



The influence of silhouette color and orientation on arrival and emergence of *Ips* pine engravers and their predators in loblolly pine

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Abstract

Insects that rely upon aggressive bark beetles (Coleoptera: Scolytidae) for generating appropriate habitats (natural enemies and associated species) must respond to a variety of stimuli used by bark beetles, including semiochemical and visual cues. In the southeastern US, *Ips* engraver beetles are non-aggressive bark beetles that exploit both standing and downed trees (vertically and horizontally oriented targets). The objective of this experiment was to evaluate whether changes in visual silhouettes (color and orientation) affected the colonization patterns of *Ips* engravers and their natural predators in loblolly pine logs. We found that the total number of *Ips* arriving at loblolly pine logs was significantly affected by color. About 48% fewer *Ips* were caught at logs painted white than those painted black, and 32% fewer than at unpainted. Of the predators arriving in sufficient numbers to evaluate, *Medetera bistriata* parent (Diptera: Dolichopodidae) and *Platysoma* spp. (Coleoptera: Histeridae) were significantly affected by color, with white logs catching fewer numbers in each case. Orientation of host logs (horizontal and vertical) affected both *M. bistriata* and *Lonchea* spp. (Diptera: Lonchaeidae) but not *Ips*. *Lonchea* were significantly and consistently more attracted to horizontal logs. *M. bistriata*, on the other hand, were inconsistently more attracted to vertical logs, i.e., the interaction between season and orientation was as strong as the main effect for orientation. *Thanasimus dubius* (F) (Coleoptera: Cleridae) and anthocorid bugs were not caught in sufficient numbers for valid analysis. Overall, these results are similar to those obtained by funnel trapping, suggesting that visual responses are robust across different environmental conditions. Further, our results suggest that color treatments could be used to manipulate behaviors of predators and prey somewhat independently. This may be important for research, to evaluate relationships at a range of densities, and management, to develop treatments that reduce losses of natural enemies when bark beetles are targeted.

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1. Introduction

Predators and prey interact in a variety of ways through multiple behaviors, each of which may impact

success and potentially be susceptible to natural selection. For bark beetles in the genus *Ips* (Coleoptera: Scolytidae), finding new host trees is crucial because, once used, a host resource is no longer available to successive generations. Attraction to a host tree from a distance appears to involve both olfaction and vision (Borden et al., 1986; Gara et al., 1965; Payne, 1986;

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Shepherd, 1966). Olfactory signals, including pheromones and host chemicals, indicate an appropriate host and cause conspecifics to move toward the source. But olfaction rarely acts alone during host selection; ancillary cues such as color are usually coincident with odor perception (Bernays and Chapman, 1994; Borden et al., 1986; Kogan, 1994; Prokopy and Owens, 1983). Visual cues may enable a precise approach to the tree, enabling beetles to land successfully on the target.

Recently, Strom et al. (1999, 2001) reported significant responses of *Dendroctonus* (Coleoptera: Scolytidae) bark beetles and their predators to modifications of visual silhouettes in both the southern and western United States using the southern pine beetle (SPB) *Dendroctonus frontalis* Zimmermann and western pine beetle (WPB) *D. brevicornis* LeConte, respectively. In these studies, trap catches of aggressive, tree-killing bark beetles (SPB and WPB) and their major predators (*Thanasimus dubius* and *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), respectively) were significantly reduced by a visual disruptant (white paint on the boles of host trees). The pattern of disruption was similar between prey and predator: both the WPB and its predator, *T. chlorodia*, were less affected by color than the SPB and *T. dubius* under similar testing.

Visual behavior of *Ips* spp. in the southeastern US has not been studied. These bark beetles, known as engravers, are generally considered to be less aggressive than *Dendroctonus* spp., often occurring in disparate hosts that offer a wide range of visual cues including weakened or injured trees, recently felled trees, logging slash, or windfalls (Drooz, 1985). Prokopy and Owens (1978) hypothesize that insects develop visual search images based upon host-use patterns and that more specific search images are more easily disrupted by visual treatments. If so, one may expect *Ips* species to be less responsive to visual treatments than *D. frontalis*, because the latter attack standing trees almost exclusively, and should therefore have a narrower acceptable range of host visual cues.

