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# Ultraviolet light detection: a function of scorpion fluorescence

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**Abstract.** The hypothesis that fluorescence in scorpions functions in the detection of ultraviolet light was tested. We reduced the fluorescence of scorpions by prolonged exposure to ultraviolet light on a 16:8 h light:dark cycle and compared their activity levels and light environment choices to unmodified scorpions in simple arenas that were half in shadow and half exposed to light. Three different lighting conditions were tested: infrared (IR) light only, IR + ultraviolet light and IR + white light. Treatments were illuminated by infrared light for videotaping. Activity level was measured by the number of transitions from the exposed to shadowed regions, and choice was measured by the percentage of time spent in the shadowed portion of the arena. Under IR + ultraviolet light, fluorescent scorpions reduced their activity levels and the variance in habitat choice increased, compared with reduced-fluorescence scorpions. There were no differences between fluorescent and non-fluorescent scorpions in the IR only condition or in the IR + white light condition. This is interpreted as evidence that fluorescence aids in the detection of and response to ultraviolet light, and possible implications of this result in natural habitats are discussed. This is the first experimental demonstration of a possible function for scorpion fluorescence.

**Keywords:** Moonlight avoidance, habitat choice, light responses

The fluorescence of scorpion cuticles is a well known, but little understood, phenomenon. Although two molecules associated with scorpion fluorescence have been isolated and identified – a ß-carboline (Stachel et al. 1999) and 4-methyl, 7-hydroxycoumarin (Frost et al. 2001) – no function of scorpion fluorescence has previously been demonstrated. This article reports the first empirical support for a function for scorpion fluorescence.

Several specific hypotheses regarding possible functions of scorpion fluorescence have been put forward, including the possibility that fluorescence functions in ultraviolet (UV) light detection (Blass & Gaffin 2008), mate identification and species discrimination (Kloock 2008), luring of prey (Kloock 2005), light amplification (Camp & Gaffin 1999), or as a sunscreen (Lourenço & Cloudsley-Thompson 1996). Some authors have hypothesized that fluorescence has no function, being either a relict trait (Frost et al. 2001) or correlated with some other functional aspect of the molecules responsible (i.e., sclerotization: Stachel et al. 1999). Those functions that have been tested to date have not received empirical support (Kloock 2005, 2008).

A recent methodological development, the ability to significantly reduce fluorescence from live scorpions (Kloock 2009), makes new tests of functional hypotheses possible by allowing us to compare the behavior of fluorescent and reduced-fluorescence scorpions in different situations. We report here on a series of experiments supporting the hypothesis that scorpion fluorescence functions in the detection of ultraviolet light.

## METHODS

**Specimens.**—Female *Paruroctonus becki* (Gertsch & Allred 1965) (Vaejovidae) were collected July–September 2008 in Kern County, California (voucher specimens deposited at the California Academy of Sciences, San Francisco). They were maintained in the laboratory in small, foam-plugged plastic vials, fed mealworm larvae and misted with water once per week until beginning the fluorescence reduction procedure. Only female scorpions were used in the experiments.

**Fluorescence reduction.**—We used a modification of the method for reducing the fluorescence from living scorpions presented in Kloock (2009) to produce a group of scorpions with significantly reduced fluorescence. The original method involved exposing scorpions for 24 h/day to low level (11μW/$cm^2$) UV lights (two 40 W fluorescent GE black light tubes) until fluorescence faded (~ 4.5 wk). Because of the potential effect of constant light exposure on scorpion circadian rhythms (Fleissner 1977a, b, c; Schliwa & Fleissner 1980; Fleissner & Fleissner 2001), and therefore behavior, we modified this technique by exposing the scorpions on a 16:8 h light:dark cycle. This extended the time for complete loss of visible fluorescence to ~6 wk, but otherwise resulted in an effect similar to that reported by Kloock (2009).

During UV exposure, scorpions were housed in small, open-topped plastic containers (13 cm length × 10 cm width × 7 cm height) with 12 ml of native soil: enough to provide a substrate, but insufficient for scorpions to bury themselves for protection from UV exposure. Scorpions were fed a single mealworm larva twice a week: if they failed to eat the larva, it was removed and a fresh larva provided at each feeding. Scorpions were also provided water twice a week by lightly misting the soil surface. Scorpions were maintained on this schedule until all experiments using them were completed.

