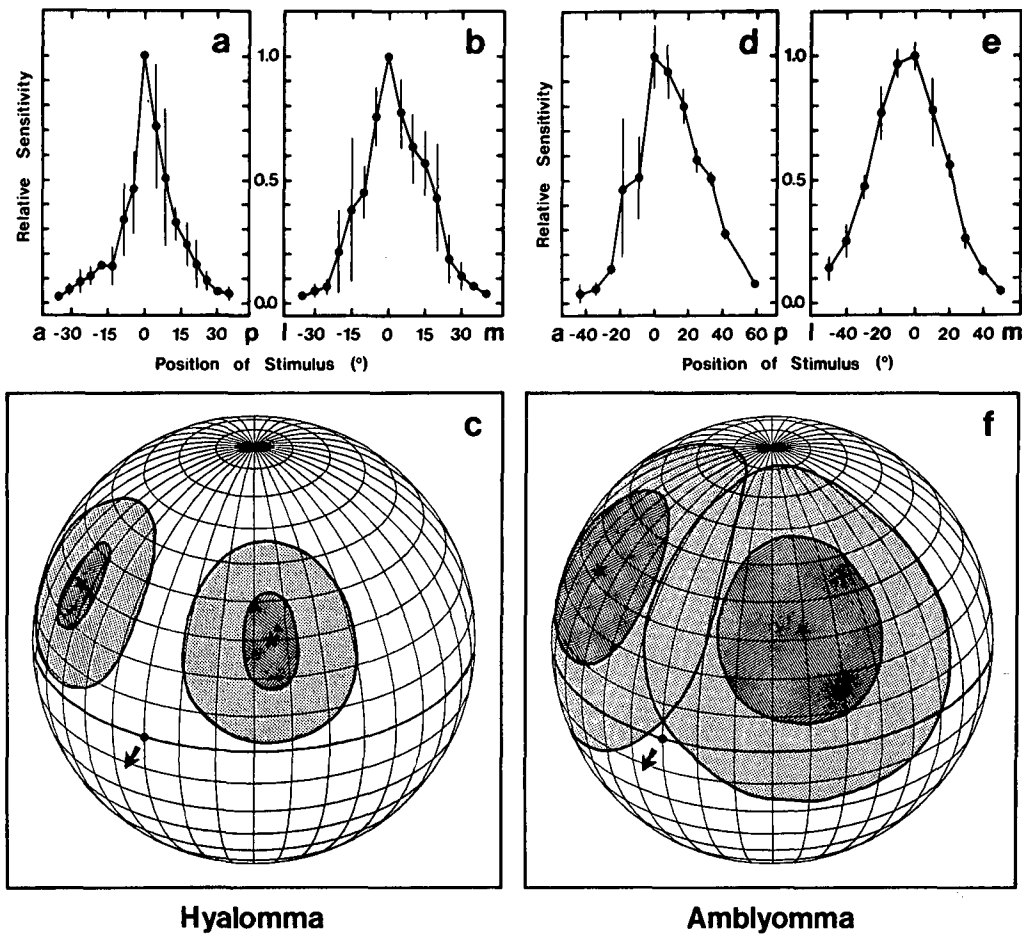
#### *Absolute threshold in Amblyomma*

The threshold irradiance was  $5.2 \times 10^8$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  (log rel *I* = -2) for  $\lambda_{\max}$  443 nm and 482 nm. This was 2 log units higher than in *Hyalomma* (Fig. 3).

When the eyes of *Amblyomma* were covered, no response ( $P > 0.10$ ) was obtained by blue light of  $\lambda_{\max}$  482 nm (response = 0%) at maximal irradiance; therefore, no threshold irradiance for extraretinal photoreceptors could be determined for this species.

#### *Angular sensitivity and visual field in Hyalomma and Amblyomma* (Fig. 8a-f)

In both species the optical axis of each eye, i.e., the center of the visual field, was directed somewhat to the side and above the horizon. In *Hyalomma* (Fig. 8c) this direction was 35° to the long



**Fig. 8.** Angular sensitivity functions and visual fields in *Hyalomma* (a, b, c) and *Amblyomma* (d, e, f) measured with the ERG. a, d Angular sensitivity functions in the horizontal direction; the stimulus was moved from posterior (p) to anterior (a); bars:  $\pm$ SD ( $n=3$ , total runs=9). b, e Angular sensitivity functions in the vertical direction; the stimulus was moved from lateral (l) to medial (m); bars:  $\pm$ SD ( $n=3$ , total runs=9). c, f Reconstruction of visual fields, based on smoothed angular sensitivity measurements. The tick was positioned in a natural posture in the center of the sphere, arrow indicates frontal direction. Equator=horizon; star=center of visual field; dark grey=visual field delimited by field width at 50% sensitivity; light grey=visual field delimited by field width at 10% sensitivity

axis of the animal and  $30^\circ$  above the horizon for natural body posture during walking. In *Amblyomma* (Fig. 8f) the corresponding angles were  $39^\circ$  and  $33^\circ$ , respectively. The size of the field (at 50% sensitivity) in *Hyalomma* was relatively small, namely  $14^\circ$  in the horizontal (Fig. 8a) and  $25^\circ$  in the vertical direction (Fig. 8b), compared with that of *Amblyomma* with  $43^\circ$  (Fig. 8d) and  $49^\circ$  (Fig. 8e), respectively.

## Discussion

Both *Hyalomma* and *Amblyomma* exhibit positive phototaxis towards a horizontal light, as do a number of other tick species, namely *Ixodes persulcatus* (Mironov 1939), *Ixodes ricinus* (Totze 1933), *Haemaphysalis leporispalustris* (George 1963), *Hyalomma marginatum* (Totze 1933), and *Boophilus decoloratus* (Goldsmid 1967). In our contribution phototaxis was used to determine the spectral sensitivity by a behavioral approach over several log units of irradiance. Maximal sensitivities were found around 380 nm and 500 nm for *Hyalomma* (Fig. 5a) and around 480 nm for *Amblyomma* (Fig. 7a). Hitherto, spectral efficiency in arachnids has been established in behavior only in the mite *Tetranychus urticae* (Naegele et al. 1966). Maximal response in phototaxis was found to light of 375 nm and 525 nm, quite similar to *Hyalomma* (Fig. 3).

Spectral sensitivity of the ERG peaks at 470 nm for both *Hyalomma* and *Amblyomma* (Figs. 5b and 7b). In *Hyalomma* there was an increase of the sensitivity in the UV. Carroll and

Pickens (1987) measured the same peak wavelength at 470 nm in *Hyalomma dromedarii*.

A comparison of the spectral sensitivity of phototaxis and ERG revealed a close similarity in *Amblyomma*, i.e., a single spectral sensitivity maximum at 480 nm in behavior (Fig. 7a) and at 470 nm in ERG (Fig. 7b). In *Hyalomma*, on the other hand, phototaxis showed two maxima (380 nm and 500 nm; Fig. 5a) and the ERG one (470 nm; Fig. 5b), but there was a prominent UV side band. There is no convincing explanation for the different peak wavelengths with phototaxis and ERG. The data indicate, however, that *Hyalomma* has at least two types of receptors, an assumption which is supported by the observation of a reverse Purkinje shift (Figs. 4 and 5a).