Insect natural enemies respond to stimuli associated with their hosts such as the response of natural enemies to kairomones (e.g., Raffa, 2001). Mass attack of trees by *Ips* requires recruitment of conspecifics. This is accomplished, in part, by semiochemicals acting in concert with short-range host cues (such as color) all

of which may be used by natural enemies. *Ips* and SPB may colonize different portions of the same tree and considerable overlap of both species often occurs. The engravers interact with many of the same natural enemies as SPB, and may serve as alternate prey for them during periods of low SPB populations (Kudon and Berisford, 1980). To exploit both hosts, natural enemies must be general in their responses to the mix of cues (olfactory and visual among others) associated with each potential host.

This study was designed to evaluate whether changes in visual cues—color (black versus white as shown with SPB and WPB) and orientation (horizontal versus vertical)—influence colonization patterns of *Ips* engravers and their natural predators in loblolly pine (*Pinus taeda*, Pinales: Pinaceae) logs in Louisiana. Given that *Ips* are less selective of host form than *Dendroctonus*, we expected that they would be less responsive to visual treatments than *D. frontalis*. We considered the natural enemy complex to be unpredictable in their responses because they may exhibit plastic behaviors that are controlled by the specific pheromone to which they are responding (semiochemical \times visual interaction), their response may be inherently more general due to overlap of their prey diets, or they may be relatively strictly coupled to particular prey and respond accordingly. Further, the study aimed to determine if visual silhouette modifications could aid research and management in developing treatments that conserve natural enemies while reducing bark beetles.

2. Methods

Arrival of predators of *Ips* engravers at recently cut loblolly pine logs was monitored over a summer, fall, and subsequent spring season—at the same site in southern Louisiana (East Feliciana Parish, latitude 30°47' north, longitude 90°57' west). Arrival of *Ips* engravers was monitored in the fall and spring seasons as well. During each season, a replicated array of color and orientation treatments was evaluated using a 'square' design (Fig. 1). Color treatments included a white, black and unaltered check, while orientation was either horizontal (approx. 15 cm above ground) or vertical. Cardinal direction was accommodated by the design, with logs positioned by treatment on each side

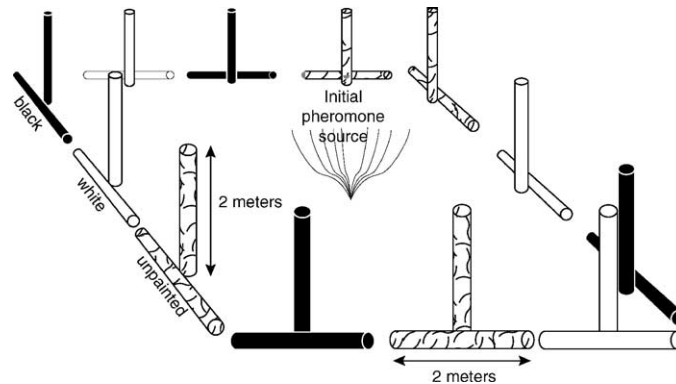


Fig. 1. Schematic of “square” design used to evaluate predator and *Ips* arrival to loblolly pine logs in Louisiana. Tones correspond with color (black, unpainted, white).

of the square. Thus, the square consisted of four replicated treatment sets, each with a horizontal and vertical pair for each of the three colors. Each side was aligned by compass in the four cardinal directions to accommodate variation in semiochemical dispersal.

At the time each seasonal evaluation was made, loblolly pines from a nearby 14-year-old plantation were felled and divided into two, 2 m logs per stem. Trees averaged 20 cm in diameter at breast height (DBH). Logs were transported immediately to the test site, positioned as described above, and color treatments applied.