**Control scorpions.**—Control and reduced-fluorescence scorpions were kept in identical containers with the same amount of soil and on identical feeding, watering, and lighting schedules with the exception that a layer of UV blocking film (Edmund Optics NT39-426) was interposed between the UV light source and the scorpions. Control and experimental scorpions were kept in a common environmental chamber with the same UV lights during UV exposure, so that environmental conditions were identical for all scorpions. Control scorpions showed no visible reduction in fluorescence over the course of the experiments.

**Basic setup.**—The basic experimental design owes considerable debt to Blass and Gaffin (2008), whose methods we have adapted and simplified for our purposes. All three experiments share the basic feature of placing scorpions in 14-cm diam.

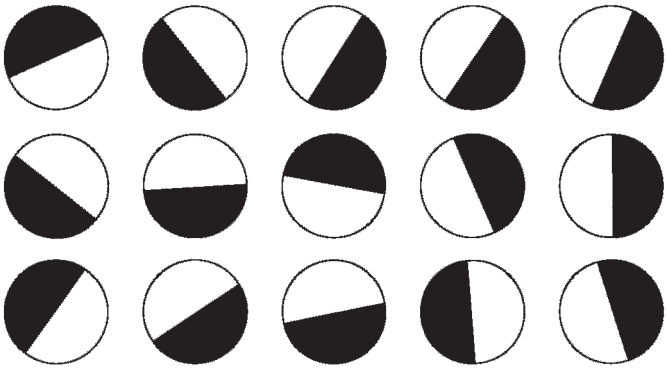

Figure 1.—Schematic of the 3 × 5 array of half-painted Petri dishes used in the experiment, showing a typical random orientation of dark and light halves.

Petri dishes, which had one-half of their exterior surface (top and bottom) painted over with water-based, non-toxic black paint (Fig. 1). No paint was on the interior surface of the Petri dish to act as a possible cue for the scorpions. Petri dishes were washed with 70% ethanol and allowed to dry for more than 20 h before each use to remove any potential chemical cues previous occupants may have deposited (Steinmetz et al. 2004).

We placed a single scorpion, either fluorescence-reduced or control, in each Petri dish, aligning the top and bottom halves so that half of the surface area of the Petri dish allowed light in, while the other half served as a light refuge. Petri dishes with scorpions were placed with the light and dark halves randomly oriented on a clear Plexiglas observation deck (Fig. 1) with an infrared sensitive video camera below and six infrared light emitting diodes (830 ± 35 nm) placed on the sides of the observation deck and reflecting off a light blue panel attached to the ceiling. This provided diffuse infrared illumination for videotaping. Scorpions have previously been shown not to respond to infrared illumination (Blass & Gaffin 2008).

Control and reduced-fluorescence scorpions were alternated in a 15 Petri dish array (three rows, five columns) and the camera adjusted to allow good visualization of all scorpions. A monitor in another room was used to ensure that all Petri dishes were easily observed, and all experiments were recorded on 42-min videotapes, which set the length of each trial. Two variables were recorded from the videotape analysis: percent time spent in the dark-covered half and the number of times scorpions moved from the exposed side to the covered side of the Petri dish (transitions). The percent time in the dark half acts as a measure of habitat choice, while the number of transitions acts as a simple measure of activity level.

In all experiments scorpions were allowed to acclimate to the array and lighting conditions for one hour before videotaping began, and the acclimation period began within 15 min of laboratory ''sunset'' to target the typical scorpion activity period (Hadley & Williams 1968). Just prior to the initiation of each experiment, each scorpion was moved into the clear portion of the Petri dish by gently tilting the dish toward the clear side; this ensured that all scorpions were visible at the beginning of the trial, and that they all experienced the lighting conditions, at least briefly, during the trial. Illumination other than the infrared needed for videotaping differed in the experiments that follow.

