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Evaluating shading bias in Malaise and window-pane traps

Kathryn M. Irvine and Stephen A. Woods

Abstract: Foresters are increasingly focusing on landscape level management regimes. At the landscape level, managed acreage may differ substantially in structure and micro-climatic conditions. Trapping is a commonly used method to evaluate changes in insect communities across landscapes. Among those trapping techniques, Malaise and window-pane traps are conveniently deployed to collect large numbers of insects for relative estimates of density. However, the catch within traps may be affected by a wide range of environmental variables including trap location, height, and factors such as exposure to sunlight and temperature. Seven experiments were conducted from 1996 through 2000 to evaluate the effects of shading on trap catch of a variety of Malaise trap designs and one window-pane trap design. Overall, differences in shading effects on trap catch were detected across different traps and taxa and suggested that, in general, more insects are collected in traps that were in direct sunlight. The effect of shading varied from a reduction in trap catch of 10 % to an increase of 7%, the results depended on trap color. Diptera, Coleoptera, and Homoptera were most likely to exhibit this bias. In contrast, trap catch of the Hymenoptera was the most variable and appeared to be sensitive to factors that might interact with sun/shade conditions

Résumé: Les forestiers mettent de plus en plus l'accent sur les modes d'aménagement des paysages. À l'échelle de l'écopaysage, la surface aménagée peut différer de beaucoup sur les plans de la structure et des conditions micro-climatiques. Le piégeage est une méthode couramment utilisée pour évaluer les changements dans lesww populations d'insectes d'un écopaysage à l'autre. Parmi les techniques de piégeage employées, les pièges Malaise et les pièges à carreau de verre sont déployés à des endroits stratégiques de façon à recueillir de grandes quantités d'insectes pour en évaluer la densité relative. Cependant, les prises à l'intérieur d'un piège peuvent être influencées par toute une gamme de variables environnementales comme l'emplacement du piège, sa hauteur, et des facteurs tels l'exposition au soleil et la température. Sept expériences ont été menées de 1996 à 2000 pour évaluer les effets de l'ombre sur le nombre d'insectes capturés dans divers modèles de pièges Malaise et dans un modèle de piège à carreau de verre. Dans l'ensemble, on a noté que les différences dans l'ombrage se répercutaient sur le nombre d'insectes capturés dans les divers pièges et sur les divers taxons, ce qui laisse à penser qu'en général, un plus grand nombre d'insectes a été capturé dans les pièges qui étaient directement exposés au soleil. Les effets de l'ombrage ont varié, et on a noté une réduction de 10 p. 100 à une augmentation de 7 p. 100 du nombre d'insectes capturés, les résultats dépendant de la couleur du piège. Ce biais était plus fréquent chez les diptères, les coléoptères et les homoptères. Par contre, le nombre d'hyménoptères capturés variait beaucoup, et semblait dépendre de facteurs qui pouvaient interagir avec l'ensoleillement et l'ombre.

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INTRODUCTION

Foresters have begun to acknowledge the importance of managing forests to maintain biodiversity in conjunction with tree production and yield. One important component of biological diversity is the Class Insecta, which contains roughly 75% of all described species (Triplehorn and Johnson 2005). Because insects respond to micro-climatic conditions they are sensitive to subtle changes in the ecosystem (Kim 1993). Also, they perform important ecosystem functions (Triplehorn and Johnson 2005). Studies that focus on the impact of silvicultural practices on insect communities are needed in order to develop strategies to maintain insect diversity and abundance within industrial forests.

Unbiased sampling methods are required to assess the effects of different silvicultural practices on insect communities and insect traps provide one method for evaluating the differences between communities that are associated with the conditions within forest stands. Window-pane traps are an effective way to sample insect communities along a vertical gradient in forest stands (Su and Woods 2001) which may reduce bias associated with differing forest structure. A Malaise trap is another efficient method used to collect large quantities of flying insects with minimal effort (Townes 1962; Steyskal 1981). While these traps might also be used along a vertical gradient most studies have been confined to the forest floor. In any case, legitimate comparisons between forest stands can only be obtained if these traps are not biased by the environmental conditions within a forest stand.

One environmental condition that differs across forest stands of different ages and management regimes is sunlight. For example, recent clearcuts (<5 years post-harvest) have little overstory vegetation, leading to higher levels of sunlight near the ground in comparison with older clearcuts (>10 years post-harvest) and mature stands. Several studies have found a greater number of species caught in Malaise traps that were deployed in stands with more open canopies (Greatorex-Davies and Sparks 1994; Lewis and Whitfield 1999; Ohsawa 2004). However the results of these studies were confounded with other differences that were associated with the different sites (e.g., height and stratification of the communities). Other authors have also provided anecdotal evidence of Malaise trap catch being higher in openings or areas with minimal surrounding vegetation (Townes 1972; Darling and Packer 1988; Hutcheson 1990). Conversely, Steinbauer et al. (2006) found that parasitoid wasps were in greater abundance in plantations that also had somewhat greater structural complexity compared to unplanted clearcuts.