The main color effect to be evaluated was white versus black; however, an unpainted (natural) treatment also was included (see Strom et al., 1999 for reflectance spectra). Because white and black Krylon[®] enamels do not apparently differ in volatile composition (S.D. Salzatore, Krylon Division of the Sherwin-Williams Co.), black paint was a ‘check’ for any semiochemical effects or microhabitat differences caused by the sealing or tactile effects of painted logs. The unpainted check provided the natural color and microhabitat treatments. Each horizontal log was placed on a discarded, dry bolt to maximize surface area available for colonization as well as to discourage predation by ground or litter-inhabiting organisms. Vertical logs were attached by wire (painted as appropriate) to metal fence posts driven into the ground. A panel of Mylar[®] (0.5 m long by 0.2 m wide) was attached to the center of each log (24 total) facing outside the square. Each panel was then coated entirely with Stikem Special[®] trapping compound

(Michel and Pelton, Emeryville, CA). To facilitate timely colonization, one packet each of ipsenol and ipsdienol (Phero Tech, Inc., Delta, BC, Canada) were attached to a 1-m stake in the center of the square. Packets were removed when attacks were observed on several test logs, signaling that naturally produced pheromones were present (after 1–2 weeks). Natural colonization of logs by *Ips* engravers was then allowed.

Each color/orientation treatment pair was randomly rotated among the sides of the square weekly. Prior to rotating, each sticky Mylar panel was removed, faced with Saran[®] wrap, and folded for transport to the laboratory for analysis. A new sticky panel was applied to each log upon repositioning. Trapping was conducted for 3 weeks after initial attacks were evident in summer and fall, and 5 weeks in the subsequent spring, coinciding with the development of *Ips* engravers under ambient environmental conditions.

Emergence of insects was evaluated in the spring and summer. When *Ips* had developed to the late larval or pupal stage (~4 weeks after attack), the center section (~0.5 m) of each log was cut, measured for surface area, and placed into a rearing drum to accumulate emerging *Ips* and predators. Emerging insects (adults and larvae) were counted and identified over 6 weeks to compare treatment effects on emergence of *Ips* and their predators. This rearing interval allowed for emergence of *Ips* engravers, and the majority of their naturally occurring predators. It is possible that a small number of diapausing clerids were not collected,

but these predators were not present in high numbers in this study.

The total number of *Ips*, *Medetera bistrata* (Diptera: Dolichopodidae), *Platysoma* spp. (Coleoptera: Histeridae), and *Lonchea* spp. (Diptera: Lonchaeidae) caught in arrival traps was subjected to three-way analysis of variance (ANOVA) to evaluate the effects of season (spring, summer, fall), log color (white, black, unpainted), and log orientation (horizontal, vertical) on behavior in a three by two factorial with all factors fixed. Each log was an experimental unit, thus there were 72 replicates (six per side \times four sides \times three seasons) available for statistical analysis of *M. bistrata*, *Platysoma* spp., and *Lonchea* spp., and 48 replicates (two seasons) for *Ips*. The total number of arriving insects caught per log was transformed either by natural log($y + 1$) or square root, depending on the data set, prior to analysis to reduce heteroscedasticity. The full ANOVA model was: $y =$ season, color, orientation, season \times color, season \times orientation, color \times orientation, season \times color \times orientation. Any interaction term that was not significant ($P > 0.20$) was eliminated from the model (pooled into error) and the model re-analyzed. Mean separation tests, using the Tukey–Kramer adjustment (SAS, 2000), were done if overall model and treatment effects were significant ($P < 0.05$). Insects that were not abundant and inconsistently present in traps (*T. dubius*, anthocorids) were not analyzed by ANOVA due to the unreliability of results when large numbers of zero counts are present.

The total number of emerging individuals in each insect group (per square meter bark surface) was analyzed similarly. These data were available from two seasons, spring and summer. *Temnochila vires-*

cens, a predator of *Ips* spp. (Billings and Cameron, 1984), was present in sufficient numbers to be included in analyses of emergence. Apparently our sticky arrival traps did not successfully trap this species. Correlation analyses were performed on pairs of interest of the number of emerging and arriving insects. For example, all insects were evaluated for the correlation between their number arriving, as estimated by sticky trap catch, and their number emerging (per square meter). Correlations were also carried out to evaluate the relationship between the number of *Ips* and the number of each predator arriving and emerging. Non-parametric correlation analysis (Kendall's Tau) was used to avoid the more restrictive assumptions of parametric correlation analysis.