**Experiments 1 and 2.**—The same set of 15 control and 15 reduced-fluorescence scorpions was used for experiments 1 and 2. The order of presentation was randomized, with eight of the control and seven of the reduced-fluorescence scorpions receiving IR only illumination first (Experiment 1). Seven control and eight reduced-fluorescence scorpions received IR+UV illumination first (Experiment 2). The scorpions were then exposed to the alternate illumination, so that each experiment achieved a total sample size of 15 fluorescent and 15 reduced-fluorescence scorpions. All trials were completed over a four-night period.

*Experiment 1:* No illumination. This experiment constitutes a control for possible effects of the fluorescent reduction treatment. We placed scorpions in the standard experimental setup described above and videotaped them for 42 min. Fluorescence reduction should have no effect in this environment. If control and fluorescence-reduced scorpions exhibit significant differences in this experiment, then behaviors being measured were changed by the fluorescence reduction procedure itself.

*Experiment 2:* IR + UV illumination. As in Experiment 1, scorpions were placed in the standard experimental setup, but UV illumination was provided by a rectangular array (52 cm × 67 cm) of nine UV LEDs (Roithner-Lasertek RLT360-1.0-15, peak emission wavelength = 361 nm, spectral ½-width = 10 nm, viewing ½-angle = 15d) equally spaced. The array was placed 1.2 m above the observation deck, allowing room for the light from each LED to overlap, providing diffuse illumination across the observation deck. Although these LEDs caused scorpions to fluoresce at short distances, at a distance of 1.2 m, scorpions under the array did not visibly fluoresce; measurement of UV power using a Mannix UV-340 light meter (range = 290–390 nm) yielded $< 1$ $\mu W/cm^2$. Although fluorescence was not detectable by human vision, the question we are asking here is whether or not it is detectable by scorpions, whose vision is much more sensitive to low light levels than humans' (Fleissner 1977c). Ultraviolet intensity was kept very low to mimic natural nocturnal conditions. If fluorescence functions in UV light detection, we expect to see significant differences between control and fluorescence-reduced scorpions in this experiment.

**Experiment 3.**—IR + White light: The expected results of Experiment 2 under the hypothesis that fluorescence functions in UV light detection are also consistent with the possibility that the fluorescence-reduced scorpions suffered damage to the retina and/or the extra-ocular light sense (Zwicky 1970) during their exposure to UV light. To test this possibility we initiated a new experiment using white light. The basic experiment was identical to experiments 1 and 2, except that additional illumination was supplied by white light from two 40W fluorescent tubes. Rather than being placed directly over the scorpions, the lights were placed to the side to provide diffuse illumination because of the higher power of these lights. These lights did not produce measurable UV light on the observation deck. This experiment used novel scorpions, treated identically to those used in experiments 1 and 2, but with a slightly smaller sample size due to the death of some of the scorpions in this group during the preparation period. For

Table 1.—Summary of transitions between light and dark regions of the Petri dish by fluorescence in experiments 1–3. All data presented use the transformation (transitions$^{-1/2}$).

| | Experiment 1 (IR only) | | Experiment 2 (IR+UV Light) | | Experiment 3 (IR+White light) | |
|---|---|---|---|---|---|---|
| Light condition | Control (fluorescent) ($n$ = 15) | Fluorescence reduced ($n$ = 15) | Control (fluorescent) ($n$ = 15) | Fluorescence reduced ($n$ = 15) | Control (fluorescent) ($n$ = 14) | Fluorescence reduced ($n$ = 13) |
| Transitions (mean ± SD) | 4.1 ± 3.2 | 4.8 ± 2.2 | 3.0 ± 2.0 | 4.7 ± 2.2 | 1.2 ± 0.43 | 1.3 ± 0.44 |
| 95% CI: | | | | | | |
| Lower limit | 2.3 | 3.6 | 1.9 | 3.5 | 1.0 | 1.1 |
| Upper limit | 5.9 | 6.1 | 4.1 | 5.9 | 1.5 | 1.6 |
| Levene's test for variances | $F$ = 2.447 $P$ = 0.129 | | $F$ = 0.182 $P$ = 0.673. | | – Non-normally distributed | |
| Test for means | Equal variances $t$-test | | Equal variances $t$-test | | Mann-Whitney $U$-test | |
| Test statistic | $t$ = 0.751, $df$ = 28 | | $t$ = 2.244, $df$ = 28 | | $U$ = 90.0 | |
| $P$ | 0.459 | | 0.033 | | 0.961 | |

Experiment 3, there were 14 control scorpions and 13 reduced-fluorescence scorpions. If scorpion vision was damaged by the fluorescence reduction treatment, we should see significant differences between control and reduced-fluorescence scorpions, in a pattern similar that of Experiment 2.