A variety of studies in the literature report the efficiency of Malaise and other traps in relation to trap color (Townes 1972; Matthews and Matthews 1983; Darling and Packer 1988). Results indicate that color affects trap catch and that different taxa exhibit different color preferences (Kennedy et al. 1961; Southwood and Henderson 2000). Thus, trap color can be altered to attract certain insect groups such as Diptera (Roberts 1970; Pickens 1990), Hymenoptera (Hollingsworth et al. 1970), and Thysanoptera (Vernon and Gillespie 1990). Although we explored traps with different color combinations, the major focus of this study was to investigate the effects of shading on trap catch for a variety of insect traps in an attempt to identify a trap that would be unbiased in comparisons of forest stands with and without the shaded condition imposed by an overstory. We conducted a series of experiments from 1996 through 2000 to evaluate the effect of artificially created shade on insect trap catch in clearcuts using Malaise and window-pane traps.

MATERIALS AND METHODS

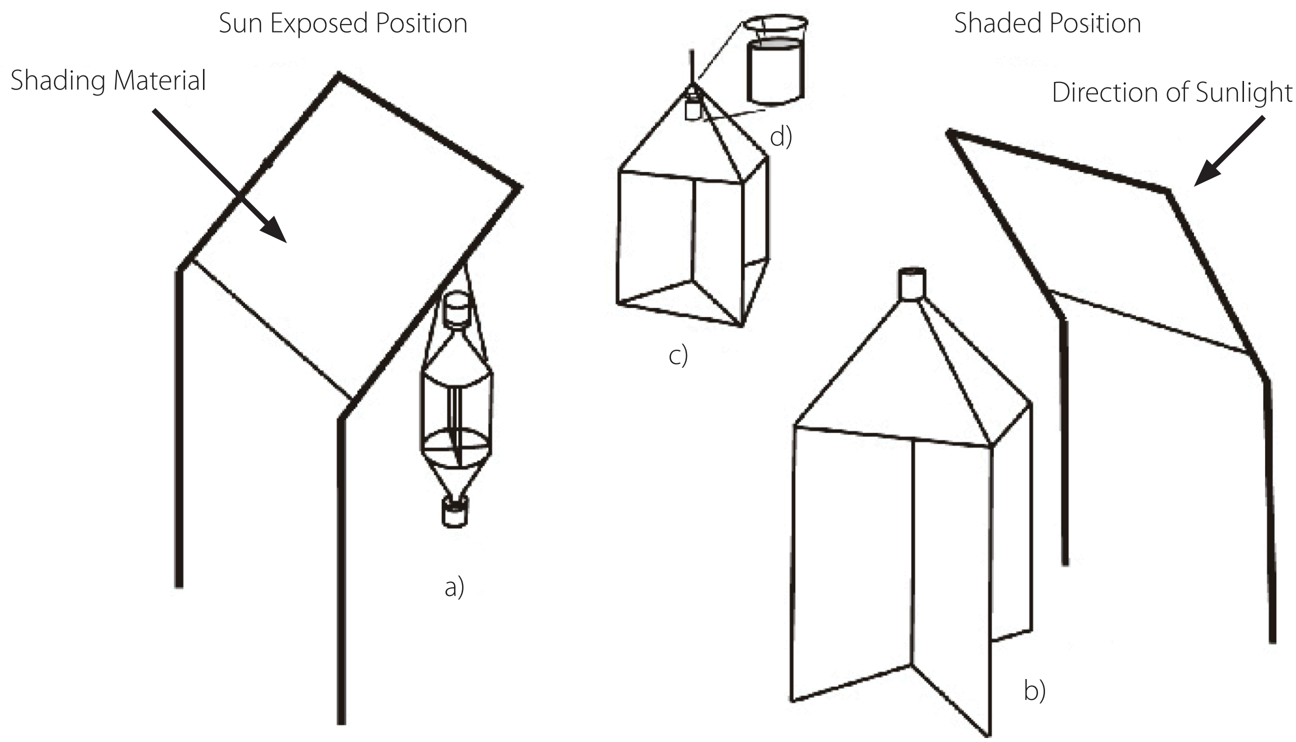
Experimental design

During each of the experiments, traps were deployed in a single previously clearcut stand each year. Artificial shade was created using frames that were constructed of electrical conduit (EMT) that was ca. 2 m high and 1.2 m across with the top portion bent at ca. 48° (Fig. 1). A fabric panel was stretched across the angled portion of the frame, with the bottom 1.2 m above the ground. The frames slid over metal bars that were sunk into the ground 15–20 cm and the frames were secured with three lines staked into the ground. The same shading technique was used throughout the five-year study.

Experiments were initially conducted in a 13.5-ha clearcut located in the Penobscot Experimental Forest in Bradley, ME (N44°52', W68°38'). The stand, harvested in December 1988, had regenerating balsam fir (*Abies balsamea* (L.) Mill), red maple (*Acer rubrum* L.), and gray birch (*Betula populifolia* Marsh.) that was 3–5 m tall. During the summer of 2000, the experiments were conducted in a different clearcut (2.4 ha) that had been harvested in the winter of 1994–1995 and received a ground application of herbicide in the summer of 1997 to reduce competition with spruce. The regeneration was composed of hardwoods similar to those described for the previous site as well as planted black spruce (*Picea mariana* (Mill.) BSP.) trees that were less than 2–3 meters tall.