The reverse Purkinje shift in *Hyalomma* could lead to an optimization of the overall sensitivity, since during daytime the relative amount of UV light is high, whereas during dawn/dusk the blue-green light (475–500 nm) is predominant (McFarland and Munz 1977; Tevini and Häder 1985). Reverse Purkinje shift has also been reported, e.g., in the receptor cells of wolf spider principal eyes (DeVoe 1972) and in the dragonfly ocellar system, i.e., in receptor cells (Chappell and DeVoe 1975), L neurons (Mobbs et al. 1981), and in the head reflex response (Stange 1981).

The extraretinal photoreceptors observed by histological methods along the outer rim of the scutum/alloscutum (Diehl et al., unpublished) seem not to be responsible for the UV/violet sensitivity, because with covered eyes, i.e., with extraretinal photoreceptors only, the threshold irradiance of violet light (log rel  $I = -1$ ) was one log unit higher than the one of green light (log rel  $I = -2$ ) (Fig. 6c). When the extraretinal photoreceptors were painted over, i.e., with eyes only, the threshold irradiance of violet and green light was the same (log rel  $I = -2$ ) (Fig. 6d). Thus, the extraretinal photoreceptors are more sensitive to long than to short wavelengths. In other arthropods maximal spectral response of extraretinal photoreceptors has been observed at 450–480 nm (Frank and Zimmerman 1969; Zwicky 1970; Truman 1976; Lees 1981). On the other hand the eyes of *Hyalomma* are sensitive to both short and long wavelengths. In addition, this suggests that both types of receptors are present in the eye. Intracellular recordings of the different types of receptors which were seen histologically in the eye (Diehl et al., unpublished) would be necessary to obtain information about different spectral receptor types. Nevertheless, this is the first evidence of high UV sensitivity in ticks.

The threshold irradiance of phototaxis in intact

*Hyalomma* was very low, i.e.,  $5.2 \times 10^6$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  or  $2.0 \times 10^{-12}$  W  $\cdot$  cm $^{-2}$  (log rel  $I = -4$ ) (Figs. 3 and 6a). In *Amblyomma* it was  $5.2 \times 10^8$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  or  $2.0 \times 10^{-10}$  W  $\cdot$  cm $^{-2}$  (log rel  $I = -2$ ). In comparison, a value as high as ca.  $10^{-5}$  W  $\cdot$  cm $^{-2}$  is reported in the mite, *Tetranychus urticae* (McEnroe and Dronka 1966), and  $8.3 \times 10^7$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  in the honey bee, *Apis mellifera carnica* (Menzel and Greggers 1985). The threshold irradiance of the oculomotor reflex in the jumping spider, *Maevia inclemens*, is ca.  $10^7$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  (Peaslee and Wilson 1989). The high absolute sensitivity observed in *Amblyomma* and *Hyalomma* would allow orientation by the use of optical cues at dawn/dusk or even during nighttime. The starlit night sky produces an irradiance of ca.  $10^{-10}$  W  $\cdot$  cm $^{-2}$  in the visible range, a night sky with full moon ca.  $10^{-7}$  W  $\cdot$  cm $^{-2}$  and twilight ca.  $10^{-4}$  W  $\cdot$  cm $^{-2}$  (Seliger and McElroy 1965; McFarland and Munz 1977; Kuchling 1986; Brady 1987, some values converted from other physical units). According to Bernadskaya (1938) and Balashov (1968) early morning and late evening activity has been observed in the closely related species *Hyalomma asiaticum* which lives in desert zones in Asia and Russia.

The fact that in *Hyalomma*, when the eyes were covered, i.e., by means of the extraretinal photoreceptors only, a threshold irradiance of  $5.2 \times 10^8$  photons  $\cdot$  s $^{-1}$   $\cdot$  cm $^{-2}$  or  $2 \times 10^{-10}$  W  $\cdot$  cm $^{-2}$  (log rel  $I = -2$ ) (Fig. 6c) was determined, indicates that the extraretinal photoreceptors also have a high absolute sensitivity. In comparison, higher threshold values have been reported for the eyeless tick species, *Argas cooleyi* (ca.  $10^{-7}$  W  $\cdot$  cm $^{-2}$ , Howell 1976), and for extraretinal photoreceptors of several insect species (ca.  $10^{-8}$  W  $\cdot$  cm $^{-2}$ , Truman 1976).

In *Hyalomma* orientation towards a light stimulus of log rel  $I = -1$  was possible even with both eyes and extraretinal photoreceptors occluded (Fig. 6e). This suggests that either the paint did not completely block the light or that an additional extraretinal photoreceptor may exist. When the dorsal surface was completely occluded, the threshold irradiance was pushed another log unit up, namely to log rel  $I = 0$  (Fig. 6f), which suggests that scattered light entering through the cuticle may also play a role in the tested phototaxis. Camin (1953) discovered photoreceptor cells on the pretarsi of the anterior legs in the snake mite *Ophionyssus natricis*, but behavioral experiments with *Hyalomma* which had their anterior pretarsi painted over yielded no evidence for a photoreceptor placed there (Kaltenrieder, unpublished). It is interesting that *Hyalomma* did not respond to irra-

diances lower than  $\log \text{rel } I = -2$  with extraretinal photoreceptors painted over, i.e., by means of their eyes only (Fig. 6d). This may suggest that both sensory inputs have to act in concert in order to maximize high sensitivity.

Using electrophysiological methods for angular sensitivity measurements we determined the optical axis in *Hyalomma* to be  $35^\circ$  in the horizontal and  $30^\circ$  in the vertical direction (Fig. 8c). In comparison, Leonovich (1986), using optical methods, determined in *Hyalomma asiaticum* values of  $15^\circ$  and  $16^\circ$ , respectively (original data in Leonovich's paper were adjusted by taking into account the body posture of *H. asiaticum* as given by this author). We do not know whether the optical axes of *H. dromedarii* and *H. asiaticum* are indeed that different or whether the difference observed is partly due to the different methods used.

The field width of *Hyalomma* was found to be rather small, namely  $14^\circ$ – $25^\circ$  (Fig. 8a, b). This is somewhat similar to that observed by the use of optical methods in principal eyes of jumping spiders, which have field widths of  $5^\circ$ – $20^\circ$  (Land 1969, 1981; Forster 1985). Field width of *Amblyomma* was seen to be much larger, namely  $43^\circ$ – $49^\circ$  (Fig. 8d, e), a value which is similar to that seen in secondary eyes of spiders, which have field widths from  $50^\circ$ – $120^\circ$  (Forster 1985; Land 1985) and in insect ocelli which have field widths of approx.  $50^\circ$  (ranging from  $27^\circ$ – $120^\circ$ ) in the horizontal and approx.  $40^\circ$  (ranging from  $23^\circ$ – $90^\circ$ ) in the vertical direction (e.g., Wilson 1978; Geiser 1985). In contrast to the eyes of *Amblyomma* and particularly *Hyalomma*, whose visual fields are larger in the vertical than in the horizontal dimension (Fig. 8c, f), insect ocelli of most species investigated so far have visual fields that are larger in the horizontal than in the vertical dimension (Geiser 1985).

The smaller size of the visual field in *Hyalomma* (Fig. 8c) compared with *Amblyomma* (Fig. 8f) together with the fact that the number of photoreceptor cells in the eye is higher in *Hyalomma* than in *Amblyomma* (Diehl et al., unpublished) suggests a higher spatial acuity for *Hyalomma* than for *Amblyomma*. This suggestion is supported by the observation that *Hyalomma* has higher form perception capabilities than *Amblyomma* (Kaltenrieder, unpublished). All these data may be interpreted as an indication that *Hyalomma*, but not *Amblyomma*, could use its visual system in host-seeking behavior.