**Statistical analysis.**—Evaluation of the hypothesis that fluorescence affects the response to UV does not depend on differences between the light treatments, but rather on the overall pattern of differences between control and reduced-fluorescence scorpions within each of the three experiments. Thus we are not interested in differences between light treatments, but instead in the differences between control and reduced-fluorescence scorpions within each experiment. The number of transitions and the percentage of time spent in the dark were analyzed separately in each experiment to determine if significant differences existed. Both variables within each experiment were analyzed for normality using the Kolmogorov-Smirnov test for normality, and homogeneity of variances was tested using Levene's test for equality of variances. Means within each experiment were compared with either the Mann-Whitney $U$ test (for non-normally distributed data) or a $t$-test (for normally distributed data), with assumptions of equal or unequal variances as dictated by the data structure. Given that the number of transitions is expected to have a Poisson distribution, the square root transform was applied a priori to normalize this variable in all tests.

## RESULTS

The number of transitions$^{1/2}$ in the IR + white light condition was not normally distributed (Kolmogorov-Smirnov $Z$ = 1.993, $P$ = 0.001). All other Kolmogorov-Smirnov tests of normality showed that the data were normally distributed (For % dark: IR only $Z$ = 0.500, $P$ = 0.964; IR+UV light, $Z$ = 0.681, $P$ = 0.743; IR + white light, $Z$ = 1.088, $P$ = 0.187. For transitions$^{-1/2}$: IR only, $Z$ = 0.834, $P$ = 0.490; IR +UV light, $Z$ = 0.683, $P$ = 0.740).

Table 1 presents the data and results of statistical tests on the number of transitions between the light and dark sides of the Petri dish. Levene's test for equality of variances revealed no differences between variances in experiments 1 and 2. Therefore, $t$-tests assuming equal variance were used to compare fluorescent and non-fluorescent scorpions while the non-parametric Mann-Whitney $U$ test was used for Experiment 3 due to the non-normality of transitions$^{1/2}$ in white light. Fluorescent and reduced-fluorescence scorpions did not differ in the number of transitions when either IR only or white light was present, but did differ when UV light was present (Table 1). Fluorescent scorpions made fewer transitions when exposed to UV light than did fluorescence- reduced scorpions.

Table 2 presents the data and results of statistical tests on the percentage of time spent in the darkened half of the Petri dish (% dark). Levene's test for equality of variances showed no difference in the variance between fluorescent and reduced-fluorescence scorpions in either the IR only or white light experiments, but a significant difference in variance in the UV light experiment was found. Thus $t$-tests assuming equal variance were applied to experiments 1 and 3, while for Experiment 2, equal variances were not assumed. There were no significant differences between the means of fluorescent and reduced-fluorescence scorpions for % dark in any of the experiments. Confidence intervals all include 50%, as expected if scorpions exhibit no preference for either side of the Petri dish.

Because of the difference in variances detected in Experiment 2, we decided to look more closely at the distribution of the percentage of time spent in the dark to see, post hoc, if any patterns emerged. Inspection of histograms suggested that the larger variation in fluorescent scorpions was caused by the tendency of these scorpions to stay in either the light or dark half of the Petri dish, with few of these scorpions having intermediate values of % dark. A simple categorization of % dark into "extreme" ($<$ 25% or $>$ 75%) vs. "moderate" (between 25% and 75%) values reveals this. With only IR light (Experiment 1), scorpions showed no tendency toward extreme values, regardless of fluorescence condition. Both fluorescent and reduced-fluorescence scorpions showed 7 "extreme" and 8 "moderate" values, ($\chi^2$ = 0.067, $df$ = 1, $P$ = 0.80). With UV light present (Experiment 2) reduced-fluorescence scorpions showed no tendency toward extremes (6 "extreme" and 9 "moderate", $\chi^2$ = 0.60, $df$ = 1, $P$ = 0.44), while fluorescent scorpions displayed a strong tendency toward extreme values (13 extreme, 2 moderate, $\chi^2$ = 8.1, $df$ = 1, $P$ = 0.0045). Scorpions exposed to white light, despite reduced activity levels (Table 1) also showed no preference for extremes (Reduced-fluorescence; 8 extreme, 5 moderate, $\chi^2$ =