3. Results

The distribution (mean number per panel) of arriving insects caught across treatments is given in Table 1. A total of 15,452 arriving individuals were trapped, with *M. bistrata* (12,749) accounting for about 82% of the total. Second most abundant were *Ips* (1248 individuals; 8%), followed by *Lonchea* spp. (1037; 7%), *Platysoma* spp. (304; 2%), *T. dubius* (61; <1%) and Anthocoridae (53; <1%). Overall ANOVA models were highly significant ($P < 0.001$) for all arriving insects, thus, relative effects of individual treatments were evaluated. Not surprisingly, season had a consistently significant effect on total catch of all species, always explaining the greatest amount of variance in arrival (Table 2).

All arriving insect species were affected by at least one visual treatment; either color or orientation had a

Table 1

Number of *Ips* spp. and predators arriving at loblolly pine logs in Louisiana (mean per panel \pm S.E./m²)

Color	Orientation	<i>Ips</i> spp. ^a	<i>M. bistrata</i>	<i>Platysoma</i> spp. ^b	<i>Lonchea</i> spp.	Anthocoridae ^c	<i>T. dubius</i>
Unpainted	Horizontal	20.9 \pm 3.3	176.8 \pm 36.1	5.3 \pm 1.2	27.8 \pm 8.0	2.1 \pm 1.2	0.2 \pm 0.1
Unpainted	Vertical	25.6 \pm 5.3	204.1 \pm 26.2	6.3 \pm 2.0	5.4 \pm 1.5	1.1 \pm 0.4	1.4 \pm 0.5
Black	Horizontal	35.3 \pm 10.6	206.8 \pm 45.5	5.2 \pm 1.5	23.8 \pm 6.6	2.0 \pm 0.6	0.5 \pm 0.2
Black	Vertical	30.5 \pm 5.5	250.1 \pm 37.9	5.2 \pm 1.2	5.8 \pm 1.3	0.1 \pm 0.1	2.3 \pm 1.0
White	Horizontal	16.8 \pm 4.6	107.0 \pm 29.6	1.2 \pm 0.3	16.9 \pm 5.0	0.5 \pm 0.4	0.3 \pm 0.2
White	Vertical	27.0 \pm 12.4	117.8 \pm 21.6	2.3 \pm 0.6	6.6 \pm 1.7	0.8 \pm 0.6	0.5 \pm 0.2

^a *Ips* spp. = *Ips avulsus*, *I. calligraphus* and *I. grandicollis* combined.

^b *Platysoma* (=Cylistix) *attenuata*, *P. cylindrica* and *P. parallelum* combined.

^c *Lycotocorus elongatus* and *Scoloposcelis mississippiensis* combined.

Table 2

Analysis of variance results from the total number of insects arriving on sticky panels placed on logs with various visual treatments^a

Effect ^{b,c}	Insect group											
	<i>M. bistrriata</i>			<i>Ips</i> ^b			<i>Platysoma</i>			<i>Lonchea</i>		
	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.
Season	125.02	<0.0001	2, 60	56.82	<0.0001	1, 47	58.65	<0.0010	2, 66	111.41	<0.0001	2, 58
Color	43.94	<0.0001	2, 60	6.24	<0.0042	2, 47	14.46	<0.0001	2, 66	2.78	<0.0705	2, 58
Orientation	21.40	<0.0001	1, 60	0.56	<0.4600	1, 47	1.21	<0.2759	1, 66	84.21	<0.0001	1, 58
Season × color	3.65	<0.0100	4, 60	NS ^d	–	–	NS	–	–	4.65	<0.0025	4, 58
Season × orientation	21.78	<0.0001	2, 60	NS	–	–	NS	–	–	8.94	<0.0004	2, 58
Color × orientation	NS	–	–	NS	–	–	NS	–	–	3.78	<0.0286	2, 58

^a Logs were painted (white, black or unpainted) and oriented (horizontal or vertical) to evaluate effects on *Ips* and predator insect behavior during three seasons in Louisiana. Season × color × orientation was NS in every case.