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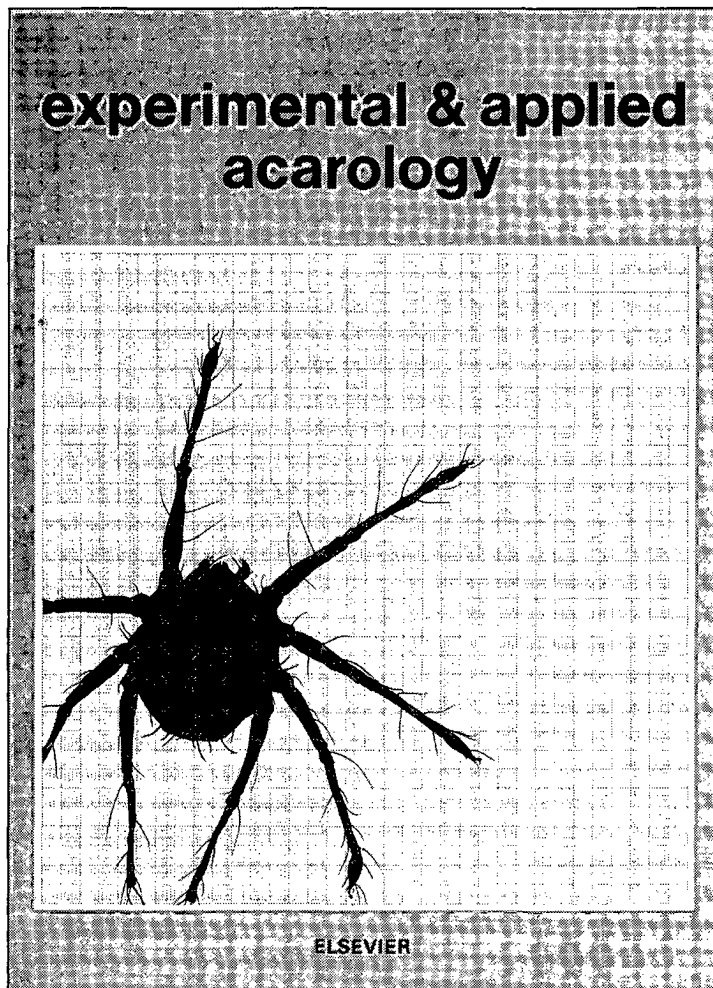
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## References

- Balashov YS (1968) Bloodsucking ticks (Ixodoidea) – vectors of diseases of man and animals [in Russian]. Akad Nauk SSSR Zool Inst, Leningrad, English translation 500 (T500) by Strekalovsky OG (1972), Departement of Medical Zoology, United States Naval Medical Research Unit No. 3, Cairo (Egypt); Misc Publ Entomol Soc Am 8:161–376
- Batschelet E (1981) Circular statistics in biology. Academic Press, London New York Toronto
- Belozerov VN (1982) Diapause and biological rhythms in ticks. In: Obenchain FD, Galun R (eds) Physiology of ticks. Pergamon Press, Oxford New York Toronto, pp 469–500
- Bernadskaya ZM (1938) Study of *Hyalomma* tick biology in sandy desert conditions [in Russian, English summary]. Tr Uzb Nauchho-Issled Vet Opyt Stn Narkom UzSSR 10:18–35
- Binnington KC (1972) The distribution and morphology of probable photoreceptors in eight species of ticks (Ixodoidea). Z Parasitenkd 40:321–332
- Brady J (1987) The sunset activity of tsetse flies: a light threshold study on *Glossina morsitans*. Physiol Entomol 12:363–372
- Camin J (1953) Observations on the life history and sensory behavior of the snake mite, *Ophionyssus natricis* (Gervais) (Acarina: Macronyssidae). Acad Sci Spec Publ 10, Chicago
- Carroll JF, Pickens LG (1987) Spectral sensitivity to light of two species of ticks (Acarina: Ixodidae). Ann Entomol Soc Am 80:256–262
- Chappell RL, DeVoe RD (1975) Action spectra and chromatic mechanisms of cells in the median ocelli of dragonflies. J Gen Physiol 65:399–419
- DeVoe RD (1972) Dual sensitivities of cells in wolf spider eyes at ultraviolet and visible wavelengths of light. J Gen Physiol 59:247–269
- El-Ziady S (1958) The behavior of *Ornithodoros erraticus* (Lucas 1849), small form (Ixodoidea, Argasidae), towards certain environmental factors. Ann Entomol Soc Am 51:317–336
- FAO (1984) Ticks and tick-borne disease control. A practical field manual, vol 1, Tick Control. Food and Agriculture Organization of the United Nations, Rome
- Forster L (1985) Target discrimination in jumping spiders (Araneae: Salticidae). In: Barth FG (ed) Neurobiology of arachnids. Springer, Berlin Heidelberg New York, pp 203–229
- Frank KD, Zimmerman WF (1969) Action spectra for phase shifts of a circadian rhythm in *Drosophila*. Science 163:688–689
- Geiser FX (1985) Elektrophysiologische Charakterisierung der Ocellen von *Apis mellifera* und *Cataglyphis bicolor*. PhD thesis, University of Zürich (Switzerland)
- George JE (1963) Responses of *Hemaphysalis leporispalustris* to light. In: Naegele JA (ed) Advances in acarology, vol 1. Comstock Publ Assoc, Ithaca New York, pp 425–430
- Goldsmid JM (1967) Observations on the behaviour of the blue tick, *Boophilus decoloratus* (Koch) (Acarina: Ixodidae). J Entomol Soc South Afr 29:74–89