Table 2.—Summary of the percentage of time spent in the dark half of the Petri dish by fluorescence in experiments 1–3.

| | Experiment 1 (IR only) | | Experiment 2 (IR+UV light) | | Experiment 3 (IR+White light) | |
|---|---|---|---|---|---|---|
| Light condition | Control (fluorescent) ($n$ = 15) | Fluorescence reduced ($n$ = 15) | Control (fluorescent) ($n$ = 15) | Fluorescence reduced ($n$ = 15) | Control (fluorescent) ($n$ = 14) | Fluorescence reduced ($n$ = 13) |
| Mean % Dark (mean ± SD) | 44.8 ± 32.8 | 40.4 ± 25.3 | 55.5 ± 37.9 | 56.8 ± 25.3 | 43.9 ± 39.6 | 44.2 ± 38.1 |
| 95% CI: | | | | | | |
| Lower limit | 26.7 | 25.3 | 34.5 | 42.8 | 34.5 | 21.2 |
| Upper limit | 63.0 | 54.4 | 76.4 | 70.9 | 76.4 | 67.3 |
| Levene's test for variances | $F$ = 1.104, $P$ = 0.302 | | $F$ = 7.945, $P$ = 0.009 | | $F$ = 0.192, $P$ = 0.655 | |
| $t$-test assumption | Equal variances | | Variances not equal | | Equal variances | |
| $t$ ($df$) | 0.418 (28) | | 0.118 (28) | | 0.022 (25) | |
| $P$ | 0.679 | | 0.907 | | 0.983 | |

0.69, $P$ = 0.41: Fluorescent; 9 extreme, 5 moderate, $\chi^2$ = 1.1, $P$ = 0.29). We should caution, however, that both the small sample size for $\chi^2$ and post-hoc nature of this analysis call for conservative use of this information in interpretation.

## DISCUSSION

These results support the hypothesis that scorpion fluorescence serves as a means for the detection of ultraviolet (UV) light at very low levels. Significant differences between the activity levels of fluorescent and reduced-fluorescence scorpions occurred only in the presence of UV light, with fluorescent scorpions changing their behavior by reducing their activity level (Table 1). Additionally, tests on variances in % dark revealed a difference between fluorescent and reduced-fluorescence scorpions only under UV light (Table 2).

Although a difference in the variance in the % dark under UV light was detected, there was no difference in the mean time spent in the two sides of the dish by fluorescent and reduced-fluorescence scorpions; in fact, no differences in the mean % dark were observed in any experiment (Table 2). No preference for either side of the Petri dish was observed in any of the conditions, as all confidence intervals include the random expectation of 50% (Table 2). Although fluorescent scorpions reduced their activity levels in response to UV light, this did not change the mean time they spent in the different light environments. In other words, the change in activity level did not result in a change in the average use of the environment. The obvious question then is whether this response to UV light has any value in a natural environment.

Scorpion surface activity is generally higher during moonless nights than moonlit nights (Skutelsky 1996), and nocturnal UV light levels correlate to moon phase (Silberglied 1979). Thus, it is possible that UV light acts as a cue for moonlight avoidance. Blass & Gaffin (2008) demonstrated avoidance of UV light, but the data here indicate no avoidance of UV (Table 1). It is very likely that the low level of UV light used in this experiment did not reach a threshold for avoidance behavior. Blass & Gaffin (2008) used a greater intensity of UV light in their experiment (0.9 lux), so were more likely to observe avoidance. More work needs to be done to determine more precisely the intensity required to elicit avoidance behavior, and whether this differs between fluorescent and reduced-fluorescence scorpions. In order to determine if avoiding UV light results in moonlight avoidance, experiments comparing fluorescent and reduced-fluorescence scorpions in moonlight and UV-filtered moonlight are necessary. Conducting tests under natural illumination conditions is a natural follow-up to the current experiment that would help determine whether simple moonlight avoidance is the main function of fluorescence. Another interesting experiment could involve measuring individual scorpion responses to UV light before reducing their fluorescence, then reducing their fluorescence and re-measuring, and finally, measuring a third time after fluorescence recovers. This would establish that the behavior of individuals changes in response to the manipulation. Unfortunately, the time involved in this set of manipulations (~ 6 weeks to remove fluorescence, plus several weeks to recover full fluorescence) would introduce the potential confounding of seasonal differences in responses.