Twelve traps were deployed in each experiment and half of the traps were shaded each week. A shaded trap had the frame on the south side of the trap; whereas, the

Fig. 1. Diagram of a window-pane trap deployed in the sun-exposed position (a); a traditional Malaise trap deployed in a shaded position (b); a smaller Malaise-type trap (c) that was hung from the shade frame in a manner comparable to the window-pane traps; and the collecting cup (d) used for the smaller Malaise traps.



exposed trap had the frame on the north side. The shade frames were switched to the alternate position every other week to minimize the influence of individual locations on the results. Individual trap locations were located within ca. 50 m of each other. Frame construction and placement were designed to maximize shading effects when the sun was at its apex. In 1996, the fabric panel was initially composed of a white muslin cloth but was changed to a green nursery cloth, which allowed 40% of total sunlight penetration, for the remaining experiments.

During the summer of 2000, two different shading materials were used with the window-pane traps (Table 1) to evaluate the effect of shade type. We suspected that the lack of shade effect observed in previous years (1995 and 1996, not reported here) may have been an artifact of the type of shading material.

Samples were collected each week when the shading frame was switched to the alternate position. Insect samples were identified to the Order level, with the exception of 1996 and 1997 when the Hymenoptera were further determined to the Family Formicidae (ants), the Superfamily Apoidea (bees), or other members of the Suborder Apocrita (wasps).

During the five-year study, three different trap types were investigated: small aerial Malaise traps (Fig. 1c) and plexiglass window-pane traps (Fig. 1a) that were suspended from the shading frame, as well as traditional Malaise traps that were erected on the ground (Fig. 1b). Because we were interested in assessing whether or not different color combinations of the collecting hood and intercept panels of the Malaise traps altered shading effects on trap catch, we used a number of different fabric colors. The specifics of the experimental design are provided in Table 1.

Aerial Malaise traps

The small aerial Malaise traps (Fig. 1c) were constructed with three color combinations of nylon mesh. Traps were either all black (black/black), all white (white/white), or black intercept panels with a white collecting hood (black/white). Two horizontal dowel rods threaded through the top of the intercept panels were crossed in the middle for support. The collecting hood was placed over the intercept panels and secured to the dowel rod ends with

Table 1. Summary by year of the types of traps and shade cover used for each experiment.

Experiment	Year	Sample dates	Trap design	Color	Shade type
1	1996	1 - 26 Aug 27 Aug - 23 Sept	aerial Malaise	black/black (4) black/white (4) white/white (4)	white muslin nursery cloth
2	1997	7 Aug - 9 Oct	aerial Malaise window-pane	black/black (3) black/white (3) white/white (3) clear/white (3)	nursery cloth
3	1998	28 Aug - 17 Oct	Malaise	clear/white (8) green/white (4)	nursery cloth
4	1999	13 July - 10 Aug	Malaise	clear/white (8) green/white (4)	nursery cloth
5		10 Aug - 9 Sept	Malaise	clear/clear (8) green/white (4)	nursery cloth
6	2000	14 June - 24 July	window-pane	clear/white (6) clear/white (6)	white muslin nursery cloth
7		3 Aug - 13 Sept	Malaise	clear/clear (8) green/white (4)	nursery cloth

Note: The number of traps used for each color is in parenthesis. For the Color column: the intercept panel color is listed first and the collecting hood color is listed second

thumbtacks. The intercept panels were 61 cm x 61 cm with a 4-sided pyramid shaped collecting hood on top. A collecting cup was suspended 2.5 cm below a circular (7.6 cm dia) piece of clear plexiglass located at the top of the pyramid. In this way, insects flying to the top of the collecting hood would hit the piece of plexiglass and fall into the collection cup that contained 30 ml of propylene glycol. To keep the panels perpendicular, a 60 cm x 60 cm floor was attached at the base of the intercept panels.

Traditional Malaise traps

The more traditional Malaise trap design was erected from the ground (Fig. 1b). The lower panels were 96 cm x 91 cm. Two types of material, green mesh and clear plastic, were used for the lower intercept panels. The upper collecting hoods were either white mesh or clear plastic (Table 1). A 1.6-m EMT center pole was sunk into the ground 5–10 cm and guy lines from the four corners secured the trap in place. An inverted large-mouth soda bottle was used to collect insects that flew upwards. A small piece of Vapona (2,2-Dichlorovinyl dimethyl phosphate) was placed in the soda bottle to kill the specimens. In 1999 and 2000, the Malaise trap design with clear plastic lower and upper panels was modified such that the collecting head contained a propylene glycol solution that killed the insects.

Window-pane traps

Plexiglass window-pane traps were constructed by intersecting two 23 cm x 30 cm plexiglass panels so they created a '+' shape when viewed from above (Fig. 1a). A 20-cm diameter white translucent funnel was attached at the bottom and top of the panels. A clear plastic specimen cup was affixed to the narrow part of the funnel. Insects that flew into the panels either dropped or continued upwards. They were collected in the cups and were killed with Vapona.

Table 2. General Linear Model (Proc GLM, SAS Institute 1996) used for total insect abundance

Factor	Error term
Trap Type	Position (Trap Type)
Treatment (sun vs. shade)	Treatment * Position (Trap Type)
Treatment * Trap Type	Treatment * Position (Trap Type)
Treatment * Taxa	Treatment * Taxa * Position (Trap Type)
Trap Type * Taxa	Taxa * Position (Trap Type)

Note: A similar model was used, minus the Treatment*Taxa and Trap Type*Taxa factors, to analyze treatment and trap type differences within each taxonomic group.