^b Arrival evaluated for spring and fall only.

^c Overall ANOVA model significant ($P < 0.05$) for all insects.

^d $P > 0.20$ and removed from model (pooled to error).

significant effect on total catch of all species occurring in sufficient numbers for valid ANOVA. The prey, *Ips* engraver beetles, were significantly affected by log color. White logs (mean = 13.8; least squares means) caught significantly fewer (~48%) *Ips* than black logs (mean = 26.5; $P < 0.003$). Unpainted logs (mean = 20.3) did not differ in catch from either white ($P < 0.11$) or black ($P < 0.33$). Catch of *Ips* was unaffected by log orientation (Table 2).

The total number of *M. bistrriata* caught was significantly affected by color and orientation. In addition, the interactions of season × orientation and season × color (Table 2) were significant. Compared to the other significant effects in the model, season × color was the weakest, suggesting that the effect of color was relatively consistent across seasons (Table 2). White logs (mean = 80.6) caught 56% fewer *M. bistrriata* than black (mean = 181.5; $P < 0.0001$) and 50% fewer than unpainted (mean = 159.8; $P < 0.0001$). Unpainted and black logs did not differ ($P = 0.34$). In contrast, response by *M. bistrriata* to log orientation was dramatically affected by season. In fall, there was a strong preference for vertical logs (mean = 118.0) compared to horizontal (mean = 40.3). This preference was weak during summer (vertical mean = 115.6, horizontal mean = 113.2) and switched, though weakly, during spring (vertical mean = 292.4, horizontal mean = 300.3).

Catch of *Platysoma* was significantly affected by color but not orientation (Table 2). White logs (mean = 1.28) again caught the fewest number, catch-

ing about 62% fewer *Platysoma* than black (mean = 3.38) and 65% fewer than unpainted (mean = 3.69; $P < 0.0001$). Black and unpainted logs did not differ in catch of *Platysoma* ($P = 0.89$). Nor did any of the interactions significantly affect catch of *Platysoma* ($P > 0.20$) either.

Unlike the other insects, *Lonchea* spp. were strongly influenced by orientation but not color (Table 2). Horizontal logs (mean = 12.98) caught about 3.4 times the number of *Lonchea* caught in vertical logs (mean = 3.86; $P < 0.0001$). Interactions among treatments also affected *Lonchea* catch: season × color, season × orientation, and color × orientation each explained a significant amount of variation in the ANOVA model. Further examination of the interaction terms shows that their significance is caused primarily by high catches on horizontal traps during the summer (Table 2).

The number of *T. dubius* and anthocorids arriving at logs was recorded (Table 1), but numbers were too low for analysis. In the southeast, *T. dubius* is only weakly attracted to *Ips* aggregation semiochemicals (Billings and Cameron, 1984; Billings, 1985). A total of 61 individual *T. dubius* were caught in 27 experimental units, leaving 45 experimental units (62.5%) with zero catches. Anthocorids were similarly distributed across 48 traps (they were evaluated during the spring and fall only): a total of 53 were caught at 19 logs, while 29 logs (60%) were blank.