The decision of whether to forage in moonlight or seek cover is influenced by factors other than UV light levels. Therefore, we must consider the possibility that the lack of UV light avoidance displayed in this experiment resulted from differences in decisions by individual scorpions about whether or not to seek cover. For example, Skutelsky (1996) found that scorpions with lower body mass:length$^3$ ratios were more likely to forage on moonlit nights than those with higher ratios, indicating that energy reserves were an important factor in the choice to forage while exposed to moonlight. We controlled the food offered to scorpions, but we did not control whether they actually ate, nor the scorpion size to prey size ratio. Therefore, motivation for foraging likely varied among the scorpions, though randomly with respect to fluorescence. If some fluorescent scorpions chose to seek cover while others chose to ''forage'' in the open, we would expect to see precisely what was observed in this experiment: reduced activity levels of fluorescent scorpions coupled with an increase in the variance of time spent in the dark caused by fluorescent scorpions choosing to spend most of their time in either the darkened or exposed habitat, with the specific choice influenced by hunger levels.

The post hoc inspection of fluorescent scorpions behavior when exposed to UV light is consistent this interpretation (with of course the caveat that it is post hoc). Fluorescent scorpions exposed to UV light exhibited a tendency to stay in one light environment that was not evident in any other treatment combination, consistent with the idea that they are making an active decision about where to spend their time in response to UV light, even if the decisions of individual scorpions differed. The reduced-fluorescence scorpions did not

exhibit this tendency. If this interpretation is correct, an experiment comparing starved to fed scorpions with and without UV present should reveal that fed scorpions seek cover from UV light while starved scorpions choose exposure to UV light, and this difference should disappear in scorpions that have had their fluorescence reduced.

Previous work on light-detection abilities of scorpions has shown UV light sensitivity in the lateral eyes (but not the median eyes; Machan 1968) and in an extra-ocular light sense localized in the metasoma (Zwicky 1968, 1970). Because the sensitivities of these senses are very similar (Zwicky 1970), we cannot at present attribute the observed changes in behavior to either one of these sensory mechanisms, and indeed it may involve both. Future experiments could attempt to determine the relative effect each of these senses has on the behavior with finer control of UV light wavelengths, and with more detailed information on the spectral sensitivities of these different mechanisms.

Machan (1968) also showed that scorpion lateral eyes have a second peak in sensitivity near the wavelength of peak fluorescence emission, which is also the region of the peak in median eye sensitivity. This dual peak in scorpion vision has suggested the possibility that scorpions possess dichromatic vision (Machan 1968; Kloock 2008). However, our results suggest another possibility. The peak in sensitivity in the UV range measured by Machan (1968) may have been caused by the eye detecting fluorescence caused by UV light, rather than by directly detecting UV light. In other words, the observed peak in sensitivity to UV light may be partially or entirely a byproduct of sensitivity to the light produced by fluorescence. If the UV sensitivity peak is actually a byproduct of fluorescence, we should see the peak in sensitivity disappear (or at least drop in amplitude) in reduced-fluorescence scorpions relative to fluorescent scorpions when the cuticle is exposed to UV light.

This study provides the first experimental evidence supporting a function for scorpion fluorescence. Further work will be necessary to link UV light detection to uses that scorpions may have for this ability in their natural habitat. Although the mechanism of detection is unclear, potentially being mediated through vision, the extra-ocular light sense or a third, as yet unknown, mechanism, the role of fluorescence in UV light detection may have implications for our understanding of fluorescence and the role of light in scorpions' sensory world.

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