Probabilistic phototactic behavior in a bark beetle: comment

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Received December 6, 1971


An alternative analysis of a study on the phototactic behavior of a bark beetle leads to two conclusions that differ from those of the original author. We find (1) that the beetles behaved in a normal manner and (2) that they could be selected for their positive response to uv. light.

Introduction

The mechanism of response by an insect to light is vital to understanding insect behavior. A paper by Kimmins (1970), entitled “Probabilistic phototactic behavior in a bark beetle,” described an important investigation of response patterns. Upon careful study of this paper, however, we reached conclusions differing in important respects from those of the author. Accordingly, we present our analysis.

Kimmins’ Methods and Observations

Kimmins (1970) subjected 200 unsexed, reproductively mature bark beetles (Ips confusus (Le Conte) (Coleoptera: Scolytidae)) to a sequence of trials in which about 40 at a time were released in an arena. After 15 min, individuals were classified as (i) trapped near an ultraviolet (uv.) light source, or (ii) trapped near one of nine other light sources with wave lengths between near infrared and near uv., or (iii) neither of the above. Details of the physical apparatus and the conduct of the trials are given by Kimmins (1970) and Kimmins (1966).4

We will follow Kimmins (1970) and refer to those beetles in class (i) as having “responded positively to uv.” From the description given by Kimmins (1970), it appears that this response could have been partly due to a particular position of uv. in the arena or to a particular pattern of accompanying lights, or to a combination of such factors. This possibility raises questions which could be resolved by further experiments employing appropriate randomization.

With this reservation, we find Kimmins’ results most informative under an alternative analysis.

Alternative Analysis

Figure 1, modified only slightly from Kimmins (1970), summarizes the observed responses in the reported trials.5 It shows that, in the initial trial of 200 beetles, 106 responded positively to uv. light, 46 did not respond positively to light, and 48 responded to light other than uv. Each of these groups was then subjected, as shown, to at least one additional trial, perhaps involving additional selection, perhaps not (cf. Fig. 1).

In subsequent trials, the initial response of a particular beetle was not necessarily repeated. Rather, according to Kimmins’ analyses, the responses within each of the groups tended to reproduce the response pattern observed in the initial trial of 200 beetles; this behavior the
The author considers anomalous. His abstract follows:

"An anomaly was observed during an investigation of the spectral response behavior of a bark beetle. Repeatable group responses were obtained in a multiple-choice test, but the response of individual beetles in the groups varied. Data are presented to illustrate this phenomenon. No explanation is presented, but it is suggested that individual photic responses to a multiple choice of wavelengths may conform to some probability distribution characteristic of the species, resulting in a constant group response which reflects this probability distribution."

Our analysis of the results leads us to two conclusions which differ from those of Kimmins: (1) we do not think that the observed results are anomalous and (2) we think individual beetles differ in their tendency to respond to uv. light.

With respect to point (1) above, the behavior observed in the initial trial and in repetitions A and B (cf. Fig. 1) is actually the expected behavior under what we consider the best a priori hypothesis and, therefore, ought not, we believe, to be considered anomalous. The hypothesis we refer to is:

H. The initial 200 *Ips confusus* are a random sample from a homogeneous population and are indistinguishable from each other with regard to response to ultraviolet light.

H is, mathematically, the simplest a priori hypothesis. It is the conventional null hypothesis of homogeneity. If there had been prior evidence of heterogeneity, we assume Kimmins would have referred to it. More importantly, the initial trial does not test H. As in other biological experimentation, the ratings in a single trial are insufficient for establishing intrinsic differences. Rather, we require the demonstration that the

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6Note that Kimmins does refer to prior evidence of homogeneity. He says, "... other experiments had failed to demonstrate a variation in photic response between the sexes."
results can be reproduced with some, although not necessarily perfect, consistency. Thus, we would believe that the presence of an individual in a particular trap after the initial trial is not an infallible demonstration of preference. Rather, the presence may contain an element of preference along with a large chance, or stochastic, component. On the basis of the initial trial, it appears that under the experimental conditions imposed by Kimmins, *I. confusus* tends to respond to uv. light about half the time. Moreover, for reasons just stated, given only the information of the first trial, we would still make precisely the same assumption about any particular beetle in Kimmins' original sample, whatever its response on the first trial.

Repetitions A and B of Kimmins' experiment do give information regarding H and are consistent with it, i.e., they provide tests of H which are not significant (cf. Kimmins (1970) page 922, paragraphs 1 and 2).

Thus, we believe that H above is (a) analogous to the null hypothesis in many kinds of experiments with other biological material, (b) mathematically the simplest a priori hypothesis, (c) consistent with the absence of prior evidence of heterogeneity, (d) not tested by the results of Kimmins' initial trial, and (e) consistent with repetitions A and B. We think this justifies our conclusion (1) above.