Data analyses

For all years, insect counts were log transformed to meet the model assumptions of normality and constant variance. For each year, an overall General Linear Model (Proc GLM, SAS Institute 1996) was run with pooled data across all taxa (total insect abundance, (Table 2). If there was a significant interaction between treatment and trap type (F-test, $P < 0.05$), then linear contrasts were used to evaluate the shading effect for each trap separately. In 2000, linear contrasts were also used to evaluate shading effects on the window-pane traps independently for each cover type.

Even if there was not a significant treatment * taxa interaction (F-test, $P > 0.05$) in the overall model, we still analyzed the effect of shading for each of the taxonomic groups. This was justified because of the known behavioral differences between taxa and the researchers' interest in specific taxa, particularly the Coleoptera and Hymenoptera. We used a similar model to that listed in Table 2 to detect whether or not there were treatment and trap effects within each taxonomic group (number of individuals per taxon). Those taxonomic groups that did not meet the model assumptions of normality or constant variance were not included.

RESULTS

Over the five-year study each trap design and color combination was tested at least twice with the exception of the window-pane trap which was only tested once with green nursery shading material. All designs showed a shade bias during at least one experiment. The direction and magnitude of bias differed between years and trap designs, but the most consistent result was that more insects were recovered from traps in the sun compared to traps in the artificial shade. We present the results for the overall model (total insect catch) and the taxonomic groups (individuals per taxa) to illustrate patterns, even though in some cases there was not a statistically significant taxa * treatment interaction in the overall model.

Aerial Malaise traps

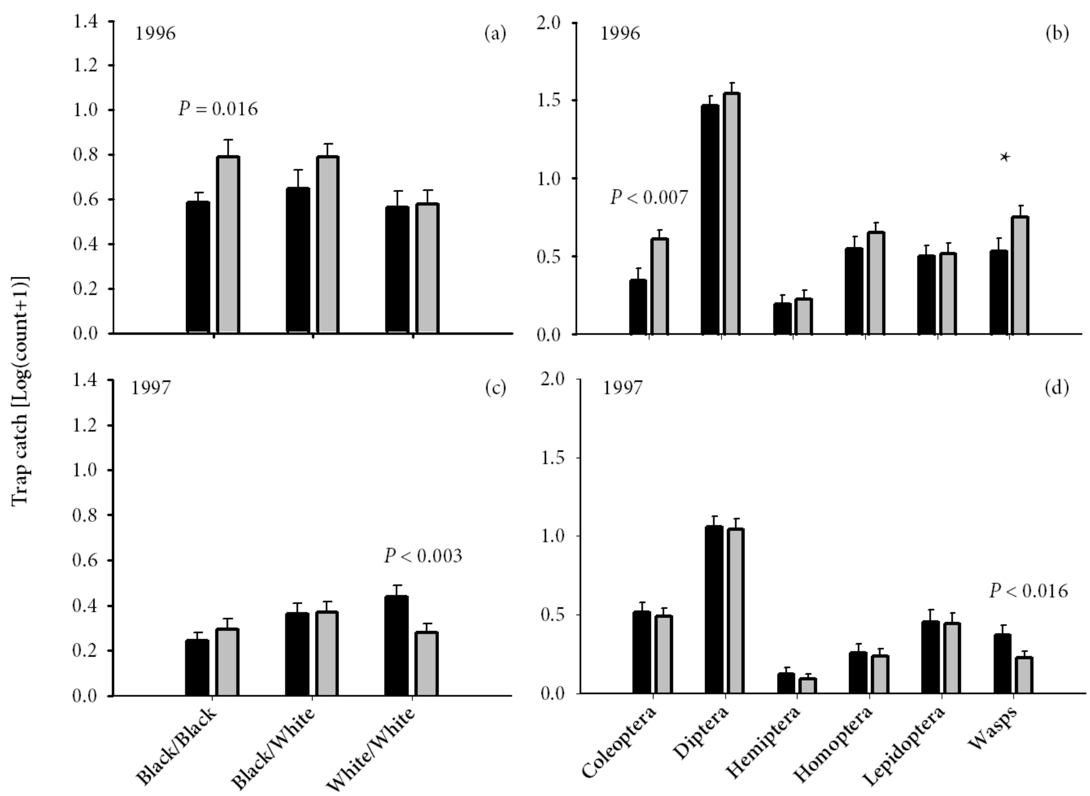
Three small aerial Malaise trap designs (white/white, black/white, and black/black) were investigated in 1996 and again in 1997. In Experiment 1, more insects (all Orders) were collected in traps in the sun than traps in the shade (Fig. 2a, $F_{1,9} = 10.79$, $P = 0.009$). The pattern was apparent for the all black and black/white designs, although the effect appears to be absent in the uniform white design. However, this result was only based on three insect sampling dates. We found no evidence for overall differences between trap designs ($F_{2,9} = 0.94$, $P = 0.429$), nor was there a trap type * shading treatment interaction ($F_{2,9} = 1.19$, $P = 0.348$). One caveat is that when trap effect was evaluated separately by taxa, more Diptera were collected in the black/black and black/white traps than the white/white traps (black/black vs white/white, $t_9 = 2.096$, $P = 0.065$; and black/white vs white/white, $t_9 = 2.37$, $P = 0.042$).

The effect of treatment (shaded vs. unshaded) on trap catch was not significantly different across the taxonomic groups (treatment * taxa interaction: $F_{5,55} = 0.695$, $P = 0.629$). However, the significant main effect was most pronounced among the Coleoptera ($F_{1,9} = 11.99$, $P = 0.007$, Fig. 2b) and possibly for Hymenoptera as well ($F_{1,9} = 3.62$, $P = 0.089$). When analyzed separately, the treatment effect was not statistically significant for the remaining Orders, although there was a consistent pattern of collecting more individuals for each taxa in the sun.

