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The effect of photobleaching on bee (Hymenoptera: Apoidea) setae color and its implications for studying aging and behavior

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Abstract. Historically, bee age has been estimated using measurements of wing wear and integument color change. These measurements have been useful in studies of foraging ecology and plant-pollinator interactions. Wing wear is speculated to be affected by the behaviors associated with foraging, nesting, and mating activities. Setal color change may be an additional parameter used to measure bee age if it is affected by sun exposure during these same activities. The objectives of this study were to experimentally assess the effect of direct sun exposure on setal color, unicellular hair-like processes of the integument, and determine whether wing wear and integument photobleaching are correlated. To quantify photobleaching of setae, we measured changes in hue of lab-reared *Bombus huntii* Greene (Apidae) exposed to natural sunlight. We found that sun exposure was a significant variable in determining setal bleaching. To assess the relationship between wing wear and setal photobleaching, we scored wing wear and measured setal hue of *B. huntii*, *Melecta pacifica fulvida* Cresson (Apidae), and *Osmia integra* Cresson (Megachilidae) from museum specimens. Wing wear and setal hue values were positively correlated for all three species; however, the strength of the relationship varies across bee species as indicated by correlation coefficient estimates. Our results suggest that setal color change is affected by sun exposure, and is likely an accurate estimate of bee age. We suggest that future investigations of bee aging consider a suite of morphometric characteristics due to differences in natural history and sociobiology that may be confounded by the use of a single characteristic.

INTRODUCTION

Morphological characters of bees, such as body size, mandible shape, tongue length, integument color, and setal color are important in studies of bee-mediated pollination, and the systematics and taxonomy of bees. Some of these traits have been

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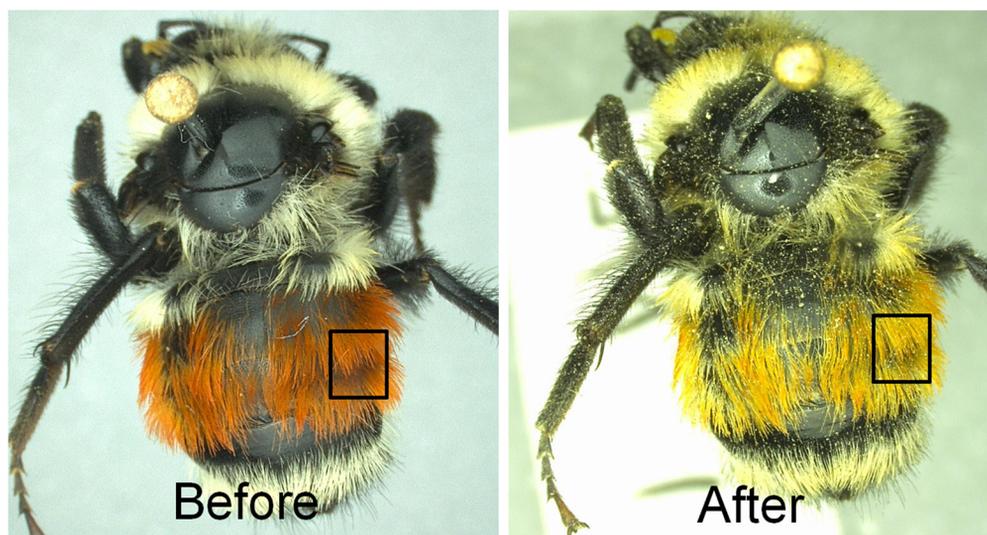


Figure 1. Unstandardized color photographs of the dorsal view of a worker of *Bombus huntii* Greene. The square box demarcates the lateral distal region of terga 2 and 3 where setal color was sampled for the ‘before’ and ‘after’ comparisons in the control and sun-exposed treatments.

shown to degrade over the lifespan of adult bees due to foraging, nesting, defense, mating behaviors (Cartar, 1992; Mueller & Wolf-Mueller, 1993), and from exposure to the elements (e.g., sun, oxidative processes). The accurate estimation of bee age can aid in evaluating the predictive utility of traits in varying degrees of degradation; thus, the quantification of these aging processes has long intrigued bee biologists (Cartar, 1992; Hendenström *et al.*, 2001; Higginson & Barnard, 2004; Michener *et al.*, 1955). The methods currently used for estimating bee age include measuring wing wear, mandible wear, and photobleaching of the integument (Mueller & Wolf-Mueller, 1993). Wing wear is measured by counting the number of nicks and tears on the wings, and mandible wear is measured by enumerating the abrasions on the mandibles. Both measurements are made with discrete quantitative values (Michener *et al.*, 1955; Mueller & Wolf-Mueller, 1993).