- Hindle E, Merriman G (1912) The sensory perception of *Argas persicus* (Oken). *Parasitology Cambridge* 5:203–216
- Hoogstraal H (1956) African Ixodoidea. I. Ticks of the Sudan (with special reference to Equatoria Province and with preliminary reviews of the genera *Boophilus*, *Margaropus*, and *Hyalomma*). Dep Navy Bur Med Surg, Washington DC
- Howell FG (1976) Influence of the daily light cycle on the behavior of *Argas cooleyi* (Acarina: Argasidae). *J Med Entomol Honolulu* 13:99–106
- Kaltenrieder M, Labhart T, Hess E (1988) Spectral sensitivity and visual field of two tick species (*Hyalomma dromedarii* and *Amblyomma variegatum*). (abstract) In: Elsner N, Barth FG (eds) *Sense organs*; Proc 16th Göttingen Neurobiol Conf. Thieme, Stuttgart New York, No. 230
- Koch B, Kraiss-Gothc A, Gothe R (1988) Zur Reaktivität von *Argas (Persicargas) walkerae* auf Lichtreize (abstract) In: 13. Tagung der Deutschen Gesellschaft für Parasitologie e.V.; 22.–25.3.1988 Neuchâtel (Switzerland), No. 7
- Kuchling H (1986) *Taschenbuch der Physik*. Harri Deutsch, Thun Frankfurt
- Labhart T (1980) Specialized photoreceptors at the dorsal rim of the honeybee's compound eye: Polarizational and angular sensitivity. *J Comp Physiol* 141:19–30
- Land MF (1969) Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J Exp Biol* 51:471–493
- Land MF (1981) Optics and vision in invertebrates. In: Autrum H (ed) *Vision in invertebrates* (Handbook of sensory physiology, vol VII/6B). Springer, Berlin Heidelberg New York, pp 471–592
- Land MF (1985) The morphology and optics of spider eyes. In: Barth FG (ed) *Neurobiology of arachnids*. Springer, Berlin Heidelberg New York, pp 53–78
- Lees AD (1981) Action spectra for the photoperiodic control of polymorphism in the aphid *Megoura viciae*. *J Insect Physiol* 27:761–771
- Leonovich SA (1986) The orientational behaviour of the tick *Hyalomma asiaticum* in a desert [in Russian, English summary]. *Parasitologiya* 20:431–439
- McEnroe WD, Dronka K (1966) Color vision in the adult female two-spotted spider mite. *Science* 154:782–784
- McEnroe WD, McEnroe MA (1973) Questing behavior in the adult American dog tick *Dermacentor variabilis* Say. (Acarina: Ixodidae). *Acarologia* 15:37–42
- McFarland WN, Munz FW (1977) The visible spectrum during twilight and its implications to vision. In: Evans GC, Bainbridge R, Rackham O (eds) *Light as an ecological factor*, vol II. Blackwell Sci Publ, Oxford London Edinburgh Melbourne, pp 249–270
- Menzel R, Greggers U (1985) Natural phototaxis and its relationship to colour vision in honeybees. *J Comp Physiol A* 157:311–321
- Mironov VS (1939) On the behaviour of the Siberian forest tick *Ixodes persulcatus* Schulze [in Russian, English summary]. *Med Parazitol Parazit Bolezni* 8:123–136
- Mobbs PG, Guy RG, Goodman LJ, Chappell RL (1981) Relative spectral sensitivity and reverse Purkinje shift in identified L neurons of the ocellar retina. *J Comp Physiol* 144:91–97
- Morel PC (1969) Contribution à la connaissance de la distribution des tiques (Acariens, Ixodidae et Amblyommidae) en Afrique éthiopienne continentale. PhD thesis, University of Paris (France)
- Naegele JA, McEnroe WD, Soans AB (1966) Spectral sensitivity and orientation response of the two-spotted spider mite, *Tetranychus urticae* Koch, from 350 m $\mu$  to 700 m $\mu$ . *J Insect Physiol* 12:1187–1195
- Panfilova IM (1976) Reaction of ixodid ticks *Ixodes persulcatus*, *Dermacentor silvarum* and *Haemaphysalis concinna* to light [in Russian, English summary]. *Zool Zh* 55:371–377
- Peaslee AG, Wilson G (1989) Spectral sensitivity in jumping spiders (Araneae, Salticidae). *J Comp Physiol A* 164:359–363
- Sachs L (1984) *Angewandte Statistik*. Springer, Berlin Heidelberg New York
- Seliger HH, McElroy WD (1965) *Light: physical and biological action*. Academic Press, New York London
- Shoukrey NM, Sweatman GK (1984) The peripheral nervous system of the tick *Argas arboreus*. *Can J Zool* 62:893–926
- Stange G (1981) The ocellar component of flight equilibrium control in dragonflies. *J Comp Physiol* 141:335–347
- Tevini M, Häder DP (1985) *Allgemeine Photobiologie*. Thieme, Stuttgart New York
- Totze R (1933) Beiträge zur Sinnesphysiologie der Zecken. *Z Vergl Physiol* 19:110–161
- Truman JW (1976) Extraretinal photoreception in insects. *Photochem Photobiol* 23:215–225
- Wilson M (1978) The functional organisation of locust ocelli. *J Comp Physiol* 124:297–316
- Zwicky KT (1970) Behavioural aspects of the extraocular light sense of *Urodacus*, a scorpion. *Experientia* 26:747–748

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## Scototaxis and target perception in the camel tick *Hyalomma dromedarii*

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### ABSTRACT

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The camel tick, *Hyalomma dromedarii*, exhibited positive scototaxis in an arena, e.g. it oriented towards a black or grey target in front of a white background. The degree of the scototactic response varied with the size and the elevation of the target, with its luminance contrast, with its shape and with the speed by which the target was moved: (1) the response to stationary and moving targets increased with increasing target size; (2) presentation of the targets at an elevation of 11°–15° induced the highest response; (3) the response decreased with decreasing luminance contrast of the target; (4) targets with the shape of a disk, a triangle standing on a vertex, a vertical bar or a silhouette of a dromedary caused high responses; a low response was observed when the target was a horizontal bar and there was no response to a striped pattern; (5) the smaller the size of a disk, the faster it had to be moved to elicit an optimum response.

The smallest disk which elicited a significant response appeared under a visual angle of 4.8° for a tick at the starting point. The smallest dromedary-shaped silhouette which elicited a significant response corresponded to the silhouette of a real dromedary at a distance of 18 m.

### INTRODUCTION

The camel ticks, *Hyalomma dromedarii* and *Hyalomma asiaticum* (Acari, Ixodidae), have single-lens eyes that protrude considerably above the body surface. These ticks have been reported to be guided mainly by visual cues towards their hosts (Mann, 1915; Pomerantzev, 1950; Zolotarev and Sinit-syna, 1965; Balashov, 1968). In a field study, Leonovich (1986) showed that *Hyalomma asiaticum* is able to orient optically towards a human from a distance of 2 m. Some fundamental characteristics of the visual system of camel ticks have recently been investigated, namely the spectral and absolute sensitivity in phototaxis (Kaltenrieder et al., 1989), the spectral sensitivity in the electroretinogram (Carroll and Pickens, 1987; Kaltenrieder et al., 1989) and the visual field (Leonovich, 1986; Kaltenrieder et al., 1989). Nothing is known

about the characteristics of visual cues which could be involved in host-seeking behaviour of these ticks.

In this paper aspects of target perception in *Hyalomma dromedarii* were studied. This was done by analysing orientation towards dark objects (scototaxis) in an arena and by investigating the effect of various features of these targets (size, elevation, shape and luminance contrast) on scototaxis. In addition, the effect of moving targets was studied.

## METHODS

### *Animals*

The camel tick, *Hyalomma dromedarii* Koch 1844, is widely distributed in eastern and northern Africa, in the Middle and Near Orient and on the Arabian peninsula, wherever dromedaries occur. Adults mainly feed on dromedaries, but also on cattle, horse, sheep and goats. Immatures can be found on dromedaries, small, burrowing mammals and lizards (Hoogstraal, 1956; Morel, 1969). *Hyalomma dromedarii* originating from Egypt (U.S. Naval Medical Research Unit No 3; Cairo) were generously supplied by Ciba-Geigy Ltd., Animal Health (CRA, St. Aubin, Switzerland), where they were reared on tails of Simmental-Redholstein calves. Unfed adults, 7–12 months after nymphal drop-off, were used.

### *Preparation*

Ticks (males and females separately) were put into glass tubes (40 mm,  $\varnothing$  19 mm; 5 ticks per tube) with perforated plastic plugs at  $27 \pm 1^\circ\text{C}$  and  $85 \pm 5\%$  rh and kept under nonrhythmic light conditions (Tungsten lamp, 80 lux; light and dark periods randomly lasting 40–100 min) for 1 to 4 weeks before an experiment. Under these conditions the ticks were most responsive (Kaltenrieder, 1989).