Experiment 2 in 1997 was a repeat of 1996 except that the window-pane was also included so that only three replicates of each aerial Malaise trap were deployed instead of four. There was not a significant main effect for treatment or trap type ($F_{1,6} = 2.51$, $P = 0.164$, and $F_{2,6} = 1.46$, $P = 0.305$, respectively; Fig. 2c), however there was a significant interaction between trap and treatment ($F_{2,6} = 11.14$, $P = 0.010$, Fig. 2c). Although not statistically meaningful, more insects were collected in the black/black design in the sun ($t_6 = 1.53$, $P = 0.177$) compared to those in the shade which is consistent with 1996. Trap catch for the black/white traps were virtually identical ($t_6 = 0.30$, $P = 0.772$) in 1997. Significantly fewer insects were collected in the all-white traps in the sun ($t_6 = 4.84$, $P = 0.003$) in 1997.

In the overall model, the effect of shade was consistent across the taxonomic groups (treatment * taxa interaction, $F_{9,54} = 1.48$, $P = 0.181$), although the Hymenoptera as a group were less abundant in the sun ($F_{1,6} = 11.03$ $P = 0.016$, Fig. 2d). There were no significant differences in the numbers

Fig. 2. Mean (± 1SE) number of insects collected from three Malaise trap designs located in shade (black bars) and sun (gray bars) in 1996 (a) and 1997 (c) and mean number of each taxon collected in shaded versus sun traps in 1996 (b) and 1997 (d). An asterisk indicates 0.05 < p < 0.10 (Linear Contrast).



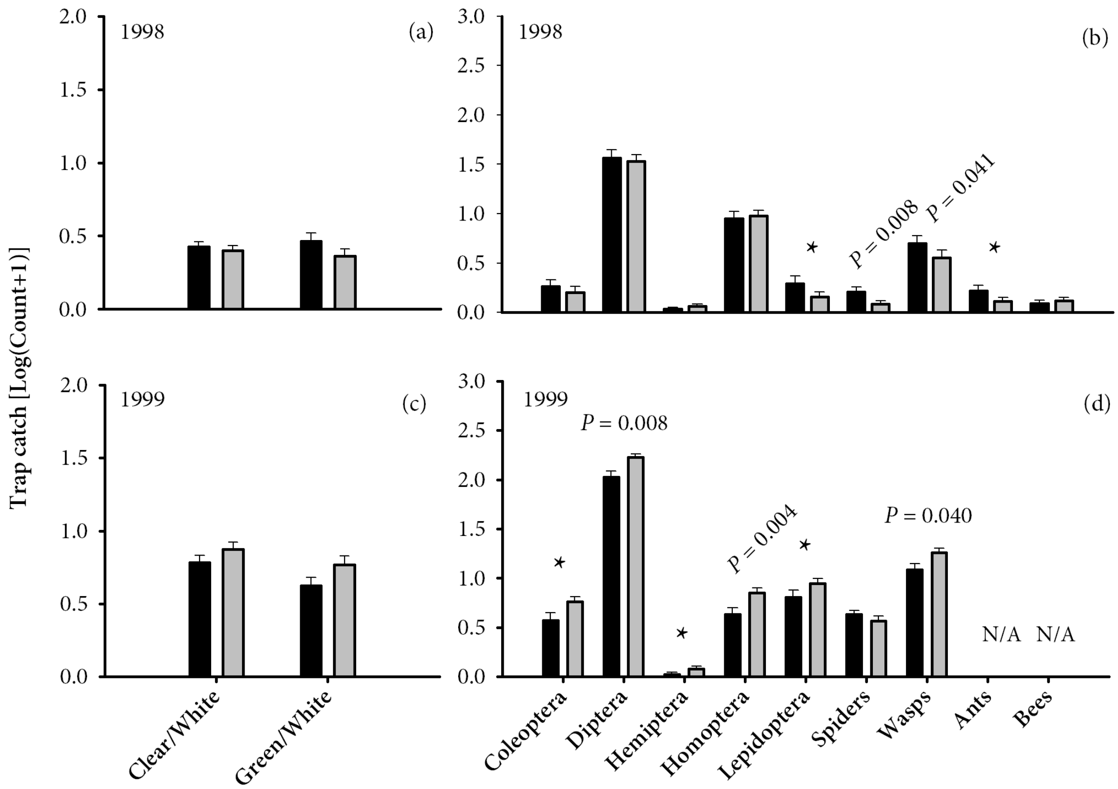
of individuals recovered for the remaining Orders (P > 0.10). Evidence for differences in catch between the three trap types at the Order level was weak at best. A trap * taxa interaction ($F_{18,54}$ = 1.72, P = 0.064) suggested possible differences that might have been attributed to the Diptera which could have a slightly greater propensity for black/white traps ($F_{2,6}$ = 4.47, P = 0.065) and the Hymenoptera for white/white traps ($F_{2,6}$ = 3.74, P = 0.088). For both taxa, the fewest numbers were collected in the black/black traps.