Unlike a quantitative variable, measuring integument color is often subjective in nature, requiring interpretation of the degree of color change or differences in color from one specimen to another, often on a qualitative scale (Mueller & Wolf-Mueller, 1993; Ruttner, 1988). While some studies have used quantitative approaches to measure bee setal color (Lozier *et al.*, 2013), none have experimentally investigated how sun exposure affects the integument or setal color of a bee. Quantitatively determining the effect of sun exposure on insect integument or setae will provide another metric to estimate bee age. Furthermore, considering the importance of integument and setal color in the context of insect evolution and taxonomy (Kettlewell, 1965), it would be practical to utilize quantitative rather than qualitative color measurements to test hypotheses.

In this study, we first examine the effect of sun exposure on red bumble bee setae, unicellular processes of the integument (Fig. 1). Unlike the study by Mueller & Wolf-Mueller (1993), we did not measure color change of the integument. We restricted our study of setal color change to phenotypes of bee species with red setae on the dorsum of the mesosoma or metasoma. Red setae are likely a result of melanin con-

Table 1. Summary of solar exposure (watts/m²) for Logan, Utah from 11 July through 25 August 2011. Average exposure for all three replicates is 49,291 watts/m². Data from the Campbell Scientific Weather Station in Logan, Utah (<http://weather.campbellsci.com/>).

Experimental Replicate	Total Solar Exposure (watts/m ²)	Trial Duration	# of Exposure Days During Each Trial
1	49,569	11 July – 21 July	8
2	49,296	28 July – 14 August	10
3	49,030	14–25 August	10

tent (Hines, 2008) and are susceptible to photobleaching and other oxidative processes (Korytowski & Sarna, 1990). We experimentally test for differences in setal color on bumble bees exposed to direct sunlight compared with bumble bees that are not exposed to direct sunlight. Setal color is measured quantitatively through digital image analysis, which is objective in nature, and differs from subjective approaches in previous studies of integument color change (Mueller & Wolf-Mueller, 1993; Ruttner, 1988). Our second objective is to test for a correlation between measurements of red setal color and measurements of wing wear across three different bee taxa. Several studies agree that wing wear is positively correlated with flight activities, which may affect the insect's life span (Cartar, 1992; Hendenström *et al.*, 2001; Rodd *et al.*, 1980). Thus, if increased wing wear is positively correlated with red setal color change (Mueller & Wolf-Mueller, 1993), then both measurements can be used with a degree of confidence as an indicator of bee age or foraging behavior.

MATERIAL AND METHODS

Sun Exposure vs. No Exposure Experiments

To test for the effect of sun exposure on the red color of the setae, we subjected lab-reared individuals of *Bombus huntii* Greene to different experimental treatments. Red setae are found on the dorsum of metasomal terga two (T2) and three (T3) (Thorp *et al.*, 1983) (Fig. 1). Colonies of *B. huntii* were grown at the USDA-ARS Pollinating Insects Research Unit in Logan, Utah, in low light conditions with no direct sunlight and < 2 h indirect red fluorescent light (Sylvania CF13EL/SUPER/RED 60 Watt equivalent 825 lumens) per day according to Strange (2010), thus assuring that setal color would not be degraded prior to light exposure. Individual adults of *B. huntii* were removed from colonies and placed into plastic vials and chilled to 10°C, then stored frozen until needed for the experiment.

At the time of the experiment, the sacrificed bees were thawed, pin mounted, and then placed approximately 5 cm apart into Schmidt boxes. We removed the fore and hind wings of each individual to expose the metasoma for the sun (ST) and control (CT) treatments. Individuals from different colonies were randomly assigned to the ST and CT, with three replicates per treatment and 18–20 individuals per replicate. Digital images of the dorsum of each bumble bee were taken with a Keyence Digital Microscope VHX-500F (Keyence Corp., Itasca, IL) and standardized with an 18% gray card before being subjected to treatment. Specimens assigned to the ST were held under full sun from 11 July to 25 August 2011 between 0800 and 1700 hours from Monday to Friday. Daily solar radiation data for this time period were obtained from the Campbell Scientific Corporation in Logan, Utah (Table 1). Individuals assigned to the

CT were held under a shaded overhang adjacent to the ST to control for concurrent weather variables (*e.g.*, relative humidity, wind, dew point). It should be noted that CT bees were still exposed to indirect sunlight. Bees in the CT for the first replicate were accidentally exposed to approximately 1 hour of sunlight per day for the first 5 days of the treatment, and when discovered were moved to an area of full shade. After the treatment period, digital images of each bee were taken in the same manner as the pre-treatment images.