With regard to (2), repetition C leads one to reject H, and therein, we believe, lies the importance of this experiment. This rejection of H does not conflict with (e) immediately above. The beetles in repetition A and in repetition series B were selected for a particular response only once. Thus, the selection process was simply not continued long enough to obtain statistically significant results.

Our analysis of repetition C is as follows. We have labeled the trial with the original beetles as $C_0$, the subsequent trial with the 106 beetles that responded to uv. as $C_1$, the subsequent trial with the 67 beetles that responded again to uv. as $C_2$, and so on until the last trial in repetition C is trial $C_7$. Then from $C_0$ to $C_5$ the selection has been consistently on the basis of response to uv. $C_5$, $C_6$, and $C_7$ are replicated trials with the 23 beetles that survived this selection process. The percentage of beetles responding to uv. in this series is as follows (cf. Kimmins 1970).

<table>
<thead>
<tr>
<th>Trial</th>
<th>% beetles responding to uv.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_0$</td>
<td>53</td>
</tr>
<tr>
<td>$C_1$</td>
<td>63</td>
</tr>
<tr>
<td>$C_2$</td>
<td>60</td>
</tr>
<tr>
<td>$C_3$</td>
<td>65</td>
</tr>
<tr>
<td>$C_4$</td>
<td>88</td>
</tr>
<tr>
<td>$C_5$</td>
<td>73</td>
</tr>
<tr>
<td>$C_6$</td>
<td>82</td>
</tr>
<tr>
<td>$C_7$</td>
<td>68</td>
</tr>
</tbody>
</table>

The obvious question to ask about this series is: is it increasing? To answer this question, the percentages of beetles responding to uv. are plotted against $n$, the number of times the beetles have been selected for response to uv. (Fig. 2). Clearly, the percentages are increasing. One can select individuals that respond more consistently to uv. Thus, H is apparently false. (For statistical verification, one can transform the observed percentages $y$ to $y' = \arcsin \sqrt{y}$ to diminish the discrepancies in the variances of percentages, weight the $y'$ by the square root of the number of beetles in the trial (to further stabilize the variances) and thus show that the resulting regression coefficient is positive and significant at the 1% level.)

We conclude that the 23 beetles in trials $C_5$ to $C_7$ tend to respond more often to uv. than does a typical member of the population. Interesting
questions then arise. If a large number of beetles were subjected to a large number of selection screenings, could a subpopulation with a high probability of attraction to uv. light be obtained?

If so, and we believe Kimmins’ experiment indicates this is the case, the results suggest that bark beetle phototaxis may have a strong individual component, possibly characteristic of a particular genotype. If breeding experiments carried out with the selected individuals showed a genetic factor was involved, the bark beetle would thus be similar to Drosophila melanogaster. Hirsch and his group have studied D. melanogaster extensively for relationships between variation in genetic material and differences in behavior (Erlenmeyer-Kimling and Hirsch 1961). In particular they showed that with this insect a major portion of the variance in phototaxis experiments was under genetic control (Hirsch and Boudreau 1958).

Repetitions D and E, we believe, are difficult to interpret because the beetles entering the tests were selected in inconsistent ways. For example, of the 90 beetles entering repetition D, 39 responded to uv. on the first trial but failed to on the second, 27 responded to uv. on the first two trials but failed on the third, 14 responded to uv. on the first three trials but failed on the fourth, 3 responded to uv. on the first four trials but failed to on the fifth. The exact history of the remaining seven cannot be determined from Kimmins’ reported results. Thus, the beetles entering repetition D have quite diverse performance records. The response during the series does not contradict our earlier conclusions, however. Indeed, during repetition D where selection is consistently for response to uv., the percent response appears to be again increasing, as Kimmins noted.

The stability of the percentages with repetitions B and E (where the same beetles are simply subjected to repeated trials) has important implications. This is evidence that individual beetles do not adapt (in the sense that they respond more often) to uv. in repeated trials. This evidence suggests that the increasing percentage in repetition C is not due to any such adaptation, but rather reflects an intrinsic variability in the initial population with respect to uv. response, which has been detected by selection in the successive screenings.

Summary and Conclusions

We believe the work of Kimmins (1970) has demonstrated an important phenomenon in the phototactic response of bark beetles. By successive screenings, he selected individual beetles from a population of I. confusus. We have given and discussed evidence that the selected beetles exhibited a greater tendency to respond to uv. light than the others (see especially Fig. 2). The greater tendency to respond is apparently an intrinsic property of the selected individuals and not due to an adaptation to uv. light.