*Arena, experimental setup and recording.* (Figs. 1a,b). Experiments were conducted at  $27 \pm 1^\circ\text{C}$  and  $55 \pm 5\%$  RH. The white arena ( $\varnothing$  204 cm) was provided with markings, surrounded and covered with white cotton cloth. The targets were presented at a distance of 100 cm from the center of the arena and at different elevations above the arena surface. To ensure uniform light distribution within the arena, a ring-shaped fluorescent lamp (32 W, Universal White, type L32W/25C; Osram) was fixed 27 cm above the center of the arena. The azimuthal light distribution around the center was ca.  $90\text{ cd/m}^2$ . A round, white shield ( $\varnothing$  50 cm) beneath the lamp gave a homogenous canopy (ca.  $60\text{ cd/m}^2$ ) for a tick in the center of the arena. Luminance measurements were carried out with a Lunasix 3 (Gossen). The walking paths of the ticks were recorded from above by a videocamera equipped with a wide-angle

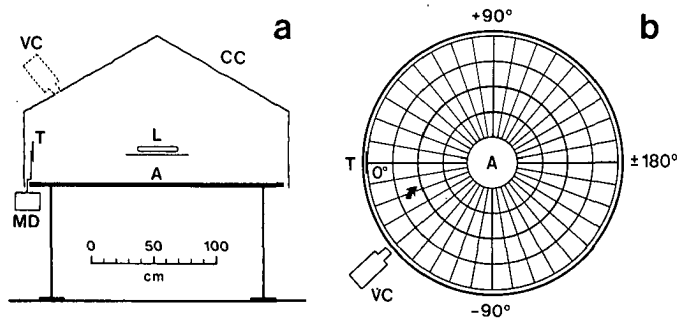


Fig. 1. Setup for measurement of scototaxis, side-view (a) and top-view (b): (A) arena, (VC) videocamera, (CC) cotton cloth, (L) lamp with shield beneath (CC and L not shown in b), (T) target, (MD) movement device. Arrow points to the 60-cm circle.

lens which allowed the surface within the 60-cm circle to be viewed. Videosignals were stored with a recorder and displayed on a black and white monitor.

### *Targets*

Two-dimensional shapes of black (if not stated otherwise) cardboard were mounted on a vertical white bar. The shapes included a disk, a square, a bar (side ratio = 1:4), an equilateral triangle, a black and white pattern made of nine equidistant stripes (arranged in a square), and the silhouette of a dromedary. The surface area of the targets varied from 31 cm<sup>2</sup> to 491 cm<sup>2</sup>. Intermediate sizes were obtained by doubling the surface of the former target. The elevations of the center (of gravity) of the targets, measured from the center of the arena, varied from 2.8 to 23.9°. Luminance contrast ratio of the white background versus the black cardboard was 16:1, and versus the grey cardboards was 6:1, 3:1 or 1.5:1.

The movement of a target, produced by a remote-controlled device, consisted of a horizontal sinusoidal oscillation of 0.25 Hz, 0.50 Hz or 0.75 Hz around the 0°-direction over a distance of 18 cm tangential to the 100-cm circle. This resulted in an average speed of 9 cm s<sup>-1</sup>, 18 cm s<sup>-1</sup> or 27 cm s<sup>-1</sup>.

### *Testing procedures*

Ticks were adapted to dim white light (Tungsten lamp, ca. 2 lux) for at least 15 min. To activate the ticks they were then exposed to a temperature of 31 ± 1°C for 3 min, gently shaken several times in their glass tube, and after removal of the plug the experimenter blew on them for 3 s. The ticks were then poured out of the tube into the center of the arena and the experimenter retreated behind a curtain 2 m from the arena. The ticks were exposed to a target for 150 s. Ten sets of five ticks were tested in order to obtain a response value. After a series of 50 ticks the arena surface was cleaned with ethanol 70%.

### *Evaluation of data*

The angular values where the ticks crossed the 60-cm circle for the first time were registered. The circle was graduated from  $0^\circ$  to  $\pm 180^\circ$ , the  $0^\circ$ -direction pointing to the center of the target (Fig. 1b). The formula that was chosen to describe the scototactic response was the same as that used in phototaxis (Kaltenrieder et al., 1989). The response ( $R$ ) was defined as:

$$R = \sqrt{n/N} \cdot r \cdot \cos \bar{\Phi} \cdot 100\%$$

where  $n$  is the number of ticks crossing the 60-cm circle,  $N$  the total number of ticks introduced in the arena,  $r$  the mean vector length (measure of concentration) and  $\bar{\Phi}$  the mean angle (measure of direction) of the sample (see Batschelet, 1981). Negative response values (obtained if  $|\bar{\Phi}| > 90^\circ$ ) were defined as 0%. The walking paths of the ticks were similar to those observed in phototaxis (Kaltenrieder et al., 1989). With decreasing attractivity, e.g. with decreasing size of the target (1) the number  $n$  decreased; (2) the mean vector length  $r$  also decreased; and (3) the mean angle  $\bar{\Phi}$  became more and more different from zero. All this together led to a decrease of the response  $R$ .

The walking speed of ticks displaying scototaxis was measured over a distance of 20 cm, namely between the 40-cm circle and the 60-cm circle.

### *Statistics*

In order to evaluate whether a sample of ticks was oriented in the direction of the target, the  $V$  test (Batschelet, 1981) was used. For comparing the response of 2 samples, the exact method of Fisher (Sachs, 1984) was used and was based on the number of ticks crossing the 60-cm circle within  $+15^\circ$  and  $-15^\circ$ . Other tests are referred to in the Results section.

## RESULTS

### *Response to stationary disks of different size presented at different elevation angles (Fig. 2)*

*Hyalomma* exhibited positive scototaxis, e.g. it oriented towards a black disk in front of a white background. The response varied with the size of the disk and with its elevation above the arena surface. The larger the size of a disk, the higher was the response and the optimum elevation of a disk was ca.  $13^\circ$ , varying between  $11^\circ$  and  $15^\circ$ .

The smallest disk that elicited a significant response ( $P \leq 0.05$ ) was the  $\varnothing 8.8$ -cm disk at  $12.4^\circ$  ( $R = 17\%$ ).

### *Response to stationary disks with different luminance contrasts (Fig. 3)*

Disks (size  $\varnothing 12.5$  cm, elevation  $13^\circ$ ) made of dark, medium and light-grey cardboard were tested in addition to the black one. Luminance contrast ratios of the white background versus the disk were from 16:1 (black) to

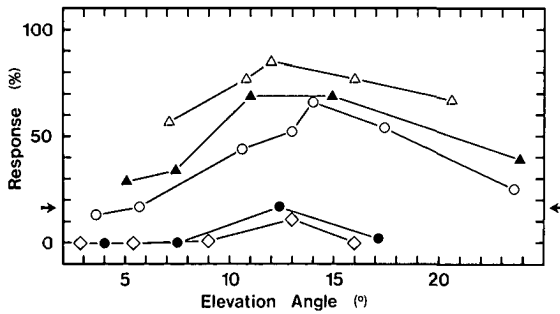


Fig. 2. Response to stationary disks of different size presented at different elevation angles:  $\Delta$   $\varnothing$ 25.0-cm disk,  $\blacktriangle$   $\varnothing$ 17.7-cm disk,  $\circ$   $\varnothing$ 12.5-cm disk,  $\bullet$   $\varnothing$ 8.8-cm disk,  $\diamond$   $\varnothing$ 6.3-cm disk. Elevation angle (of center of disk) as measured from the center of the arena. Each symbol represents the response obtained with 50 ticks. Arrows indicate lowest response with significant orientation ( $P=0.05$ ).