To estimate the 'before' and 'after' effects on the setae on the terga, we measured hue (H) on the red-banded terga. We chose to analyze H , which is a component of the Hue, Saturation, and Lightness (HSL) digital color model and has been successfully quantified in a handful of insect studies (Davis *et al.*, 2007; Lozier *et al.*, 2013). All images were standardized to the 18% gray card using Adobe Photoshop CS2 (Adobe, San Jose, CA). Grey point filter was set by using an average value of the grey card from a digital photo taken in the same manner as the bee photos (Filter/Blur/Average). This saved grey point filter was then applied to each of the bee photos (Image/Adjustment/Load). After color standardization, on each image, a central point on the apex of the lateral distal region on T2 was sampled for the color measurements (Fig. 1). From the central point, a box was drawn with a 15 pixel radius to encompass portions of the setae on T2 and T3. H measurements lying within the area of the square on the lateral distal region were averaged to represent the average H measurements on T2 and T3 of the insect terga. Color measurements were conducted in GIMP v2.8.2 (Kimball *et al.*, 2012).

Sun Exposure vs. Wing Wear

To test for correlation between hue variability of red setae and wing wear (W), we surveyed specimens of three bee species obtained from the USDA-ARS National Pollinating Insect Collection also in Logan, Utah. We measured H and W on museum archived *B. huntii*, and two solitary bee species, *Melecta pacifica fulvida* Cresson and *Osmia integra* Cresson. For the purposes of this study, we define the color red to include fulvous (Hurd & Linsley, 1951) and rufo-fulvous (Sandhouse, 1939), which are used by taxonomists to describe the dorsal thoracic pubescence of *M. pacifica fulvida* and *O. integra*, respectively. In addition, specimens of *O. integra* were restricted to populations from the intermountain western U.S. (*e.g.*, Utah and Wyoming) to preclude the use of phenotypes with yellow setae common in the eastern U.S. (Mitchell, 1962). H was quantified on the red setal region between the wing bases on the thorax of *M. pacifica fulvida* and *O. integra* whereas H was measured on the lateral distal region of T2 on the metasoma of *B. huntii*. Imaging and color sampling methods of the museum specimens follow the methods described in the sun-exposure experiment above. W was scored by two independent observers and the two values were averaged. W scoring follows the methods outlined in Mueller & Wolf-Mueller (1993) and Michener *et al.* (1955). Briefly, W was estimated between 0–6, with 0 representing little or no W and 6 representing extreme W (Mueller & Wolf-Mueller, 1993).

Interpretation of Setal Color Change and Statistical Analyses

While H has a circular distribution of values (0–360), the lowest measured average H in our preliminary investigation is $H_{CT} = 1.5$, whereas the largest measured H is $H_{ST} = 40$. Because our actual measurements of H constitute less than one tenth of the pos-

sible integer values in the distribution of H , we chose to use statistical analyses for linear and not circular data. In our analysis and interpretation, a change in H from 'dark red' to 'light red' of the insect setae will be defined as a 'lightening or photobleaching of setal color'. Lighter setae result in larger values of H , whereas smaller values of H indicate darker setae.

We utilized a general linear model (PROC GLM; SAS ver. 9.3) to test for the effects of replicate, treatment (ST and CT), and the interaction of these two variables on H blocked by time of data collection (before and after). We used the Tukey's multiple comparison method to determine significant differences in H for each time and treatment combination. To test for a correlation between H and W , we estimated the Kendall rank-sum Correlation Coefficient (τ).