Traditional Malaise traps

The larger clear/white and green/white Malaise trap designs were deployed at ground level in 1998 (Experiment 3) and again in 1999 (Experiment 4). In 1998, we found no statistical evidence for a shading effect or trap type effect in the overall analysis either as a main effect ($F_{1,10}$ = 2.42, P = 0.151 and $F_{1,10}$ = 0.04, P = 0.836, Fig. 3a), or a trap design * treatment interaction ($F_{1,10}$ = 0.84, P = 0.381). However, there was a significant taxa * treatment interaction in the overall model ($F_{9,99}$ = 2.70, P = 0.007) suggesting the effect of shade on trap catch was not consistent across the taxonomic groups.

When taxa were analyzed individually, significantly fewer spiders ($F_{1,10}$ = 10.97, P = 0.008) and wasps ($F_{1,10}$ = 5.50, P = 0.041) were captured in traps in the sun compared to those in the shade. There was also suggestive, but inconclusive evidence that fewer Lepidoptera ($F_{1,10}$ = 4.40, P = 0.062) and ants ($F_{1,10}$ = 4.91, P = 0.051) were collected in traps in the sun, whereas the remaining taxa clearly did not display significant treatment differences (P > 0.10, Fig. 3b). Thus, a shade bias was only detectable at the Order level with some Orders having higher numbers in the shade and others not. One note of interest was that there was a significant interaction between trap type and shade effect for bees ($F_{1,10}$ = 6.81, P = 0.026) with more bees recovered in the clear/white traps in the sun (t_4 = 2.84, P = 0.047) compared to the green/white traps in the sun.

Fig. 3. Mean (± 1SE) number of insects collected from two Malaise trap designs located in shade (black bars) and sun (gray bars) in 1998 (a) and 1999 (c) and mean number of each taxon collected in shaded versus sun traps in 1998 (b) and 1999 (d). An asterisk indicates $0.05 < P < 0.10$ (Linear Contrast).



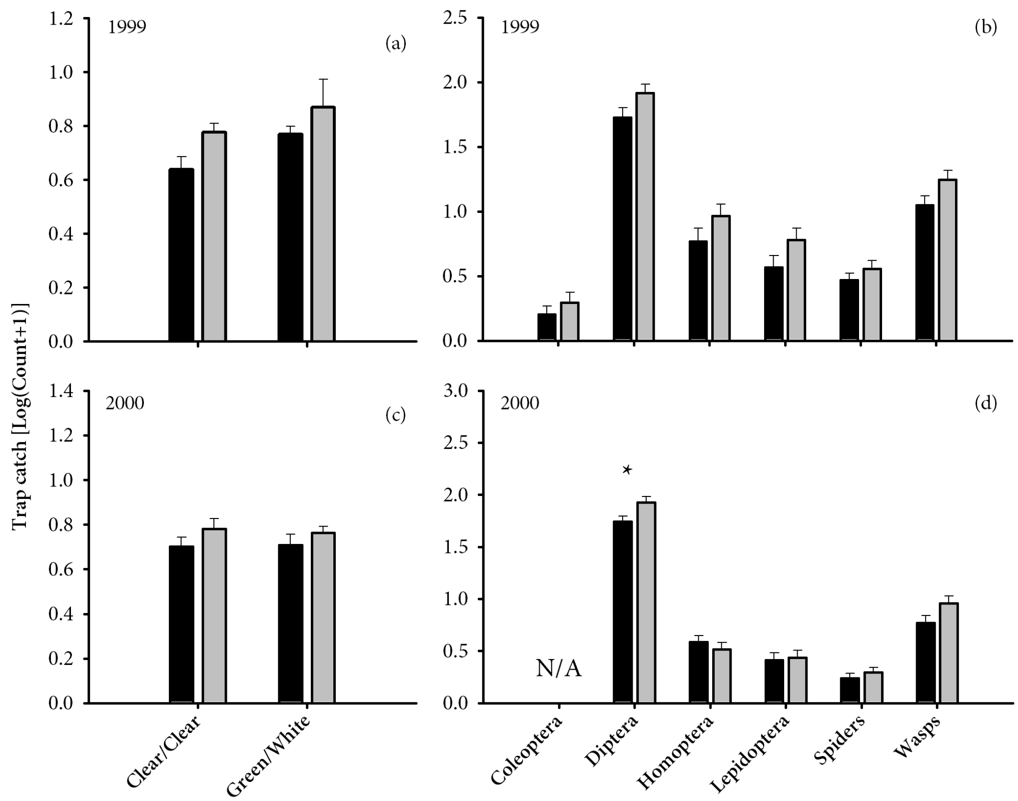
In Experiment 4 (1999, using the same traps as Experiment 3), more insects were captured with both trap color combinations in the sun compared to those in the shade (treatment main effect, $F_{1,10} = 7.64$, $P = 0.020$). Also, more insects were caught in the clear/white traps (trap type main effect, $F_{1,10} = 7.82$, $P = 0.019$). There was not a significant treatment * trap design interaction ($F_{1,10} = 0.16$, $P = 0.698$, Figure 3c).