Emergence of insects from logs was evaluated in summer and spring (Table 3). As with arrival, insects

Table 3
Emergence from loblolly pine logs in Louisiana (mean insects per log \pm S.E./m²)

Color	Orientation	<i>Ips</i> spp. ^a	<i>M. bistrriata</i>	<i>Platysoma</i> ^b spp.	<i>Lonchea</i> spp.	<i>Anthocoridae</i> ^c	<i>T. dubius</i>	<i>T. virescens</i>
Unpainted	Horizontal	236.4 \pm 110.9	28.7 \pm 3.7	14.0 \pm 3.3	195.5 \pm 31.3	0.5 \pm 0.5	0.5 \pm 0.3	3.4 \pm 1.1
Unpainted	Vertical	238.2 \pm 122.3	22.0 \pm 4.6	22.2 \pm 6.7	143.2 \pm 46.8	5.0 \pm 4.5	0.4 \pm 0.4	5.8 \pm 2.8
Black	Horizontal	168.5 \pm 42.5	21.8 \pm 3.9	16.2 \pm 4.5	162.2 \pm 28.3	4.4 \pm 3.3	0.2 \pm 0.2	9.7 \pm 2.7
Black	Vertical	224.6 \pm 79.4	15.9 \pm 5.6	9.9 \pm 1.2	97.1 \pm 21.7	2.1 \pm 2.1	6.3 \pm 1.8	14.4 \pm 4.0
White	Horizontal	314.9 \pm 108.2	12.3 \pm 3.6	1.7 \pm 1.2	152.5 \pm 56.0	1.3 \pm 1.3	1.7 \pm 1.1	2.7 \pm 1.0
White	Vertical	324.5 \pm 101.2	13.9 \pm 4.6	5.5 \pm 2.5	123.4 \pm 33.1	0.0 \pm 0.0	0.3 \pm 0.3	6.7 \pm 4.3

^a *Ips* spp. = *Ips avulsus*, *I. calligraphus* and *I. Grandicollis*.

^b *Platysoma* (= *Cylistix*) *attenuata*, *P. cylindrica* and *P. parallelum*.

^c *L. elongatus* and *S. mississippiensis*.

whose total numbers were too sporadic to yield reliable analyses were reported but not subjected to ANOVA. An additional species, *T. virescens*, emerged from logs in sufficient numbers to be included in evaluations. The overall ANOVA model (same as for arrival data) did not explain a significant amount of the variance for *M. bistrriata* and *Lonchea*, so individual treatment terms were not evaluated for these insects. As with arrival, season significantly affected emergence of *Ips*, *Platysoma*, and *T. virescens* being the largest effect in each case (Table 4). Effects with color were in all cases the next largest: color for *Platysoma*, and *T. virescens*, and season \times color for *Ips* (Table 4). Despite their lower landing numbers on white logs, significantly more *Ips* emerged from white logs (mean = 312.0) than from black (mean = 191.3) or unpainted (mean = 178.5). Black and unpainted did not differ significantly (Table 4).

Significantly fewer *Platysoma* emerged from white logs (mean = 2.64) than from black (mean = 14.3;

$P < 0.0001$) or unpainted (mean = 18.4; $P < 0.0001$), which did not differ ($P = 0.46$). Emergence of *T. virescens* was also significantly affected by log color. Black logs (mean = 13.08) produced significantly more *T. virescens* than did unpainted (mean = 4.74; $P < 0.0003$) or white (mean = 3.65; $P < 0.0001$), which were the same ($P = 0.69$). In addition, *T. virescens* was the only insect for which log orientation significantly affected emergence (Table 4). Vertical logs (mean = 8.4) produced about 1.7 times the number of emerging *T. virescens* than horizontal (mean = 5.0; $P < 0.02$). Two interaction terms (season \times color (*Ips* spp.) and season \times orientation (*T. virescens*)) significantly affected the number of insects emerging from logs (Table 4).

Non-parametric correlation analyses were used to evaluate monotonic relationships between combinations of arriving and emerging insects in the spring (those data for which we had particular experimental units labeled) (Table 5). A total of 13 correlations were

Table 4

Analysis of variance results from the total number of insects emerging from logs (per square meter) with different visual treatments in two seasons in Louisiana

Effect ^{a,b}	Insect group								
	<i>Ips</i>			<i>Platysoma</i>			<i>T. virescens</i>		
	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.
Season	242.11	<0.0001	1, 29	22.86	<0.0001	1, 31	49.78	<0.0001	1, 30
Color	10.95	<0.0003	2, 29	22.37	<0.0001	2, 31	15.95	<0.0001	2, 30
Orientation	0.05	<0.82	1, 29	0.95	<0.34	1, 31	5.72	<0.023	1, 30
Season \times color	14.04	<0.0001	2, 29	NS	>0.20	–	NS	>0.20	–
Season \times orientation	NS ^c	>0.20	–	NS	>0.20	–	4.48	<0.043	1, 30

^a Overall ANOVA model not significant ($P < 0.05$) for *M. bistrriata* and *Lonchea*.