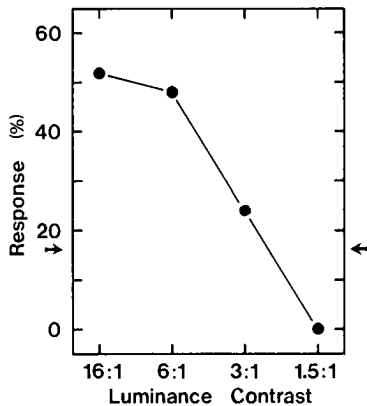


Fig. 3. Response to stationary disks with different luminance contrasts. Disks ( $\varnothing$ 12.5 cm) were presented at an elevation of  $13^\circ$ . Luminance contrast ratio=luminance of the white background vs. luminance of the disk. Each symbol represents the response obtained with 50 ticks. Arrows indicate lowest response with significant orientation ( $P=0.05$ ).

1.5:1 (light grey). The response dropped with decreasing contrast between disk and white background.

#### *Response to stationary targets with different shapes (Fig. 4)*

All targets had a surface area of  $123 \text{ cm}^2$  ( $\sim$  surface area of  $\varnothing$ 12.5-cm disk) and were presented at an elevation of  $13^\circ$ . High responses were observed to the disk ( $R=52\%$ ), to the triangle standing on a vertex ( $R=51\%$ ) and to the vertical bar ( $R=48\%$ ). The other compact targets induced medium responses ( $R=25\%$ – $43\%$ ). A low response was observed to the horizontal bar ( $R=19\%$ ) and no significant response ( $P>0.10$ ) to the black-and-white

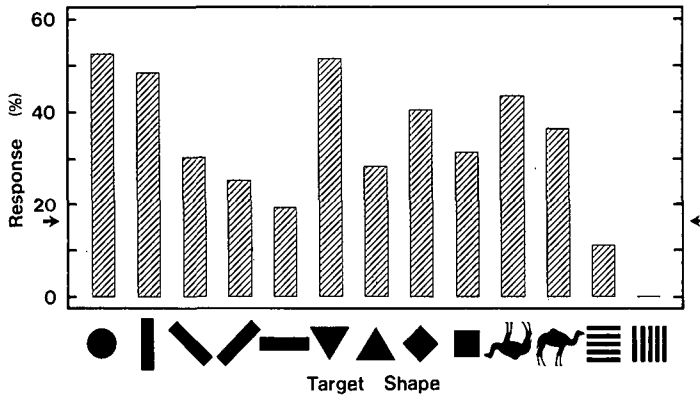


Fig. 4. Response to stationary targets with different shapes. All targets had a surface area of 123 cm<sup>2</sup> (~ surface area of Ø12.5-cm disk) and were presented at an elevation of 13°. Each symbol represents the response obtained with 50 ticks. Arrows indicate lowest response with significant orientation ( $P=0.05$ ).

striped pattern. However, the differences in the response were statistically significant ( $P \leq 0.05$ ) only between the horizontal bar and the three targets which induced high responses.

#### *Control experiments with stationary targets*

Two control experiments with 50 ticks each were made: (1) no target was presented in the arena, the distribution of *Hyalomma* on the 60-cm circle was random ( $P > 0.10$ ; Raleigh test and Rao's spacing test: Batschelet, 1981); (2) only the white bar which served as a holder for the targets was presented in the 0°-direction. The ticks were not oriented in the direction of the bar nor in any other direction ( $P > 0.10$ ).

#### *Response to disks moving at different speeds (Fig. 5).*

Moving disks of various sizes were presented at an elevation of 13°. The response of *Hyalomma* varied with the size of the disk and with its speed. As for stationary disks, the larger the size of a disk, the higher was the response. The response to the Ø25.0-cm disk was significantly higher ( $P \leq 0.05$ ) when it was moving at 9 cm s<sup>-1</sup> than at 27 cm s<sup>-1</sup> and the response to the Ø12.5-cm disk was higher ( $P \leq 0.05$ ) when it was moving at 18 cm s<sup>-1</sup> than at 27 cm s<sup>-1</sup>. All other comparisons yielded nonsignificant differences ( $P > 0.05$ ). The plot of the optimum speed as a function of disk size (Fig. 5; inset) revealed that the smaller the size of a disk, the higher was its optimum speed.

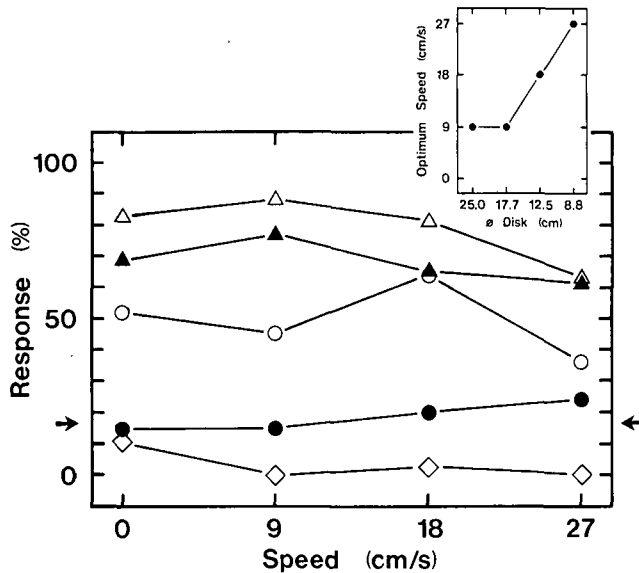


Fig. 5. Response to disks of different size moving at different speeds:  $\Delta$   $\varnothing$ 25.0-cm disk,  $\blacktriangle$   $\varnothing$ 17.7-cm disk,  $\circ$   $\varnothing$ 12.5-cm disk,  $\bullet$   $\varnothing$ 8.8-cm disk;  $\diamond$   $\varnothing$ 6.3-cm disk. Disks were presented at an elevation of  $13^\circ$ . For three disks ( $\varnothing$ 25.0-cm,  $\varnothing$ 17.7-cm and  $\varnothing$ 8.8-cm) the values at speed  $0 \text{ cm s}^{-1}$  were taken from Fig. 2. Each symbol represents the response obtained with 50 ticks. Arrows indicate lowest response with significant orientation ( $P=0.05$ ). Inset: Optimum speed as a function of disk size, based on data from the main figure.

*Comparison of the response to stationary and moving disks with the response to stationary and moving silhouettes of dromedaries presented at the horizon (Fig. 6)*

There was a significant response ( $P \leq 0.05$ ) to the moving disk with the surface area of  $61 \text{ cm}^2$ , but no significant response to the stationary disk of this size ( $P > 0.10$ ). Similarly, for larger disks ( $123 \text{ cm}^2$  and  $245 \text{ cm}^2$ ) there was a tendency towards a higher response when the disks were moved. This contrasts with the observations made with silhouettes where two sizes ( $61 \text{ cm}^2$  and  $123 \text{ cm}^2$ ) induced no significant response when moved ( $P > 0.10$ ), but a significant response when stationary ( $P \leq 0.05$ ). Similarly, for the two larger silhouettes ( $245 \text{ cm}^2$  and  $491 \text{ cm}^2$ ) there was a tendency towards a lower response when they were moved. With each target surface, the moving disk and the stationary silhouette induced a very similar response.