There was, however, a significant interaction between treatment and taxa ($F_{9,99} = 2.42$, $P = 0.016$). Consistent with the overall model, significantly more Diptera ($F_{1,10} = 10.87$, $P = 0.008$), Homoptera ($F_{1,10} = 13.53$, $P = 0.004$), and Apocrita ($F_{1,10} = 5.57$, $P = 0.040$) were recovered from traps in the sun compared to those in the shade (Fig. 3d). There was also suggestive, but inconclusive evidence that more Coleoptera ($F_{1,10} = 3.34$, $P = 0.098$), Hemiptera ($F_{1,10} = 3.53$, $P = 0.090$), and Lepidoptera ($F_{1,10} = 3.75$, $P = 0.082$) were captured in traps in the sun as well. The spiders were the only group that were clearly without a significant treatment bias ($F_{1,10} = 1.53$, $P = 0.244$; Fig. 3d). When analyzed at the Order level, the higher numbers of insects trapped in clear/white traps was most pronounced among the Coleoptera ($F_{1,10} = 23.25$, $P < 0.0001$) and possibly the Apocrita ($F_{1,10} = 3.63$, $P = 0.086$) as differences in the other taxa were not significant ($P > 0.10$).

In Experiments 5 and 6, clear/clear and green/white traps were deployed. Results from Experiment 5 (1999) suggest the possibility that more insects (Fig. 4a; treatment main effect, $F_{1,10} = 3.52$, $P = 0.090$; treatment * trap design interaction, $F_{1,10} = 0.15$, $P = 0.710$) may be captured in both traps in full sunlight. However, the treatment * taxa interaction was not significant ($F_{9,99} = 1.35$, $P = 0.221$; Fig. 4b) and none of the orders proved significant when analyzed separately ($P > 0.10$). It may be of interest to note however, that all taxa had means that were higher for traps in the sun.

There was no evidence for an overall difference between traps (trap main effect, $F_{1,10} = 2.02$, $P = 0.186$), although there was a significant trap * taxa interaction ($F_{9,90} = 6.11$, $P < 0.001$). Homoptera ($F_{1,10} = 12.83$, $P = 0.005$), Lepidoptera ($F_{1,10} = 8.32$, $P = .016$), and spiders ($F_{1,10} = 9.15$, $P = 0.013$) were more abundant in green/white traps whereas the wasps were more abundant in the clear/clear traps ($F_{1,10} = 4.04$, $P = 0.072$). Diptera and Coleoptera did not vary with trap type

Fig. 4. Mean (± 1SE) number of insects collected from two Malaise trap designs located in shade (black bars) and sun (gray bars) in 1999 (a) and 2000 (c) and mean number of each taxon collected in shaded versus sun traps in 1999 (b) and 2000 (d). An asterisk indicates 0.05 < P < 0.10 (Linear Contrast).



(P > 0.10) but the means were consistent with non-wasps.

In Experiment 6 (2000), there was stronger evidence that more insects were collected in traps in the sun than those in the shade for both the clear/clear and green/white traps (treatment main effect, $F_{1,10} = 11.22$, $P = 0.007$; treatment * trap design interaction, $F_{1,10} = 1.01$, $P = 0.339$, Fig. 4c).

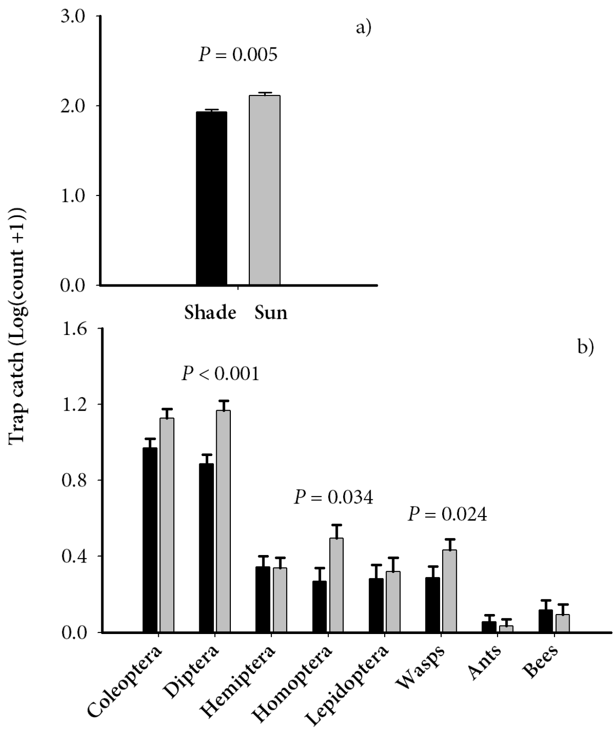
In general, the effect of shade on trap catch was consistent across the taxonomic groups (treatment * taxa interaction $F_{9,99} = 1.51$, $P = 0.155$; Fig. 4d). The effect appeared to be most pronounced for the Diptera ($F_{1,10} = 4.34$, $P = 0.064$) and to a lesser degree the wasps ($F_{1,10} = 3.00$, $P = 0.114$). Within the Lepidoptera, a treatment * trap interaction was detected ($F_{1,10} = 5.13$, $P = 0.047$). The clear/clear traps had a detectable shade bias ($t_{1,10} = 2.65$, $P = 0.024$) with more being recovered in the sun, whereas the green/white trap were not significant ($t_{1,10} = 1.11$, $P = 0.317$, Fig. 4d) and recovered fewer in the sun.

Once again there was no significant difference between trap types ($F_{1,10} = 0.94$, $P = 0.355$), but there was a significant trap * taxa interaction ($F_{9,90} = 5.51$, $P < 0.001$). More spiders ($F_{1,10} = 5.56$, $P = 0.040$) were collected in the green/white traps and more wasps ($F_{1,10} = 3.63$, $P = 0.086$) in the clear/clear traps, whereas the other taxa were clearly not significant ($P > 0.10$).