^b Season \times color \times orientation and color \times orientation were not significant ($P < 0.20$) in every case.

^c $P > 0.20$ and removed from model (pooled to error).

Table 5

Non-parametric correlations (Kendall's Tau) between insects arriving and emerging across visual treatments during the spring in Louisiana (A: arriving; E: emerging)

Insect group	Insect group	Correlation (<i>T</i>)	<i>P</i>
<i>Ips</i> spp. (A)	<i>Platysoma</i> spp. (A)	0.39	0.009
<i>Ips</i> spp. (A)	<i>M. bistriata</i> (A)	0.42	0.005
<i>Ips</i> spp. (A)	<i>Lonchea</i> spp. (A)	-0.09	0.53
<i>Ips</i> spp. (A)	<i>T. dubius</i> (A)	0.33	0.041
<i>Ips</i> spp. (E)	<i>Platysoma</i> spp. (E)	-0.45	0.002*
<i>Ips</i> spp. (E)	<i>M. bistriata</i> (E)	-0.06	0.69
<i>Ips</i> spp. (E)	<i>Lonchea</i> spp. (E)	-0.13	0.37
<i>Ips</i> spp. (E)	<i>T. dubius</i> (E)	-0.01	0.93
<i>Ips</i> spp. (A)	<i>Ips</i> spp. (E)	0.0	1.00
<i>Platysoma</i> spp. (A)	<i>Platysoma</i> spp. (E)	0.31	0.04
<i>M. bistriata</i> (A)	<i>M. bistriata</i> (E)	0.37	0.011
<i>Lonchea</i> spp. (A)	<i>Lonchea</i> spp. (E)	0.09	0.57
<i>T. dubius</i> (A)	<i>T. dubius</i> (E)	0.15	0.38

* $P < 0.05$ after Dunn-Sidak adjustment for 13 comparisons (adjusted critical value of P is 0.004).

done (Table 5), giving a corrected critical P -value of 0.004 (Dunn and Sidak correction, Sokal and Rohlf, 1995). Under these conditions, only one correlation was significant, that of *Ips* and *Platysoma* emerging ($T = -0.45$; $P < 0.002$). Two marginally significant correlations were also of interest: the number of *Ips* and *Platysoma* arriving ($T = 0.39$; $P < 0.009$), and *Ips* and *M. bistriata* arriving ($T = 0.42$; $P < 0.005$). Thus, there is some evidence that the number of arriving *Platysoma* and *M. bistriata* are positively related to the number of *Ips* arriving, and that the number of *Platysoma* emerging is negatively correlated with the number of emerging *Ips*.

4. Discussion

Prokopy and Owens (1978) propose that visual specialization to host plant appearance may make insects susceptible to visual disruptants. In the southeastern United States, *Ips* bark beetles reproduce predominantly in trees with reduced resistance, including recently felled or storm damaged trees. This pattern of host use implies that *Ips* may be relatively unspecialized with regard to visual form because they exploit both vertical and horizontal host material. In this experiment, unnatural (white) silhouettes reduced

Ips arrival by 32–48%. While significant, this is considerably less than the effect observed in the sympatric *D. frontalis* (68–78%, Strom et al., 1999), a species that strongly prefers standing (dark, vertically oriented) trees. The visual generality of *Ips*, along with their being less affected by silhouette colors (compared to *Dendroctonus*), supports the idea that their natural visual behavior may affect their susceptibility to visual disruption.