RESULTS

Sun Treatment vs. Control Experiment

For all ST, bees were visually much lighter in appearance (Fig. 1) than bees in the CT. Replicate was the only significant effect on variations of bumble bee H before any CT or ST ($F = 13.14$, $df = 2$, $P < 0.001$). Treatment ($F = 1.58$, $df = 1$, $P = 0.2118$) and the interaction of treatment and replicate ($F = 0.22$, $df = 2$, $P = 0.8053$) had no significant effect on H at the beginning of the experiment. After treatment, replicate remained a significant factor in H differences ($F = 91.25$, $df = 2$, $P < 0.001$). Treatment was also highly significant in H differences ($F = 249.27$, $df = 1$, $P < 0.001$). However, there was no significant interaction of these two variables on H ($F = 0.93$, $df = 2$, $P = 0.3964$). Multiple comparisons show no significant difference in H between any pre-treatment groups. Groups exposed to the full ST were all significantly greater than the corresponding measurements taken before treatments, and greater than the after-treatment values for the CT bees (Fig. 2). Groups exposed to the shade did not have different H after treatment as compared to before, with the exception of replicate 1 (Fig. 2).

Sun Exposure vs. Wing Wear

Bees with a high degree of W (e.g., $W = 6$) were more likely to have lighter red setae, whereas bees with a low degree of W (e.g., $W = 0$) were more likely to have darker red setae (Fig. 3). We found a significant, positive correlation (τ) between H and W across all three bee species (*B. huntii*: $\tau = 0.55$, $P < 0.001$, $n = 30$; *M. pacifica fulvida*: $\tau = 0.57$, $P < 0.001$, $n = 30$; *O. integra*: $\tau = 0.60$, $P < 0.001$, $n = 30$) (Fig. 3). Thus, photobleaching of the red setae across all three species remains correlated with W as noted in previous studies (Mueller & Wolf-Mueller, 1993).

DISCUSSION

The results of our study reveal that red bee pile does fade when exposed to direct sunlight. We found no interaction between treatment and replicate in our experiments, with specimens experiencing a significant degree of photobleaching in the ST compared with the CT. We also found that a small degree of fading occurred in the control groups (CT), likely reflecting oxidative processes (Korytowski & Sarna, 1990) or perhaps due to indirect solar exposure (Fig. 2). Our results further suggest that limited sun exposure to insect setae can still result in dramatic photobleaching. Un-