*Control experiments with moving targets*

Three control experiments with 50 ticks each were made: (1) no target was presented in the arena, but the apparatus which performed the oscillation movement and hence produced a metallic sound was switched on, the distribution of *Hyalomma* on the 60-cm circle was random ( $P > 0.10$ ; Raleigh test and Rao's spacing test: Batschelet, 1981); (2) only the white bar which served as a holder for the targets was presented and oscillated around the  $0^\circ$ -direction with an average speed of  $18 \text{ cm s}^{-1}$ , the ticks were not oriented in the  $0^\circ$ -

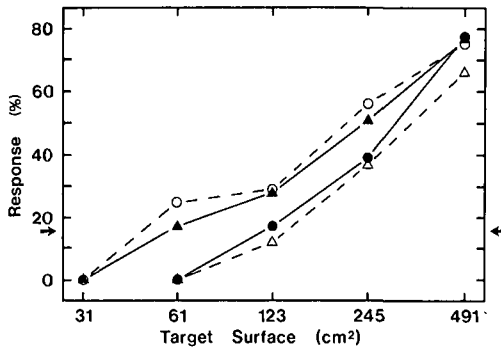


Fig. 6. Response to stationary and moving disks and silhouettes of dromedaries: ● stationary disk, ○ moving disk, ▲ stationary silhouette, △ moving silhouette; solid lines = stationary targets, dashed lines = moving targets. The silhouettes were presented at the horizon and the corresponding disks (same surface area) slightly above it in order to present the centers of the targets at the same elevation. Both target types were moved with the optimum speed for disks according to Fig. 5 (inset). Each symbol represents the response obtained with 50 ticks. Arrows indicate lowest response with significant orientation ( $P=0.05$ ).

direction nor in any other direction ( $P>0.10$ ); (3) a disk (size  $\varnothing 12.5$  cm  $\sim 123$  cm<sup>2</sup>, at an elevation of  $13^\circ$ ) or a silhouette of a dromedary (surface area 123 cm<sup>2</sup>, at the horizon) were presented separately, while the oscillation apparatus was switched on, but disconnected from the holder with the target. The responses ( $R=46\%$  and  $26\%$ , respectively) were not different ( $P>0.50$ ) from the responses obtained without running apparatus ( $R=52\%$  and  $28\%$  respectively).

#### *Walking speed*

The walking speed of *Hyalomma* which displayed scototaxis was determined to be  $4.6 \pm 0.7$  cm s<sup>-1</sup> ( $n=70$ ).

#### DISCUSSION

*Hyalomma* exhibited positive scototaxis towards various two-dimensional targets. The response to stationary and moving targets increased with increasing target size (Figs. 2 and 5). This has also been observed in a number of insect species (e.g. Jander and Voss, 1963; Voss, 1967; Hodgson and Elbakhiet, 1985; Allan and Stoffolano Jr., 1986; Atkins et al., 1987). Similar observations have also been made in studies on prey-catching behaviour of jumping spiders, where the response increased up to a certain target size (Drees, 1952; Forster, 1985).

The targets induced the highest response at an elevation of  $11$ – $15^\circ$  (Fig. 2). This contrasts somewhat with the observation that the center of the visual

field of an eye was at an elevation of  $30^\circ$  (Kaltenrieder et al., 1989). This discrepancy may be explained in three ways: (1) from the position in the center of the arena where a tick started to orient towards a disk, the center of a disk appeared at an elevation of  $13^\circ$ , this angle gradually shifted to  $30^\circ$  when the tick crossed the 60-cm circle; (2) a walking tick shows considerable yaw and pitch movements of the body (Kaltenrieder, 1989): the pitch of the body is  $\pm 10^\circ$ , therefore the center of the visual field will occasionally reach  $20^\circ$ , the vertical field width (50% sensitivity) is  $25^\circ$ , i.e. its lower rim is at  $17.5^\circ$  (Kaltenrieder et al., 1989), with the additional pitch down at  $7.5^\circ$ ; (3) it could well be that the lower part of the visual field is more effective in inducing scototaxis.

The smallest disk which elicited a significant response was the  $\varnothing 8.8$ -cm disk, not only when it was moving at  $18 \text{ cm s}^{-1}$  and  $27 \text{ cm s}^{-1}$  at an elevation of  $13^\circ$  (Fig. 5), but also when it was stationary at  $12.4^\circ$  (Fig. 2). For a tick at the starting point this target appears under a visual angle of  $4.8^\circ$ . A comparison with jumping spiders shows that for the latter a (moving) target must appear under a minimal visual angle of  $1\text{--}4^\circ$  to elicit prey-catching behaviour (Homann, 1928; Heil, 1936; Drees, 1952; Land, 1972; Duelli, 1978, Forster, 1985). This angle is somewhat smaller than the minimal visual angle determined in *Hyalomma* but, in an eye of a spider, 1000 or more photoreceptors are present (Land, 1972) compared with the 53–62 in *Hyalomma* (according to A. Diehl personal communication) or 20–25 (according to El Shoura, 1988). Therefore the visual acuity in *Hyalomma* is reasonably high. In tsetse flies an object must appear under a minimal angle of  $1\text{--}2^\circ$  to be attractive (Chapman, 1961).

The higher the luminance contrast of a target, the higher was the scototactic response (Fig. 3). This has also been observed in the ant *Formica rufa* (Jander and Voss, 1963) and in tsetse flies (Turner and Invest, 1973). In *Hyalomma* a disk with a luminance contrast of 3:1 was necessary to elicit scototaxis, which indicates rather low luminance-discrimination capabilities. This corresponds with the observation that in phototaxis the sensitivity range was seen to be large, encompassing 5 log units of irradiance (Kaltenrieder et al., 1989).

The comparison of various stationary target shapes (presented at an elevation of  $13^\circ$ ) revealed a high scototactic response for the disk, the vertical bar and the triangle standing on a vertex. When the disk and the silhouette of a dromedary were presented stationary at the horizon, there was a clear tendency that the silhouette elicited a higher response than the disk (Fig. 6). This suggests that the naturally matching target, if appropriately placed in space, would be best stimulus for scototaxis. Whether this implies form-discrimination capabilities in *Hyalomma* cannot be stated without further experiments. In view of the relatively small number of photoreceptor cells this seems unlikely. The vertical bar elicited a higher response than the horizontal one (Fig. 4), possibly because the visual field of an eye has the shape of an upright oval (Kaltenrieder et al., 1989). A higher response to a vertical bar

than to a horizontal one has also been observed e.g. in the ant *Formica rufa* (Jander and Voss, 1963), in the locust *Schistocerca gregaria* (Wallace, 1958) and in tsetse flies (Brady and Shereni, 1988), but not in the cricket *Acheta domesticus* (Kieruzel and Chmirzynski, 1982; Atkins et al., 1987) nor in the stable fly *Stomoxys calcitrans* (Brady and Shereni, 1988), where the opposite is the case. It is unlikely that the higher number of stimulus changes (Reizwechsel; see Jander and Voss, 1963) in the horizontal direction is responsible for the higher response to the vertical bar, because in *Hyalomma* the frequencies of the yaw and pitch oscillations are similar (ca. 4 Hz; Kaltenrieder, 1989). However, the relatively small visual field (Kaltenrieder et al., 1989) can functionally be increased by these oscillations. This was confirmed by the large angular range within which scototaxis could be elicited (Fig. 2). Jumping spiders increase the visual field of their principal eyes by scanning movements of the eye retina (Land, 1969). There is no explanation for the lack of a significant response to the striped pattern (Fig. 4), as one would expect it to appear as a big square (with a surface area of 225 cm<sup>2</sup>) having a luminance contrast of ca. 9:1. Obviously *Hyalomma* perceives this pattern differently.

The scototactic response could be altered by moving targets (Fig. 5). The angular speeds tested ranged from ca 5° s<sup>-1</sup> to 15° s<sup>-1</sup>, which corresponds to the speed range in which a visual stimulus is highly attractive for a jumping spider (Drees, 1952; Forster, 1985).