Many bark beetle predators feed on various prey species in the same host tree. For non-semiochemical cues, this polyphagous habit seems less appropriate because habitats used by prey can vary significantly in abiotic cues, e.g., ambient light (Endler, 1993) or host color (Prokopy and Owens, 1983). In this search for appropriate prey, many natural enemies may, of necessity, use the same environmental cues used by their prey for host selection. In the southeastern US, it appears that visual cues differentially affect *Ips* spp. and associated insects. For example, *T. dubius*, a predator highly attracted to *D. frontalis* semiochemicals and weakly attracted to those produced by *Ips* spp. (Billings and Cameron, 1984; Billings, 1985) appears to be consistently affected by visual treatments. White silhouettes caught about 85% fewer *T. dubius* when *D. frontalis* semiochemicals were eluted (Strom et al., 1999) and 73% fewer when *Ips* colonization produced the attractant (this study). These results suggest that the response of *T. dubius* to visual stimuli is consistent across olfactory stimuli. This makes them considerably more visually sensitive than their *Ips* prey; such responsiveness being similar to that of *D. frontalis*, a prey with which they are more closely associated.

Platysoma also appear to be more responsive to silhouette color than *Ips*. Because we did not separate *Platysoma* to species, our ability to elucidate behavioral responses is limited, and their prey generality is uncertain. They are consistently associated with *Ips* spp. (Overgaard, 1968; Erbilgin and Raffa, 2001), and are known to prey on *Dendroctonus* as well (Moore, 1972; Taylor et al., 1992). Unlike *T. dubius*, their comparatively small size implies that their distribution need not necessarily be limited to tree boles. We would therefore predict them to be less visually responsive than *T. dubius*, and the result that they were not affected by orientation was expected; however, that their response to visual treatments was similar to *T.*

dubius was somewhat surprising. One possible explanation is that our pooling to genus masked differences in the behavior of individual species; at least three *Platysoma* species are commonly associated with bark beetles in the southeast (Moser et al., 1971).

Within the Diptera, there were significant behavioral differences between the species we observed. *M. bistrriata*, by far our most common species, responded strongly to color treatments. *M. bistrriata* is consistently associated with *D. frontalis* and *Ips* spp., often in high numbers (Williamson, 1971; Moser et al., 1971; Camors and Payne, 1973; Dixon and Payne, 1979). The response to orientation also was significant and varied by season. *Lonchea* spp. are considered predators of *Ips* (Reid, 1957) and, perhaps, ambrosia beetles (Dixon and Payne, 1979). Their arrival was unaffected by color, but they strongly preferred horizontally oriented silhouettes. *Lonchea* were the only group consistently influenced by silhouette orientation. This result suggests that *Lonchea* prefer to colonize horizontal hosts, and emergence data lend support this finding, albeit not strongly.

Use of host logs to evaluate behavior of the *Ips* assemblage provides a more natural framework for some variables than typical traps (e.g., pheromone concentration) and allows evaluation of treatment effects on the F₁ generation. A drawback to this approach, however, is that it necessarily confounds the behaviors of the primary responder (*Ips* in our case) and other members of the assemblage. That is, because *Ips* responded to color treatments, natural enemies could be responding either to *Ips* density or the visual treatments. Both *M. bistrriata* and *Platysoma* spp. were positively correlated with the number of *Ips* arriving. It is clear that visual treatments affected the relationship between members of this assemblage.

Our results suggest that color treatments could be used to manipulate behaviors of predators and prey somewhat independently. This may be important for research, to evaluate relationships at a range of densities, and management, to develop treatments that reduce losses of natural enemies when bark beetles are targeted. Manipulating natural enemy densities is usually done in laboratory settings or with cages, both of which have limitations. The use of treatments that enhance behavioral differences (olfactory or visual) between prey and predators, allows more options for

research and management. For example, the numbers of arriving *Ips* and *Platysoma* were correlated positively, while their emergence was correlated negatively. This could be interpreted to indicate that histerids played a role in reducing the number of emerging *Ips*. Color (and insect vision) is a tool to evaluate and experimentally alter density-dependent biological relationships for research and pest management.

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