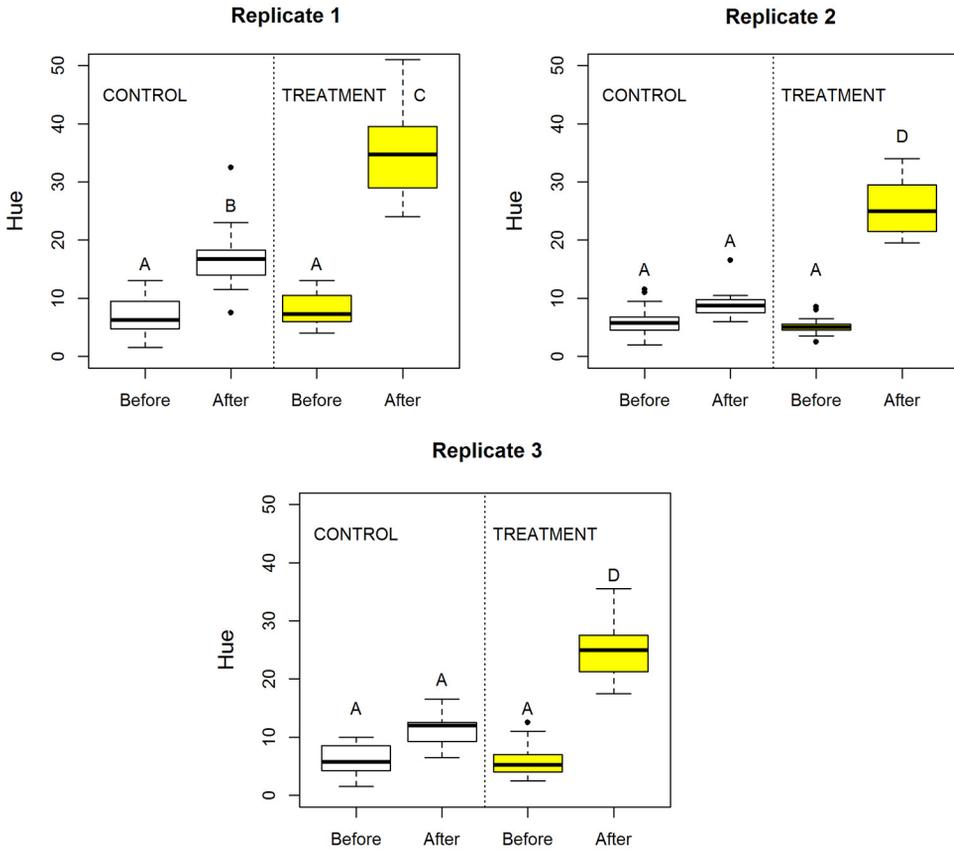


Figure 2. Data distributions of ‘before’ and ‘after’ measurements of setal color on the lateral distal region of the terga 2 and 3 for the control and sun-exposed treatments. Setal color was measured using the color property hue (*H*). Letters above each boxplot correspond to a significant difference between treatments of at least 0.05 based on Tukey’s adjusted multiple comparison tests.

like replicates 2 and 3, the replicate 1 CT was inadvertently exposed to approximately 1 hour of direct morning sunlight per day (between 9am and 10am) due to misplacement of the specimens under the shade overhang early in the experiment. This limited exposure was sufficient to significantly increase *H* (Fig. 2). The solar radiation data (Table 1) also reveals that the ST and CT of replicate 1 were exposed to the greatest amount of solar radiation over the shortest amount of days. Thus, differences in sun intensity and exposure may also explain the differences in post treatment *H* of CT replicate 1 relative to 2 and 3 (Fig. 2).

In our study, we tested the correlation between wing wear and photobleaching across multiple bee species. We chose to measure wing wear on museum specimens as it has biological significance on a bee’s life span and foraging efficiency (Cartar, 1992; Higginson & Barnard, 2004). Furthermore, qualitative measurements of setal color lightening has revealed a strong correlation with wing wear, with highly worn out wings correlated with lightened insect integument (Mueller & Wolf-Mueller, 1993). While several studies have quantified color with a digital color model (Davis *et al.*, 2007; Lozier *et al.*, 2013), no study has formally articulated the relationship between the quantitative measurements of color and wing wear. Our quantitative approach

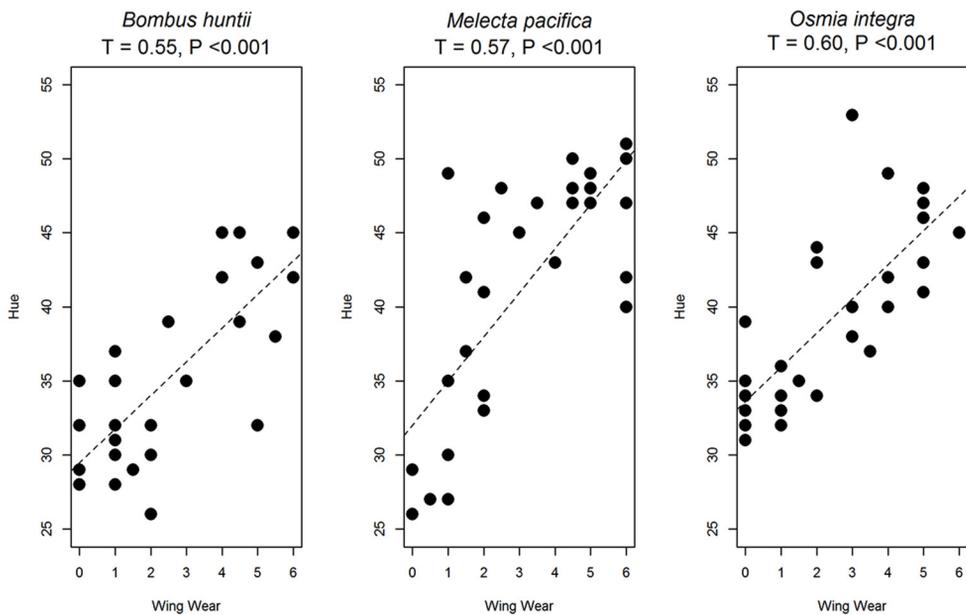


Figure 3. Correlation (τ) between wing wear (W) and setal color (hue, H) of three bee species: *Bombus huntii* Greene, *Melecta pacifica fulvida* Cresson, and *Osmia integra* Cresson. Larger H values represent increased photobleaching of setae, whereas smaller values of H represent less photobleaching of setae. Larger W represents increased wing wear, whereas smaller W represents decreased wing wear.

agrees with past investigations of color that have used qualitative methods of measuring color (Mueller & Wolf-Mueller, 1993).