In order to estimate whether the visual system of *Hyalomma* plays a principal role in host-seeking behaviour the walking speed of a tick is worth considering. The smallest stationary silhouette of a dromedary which elicited scototaxis had a surface area of 61 cm<sup>2</sup> and a height of 11 cm (Fig. 6). For a tick at the starting point this silhouette appeared like a silhouette of a real dromedary seen from a distance of ca. 18 m (taking a height of 200 cm for real dromedary). With the measured walking speed of 4.6 cm s<sup>-1</sup> *Hyalomma* would need ca. 6.5 min to reach its host. This seems feasible and matches with the observation that *Hyalomma* showed a higher response to a stationary than to a moving silhouette (Fig. 6).

In conclusion, the pronounced and nuanced target perception together with the earlier-found high absolute light sensitivity and the contrast-enhancing reverse Purkinje shift in spectral sensitivity (Kaltenrieder et al., 1989) suggest that *Hyalomma* may well use its visual system in host-seeking behaviour.

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#### REFERENCES

- Allan, S.A. and Stoffolano, J.G., Jr., 1986. The importance of pattern in visual attraction of *Tabanus nigrovittatus* Macquart (Diptera: Tabanidae). *Can. J. Zool.*, 64: 2273–2278.
- Atkins, G., Atkins, S. and Schoun, D., 1987. Scototaxis and shape discrimination in the female cricket *Acheta domestica* in an arena and on a compensatory treadmill. *Physiol. Entomol.*, 12: 125–133.
- Balashov, Y.S., 1968. Bloodsucking ticks (Ixodoidea) – vectors of diseases of man and animals. *Akad. Nauk. SSSR Zool. Inst., Leningrad.* (in Russian). English translation 500 (T500) by O.G. Strekalovsky, 1972, *Misc. Publ. Entomol. Soc. Am.*, 8: 161–376.
- Batschelet, E., 1981. *Circular Statistics in Biology*. Academic Press, London, 371 pp.
- Brady, J. and Shereni, W., 1988. Landing responses of the tsetse fly *Glossina morsitans* Westwood and the stable fly *Stomoxys calcitrans* (L.) (Diptera: Glossinidae & Muscidae) to black-and-white patterns: a laboratory study. *Bull. Entomol. Res.*, 78: 301–311.
- Carroll, J.F. and Pickens, L.G., 1987. Spectral sensitivity to light of two species of ticks (Acarina: Ixodidae). *Ann. Entomol. Soc. Am.*, 80: 256–262.
- Chapman, R.F., 1961. Some experiments to determine the methods used in host-finding by the tsetse fly, *Glossina medicorum* Austen. *Bull. Entomol. Res.*, 52: 83–97.
- Drees, O., 1952. Untersuchungen über die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). *Z. Tierpsychol.*, 9: 169–207.
- Duelli, P., 1978. Movement detection in the posterolateral eyes of jumping spiders (*Evarcha falcata*, Salticidae). *J. Comp. Physiol.*, 124: 15–26.
- El Shoura, S.M., 1988. Fine structure of the sight organs in the tick *Hyalomma (Hyalomma) dromedarii* (Ixodoidea: Ixodidae). *Exp. Appl. Acarol.*, 4: 109–116.
- Forster, L., 1985. Target discrimination in jumping spiders (Araneae: Salticidae). In: F.G. Barth (Editor), *Neurobiology of Arachnids*. Springer, Berlin, pp. 203–229.
- Heil, K.H., 1936. Beiträge zur Physiologie und Psychologie der Springspinnen. *Z. Vergl. Physiol.*, 23: 1–25.
- Hodgson, C.J. and Elbakhiet, I.B., 1985. Effect of colour and shape of 'target' hosts on the orientation of emigrating adult apterous *Myzus persicae* in the laboratory. *Entomol. Exp. Appl.*, 38: 267–272.
- Homann, H., 1928. Beiträge zur Physiologie der Spinnenaugen. *Z. Vgl. Physiol.*, 7: 201–268.
- Hoogstraal, H., 1956. African Ixodoidea. I. Ticks of the Sudan (with special reference to Equatoria Province and with preliminary reviews of the genera *Boophilus*, *Margaropus*, and *Hyalomma*). *Dep. Navy Bureau of Medicine and Surgery, Washington D.C.*
- Jander, R. and Voss, Ch., 1963. Die Bedeutung von Streifenmustern für das Formensehen der roten Waldameise (*Formica rufa* L.). *Z. Tierpsychol.*, 20: 1–9.
- Kaltenrieder, M., 1989. Spektrale und absolute Empfindlichkeit, Sehfeld und Skototaxis der Zeckenarten *Hyalomma dromedarii* und *Amblyomma variegatum*. Ph.D. thesis, University of Neuchâtel, Switzerland, 92 pp.
- Kaltenrieder, M., Labhart, T. and Hess, E., 1989. Spectral sensitivity absolute threshold and visual field of two tick species, *Hyalomma dromedarii* and *Amblyomma variegatum*. *J. Comp. Physiol. A*, 165: 155–164.
- Kieruzel, M. and Chmurzynski, J.A., 1982. Visual preferences for certain flat patterns in the house cricket and their conditionally acquired changes. *Biol. Behav.*, 7: 119–135.
- Land, M.F., 1969. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J. Exp. Biol.*, 51: 471–493.
- Land, M.F., 1972. Mechanisms of orientation and pattern recognition by jumping spiders (Sal-

- ticidae). In: R. Wehner (Editor), *Information Processing in the Visual Systems of Arthropods*. Springer, Berlin, pp. 231–247.
- Leonovich, S.A., 1986. The orientational behaviour of the tick *Hyalomma asiaticum* in a desert. *Parazitologiya*, 20: 431–439. (in Russian, with English summary).
- Mann, W.M., 1915. A cursorial tick. *Psyche Camb.*, 22: 60.
- Morel, P.C., 1969. Contribution à la connaissance de la distribution des tiques (Acariens, Ixodidae et Amblyommidae) en Afrique éthiopienne continentale. Ph.D. thesis, University of Paris, France, 388 pp.
- Pomerantzev, B.I., 1950. Fauna of USSR Arachnida, Vol. IV. Ixodid Ticks (Ixodidae). Academy of Sciences USSR, Moscow/Leningrad. (in Russian) English translation by A. Elbl, 1959. The American Institute of Biological Sciences, Washington.
- Sachs, L., 1984. *Angewandte Statistik*. Springer, Berlin, 552 pp.
- Turner, D.A. and Invest, J.F., 1973. Laboratory analyses of vision in tsetse flies (Diptera, Glossinidae). *Bull. Entomol. Res.*, 62: 343–357.
- Voss, Ch., 1967. Über das Formensehen der roten Waldameise (*Formica rufa*-Gruppe). *Z. Vergl. Physiol.*, 55: 225–254.
- Wallace, G.K., 1958. Some experiments on form perception in the nymphs of the desert locust, *Schistocerca gregaria* Forskål. *J. Exp. Biol.*, 35: 765–775.
- Zolotarev, Y.K. and Sinitsyna, Y.Y., 1965. Chemoreceptive organs on the forelegs of ixodid ticks Vest. Mosk. Gos. Univ., 20: 17–25. (in Russian). English translation 314 (T314) by Department of Medical Zoology, United Statesm Naval Medical Research Unit No 3, Cairo, Egypt.

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