The strength of the relationship between wing wear and setal photobleaching may reflect a species' behavior and sociobiology. While our results indicate a significant and positive relationship between setal photobleaching and wing wear (Fig. 3), each of the three species we tested exhibit very different sets of activities associated with behavior and sociobiology. *Osmia integra* is a ground-nesting solitary species, in which there is no cooperation between females in nesting and foraging activities (Michener, 2007). Instead, a single female excavates a nest in sand or loose soil, forages for pollen and nectar resources, and provisions each cell with adequate resources necessary for a single offspring before depositing an egg, closing the cell and repeating the process (Gordon, 2003). *Melecta pacifica fulvida* is also a non-social species, however it is a cleptoparasite of species of *Anthophora* Latreille (Michener, 2007). While cleptoparasites do not build and provision their own nests, behaviors associated with this lifestyle likely exposes *M. pacifica fulvida* to extended durations of flight time, and therefore increased wing wear and exposure to the sun. *Bombus huntii* is a social species exhibiting divisions of labor in which individuals share foraging, nest maintenance, and brood care activities with other sister workers. In addition, nests are constructed in existing cavities, such as abandoned rodent burrows (Michener, 2007), which require little or no excavation. Consequently, individual workers of *B. huntii* may not be as exposed to the same degree of environmental conditions leading to wing wear and setal photobleaching as would *O. integra* and *M. pacifica fulvida*. In fact, although *B. huntii* also exhibited a significant relationship between setal photobleaching and wing wear, the correlation coefficient was also a degree smaller than *O. integra* and *M. pacifica fulvida*

(Fig. 3). Further work is necessary, ideally with multiple bee taxa, to test whether a generalization can be made on the correlation strength of wing wear and photobleaching with behavior and sociality. Several studies do support the hypothesis that the degree of wing wear is affected by the behaviors exhibited during an individual bee's lifetime (Cartar, 1992; Rodd *et al.*, 1980). The addition of setal photobleaching will add another metric for investigations into the ecology and evolution of bees.

Objectively measuring color with properties of the digital color model has the capacity to fuel investigations in bee evolution and ecology (Cartar, 1992; Lozier *et al.*, 2013; Rodd *et al.*, 1980). Our study is limited to an investigation of photobleaching of red setae on the dorsum of the mesosoma or metasoma of three bee species. We did not investigate photobleaching on other regions of the body that have setae like the clypeus or vertex of the head, or the ventral regions of the mesosoma and metasoma. It is likely that dorsal regions of the insect body experience the greatest photobleaching due to immediate exposure to the sun (Fig. 1); however, other body regions could be investigated to test whether photobleaching occurs to the same magnitude on the insect body, specifically the ventral regions. Furthermore, the density of the setae on the insect body may be affected differentially by sun exposure; bees with less dense setae may be subject to greater photobleaching than bees with highly dense setae. However, this hypothesis remains to be tested in a controlled experiment. We also suggest that future investigations on the effect of sun exposure on setal color should include bees with phenotypes that exhibit different setal colors like yellow, black, or white (Mueller & Wolf-Mueller, 1993; Ruttner, 1988). As differences in setal colors are likely due to differences in melanin content (Hines, 2008), we hypothesize that different setal colors may exhibit differential responses to photobleaching over sun exposure time and intensity (Table 1). Previous studies have found that yellow integument color does change over time with increased sun exposure (Mueller & Wolf-Mueller, 1993). However, the effect of sun exposure on other integument colors like green and blue associated with species like *Agapostemon texanus* Cresson or *Osmia lignaria* Say remains to be studied. Future investigations could combine experiments that test for differences in photobleaching on both the integument and setae of a diversity of bee species.

Considering that many bee taxonomic diagnoses depend on color descriptions to differentiate species, we advise careful consideration to be made during the examination of degraded insect specimens. The inability to assign species names to degraded specimens has been specifically observed in bumble bees, which rely heavily on color diagnoses of their setae. Thus, when degraded specimens do arise, especially with species that depend on setal coloration for species identification, it would be advisable to pursue other routes of identification such as non-degrading morphological characteristics and molecular markers.

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