Window-pane traps and shade type

Experiment 7 was designed to evaluate the role of shading material on window-pane traps. There was a significant interaction between the type of shading cover and treatment ($F_{1,10} = 11.58$, $P = 0.007$) suggesting that the effect of shade on trap catch apparently depends on the type of shading material used. Shading effects were therefore evaluated separately for each shading material (white and green). A shade bias was detectable in the window-pane traps using the green nursery shading material ($t_{10} = 3.61$, $P = 0.005$), but not with the white muslin cloth ($t_{10} = 1.45$, $P = 0.178$). Because we believe the green shading material to be more like natural shading, the results are only presented

Fig. 5. Mean (± 1SE) number of insects collected from plexiglass window-pane traps located in the shade (black bars) and sun (gray bars) in 2000 (a) and mean number of each taxon collected in shaded versus sun traps in 2000 (b).



from traps under the green shading material (Fig. 5).

There was also a significant shade treatment * taxa interaction ($F_{9,90} = 2.52$, $P = 0.013$) using the green shading material. We found significantly more individuals of Diptera ($F_{1,10} = 27.60$, $P < 0.001$), Homoptera ($F_{1,10} = 5.03$, $P = 0.034$), and aculeate wasps ($F_{1,10} = 7.04$, $P = 0.024$) in the window-pane traps in the sun compared to those in the shade (Fig. 5b). There were no significant differences in the numbers of Coleoptera or Lepidoptera recovered from window-pane traps ($P > 0.10$), but the means were higher for these taxa as well.

Trap averages

When log means were converted back to count estimates and averaged across experiments for each trap, a negative shade bias was most pronounced in black/black, clear/clear and plexiglass traps which are the least apparent to the human eye and collected 9.8 to 10.0% fewer insects from the shaded traps. Approximately 5% (4.4–5.6%) fewer insects were collected in the shaded Malaise traps with white tops, with the exception of the white/white trap. Trap catches in the white/white traps actually averaged 7.6% more insects in the shaded traps.

DISCUSSION

A shading bias was observed in all but one of the seven experiments (1999, clear/clear and green/white traps) conducted over the 5-year period. The magnitude of the differences and direction of the bias varied between years and trap type. The variation may in part be due to the fact that experiments with the same traps were run on different years and different dates (Table 1). Despite this variation, on average, the shade had a negative effect on trap catch in all but the white/white traps where there appeared to be a positive shade effect. It seems possible that the trap shading might cast a shadow on the foliage of the plants to the north of the trap, decreasing the apparency of these plants and making them less attractive to insects associated with open clear-cut habitat. Alternately, the white material in some of these experiments may actually serve as an attractant, which under shaded conditions, creates greater contrast with the background. Roberts (1970) attributed differences in trap catch to differences in contrast between the background and Malaise traps. In this study, the traps with white collecting hoods may have reduced the effect of shade in comparison to those traps with no white because a greater proportion of taxa were attracted to traps with white under shaded conditions. In traps with a white intercept panel and a white collecting hood, the white actually seemed to reverse the sampling bias. The attractiveness of white material could also explain why the off-white muslin material, in previous experiments, might have negated the general bias associated with shading when using window-pane traps. If true, then the attraction to white would likely change the species composition, as well as total numbers trapped. Although the magnitude of these biases may not be large (+/- 10%), these results are contrary to the original description of the Malaise traps (Townes 1962), and possibly to the assumptions of many researchers using these traps.

The taxa that were most consistently favored in unshaded traps included the Diptera, Homoptera, and perhaps Coleoptera (Figs. 2–4). The Hymenoptera stand out as a taxon that was the most variable; possibly dependent on other conditions. In general, they displayed the same bias in favor of exposed traps but the reverse pattern was found to be significant in two experiments. Insect trap catch has been found to be affected by weather factors, such as air temperature, wind speed, vapor pressure, precipitation, and solar radiation (Nasr et al. 1984; Vogt 1986; Pitcairn et al. 1990; Horton et al. 1997; Butler et al. 1999; Briers et al. 2003). All of these factors, as well as the abundance of floral resources, can vary significantly from year to year and season to season, which may be a reason for the discrepancy in the results for the Hymenoptera.

This study did not address the potential bias associated with sampling for specific families or lower taxonomic levels with Malaise or window-pane traps and further research is clearly indicated. As was found by Ohsawa (2004, 2005), within the Coleoptera, Elaterids were associated with more open canopies whereas Curculionidae were not associated with canopy openness. Because we did not sort our samples to a lower taxonomic level, our results likely reflect biases of the more abundant species.

Several researchers have found greater abundance of species within forest stands with less shade (Greatorex-Davies and Sparks 1994; Lewis and Whitfield 1999; Ohsawa 2004). The results of our studies suggest that researchers should use caution when interpreting the results from using Malaise and window-pane traps to compare insect communities from sites with differing amounts of overstory vegetation. In this study, the effects of shading appear to reduce trap catch even when the insect communities are the same. That white might serve as an attractant further compounds data interpretation. The area from which the white material serves to draw insects is likely greater in an open environment than an environment in which vision is limited by the presence of vegetation.

In two different years, 1996 and 1997, the bicolor Malaise traps displayed minimal bias both times they were deployed. Perhaps, this design, which was the color scheme suggested in the original design by Townes (1962), is the best choice to minimize shade bias on insect trap catch. Another solution might be to use a combination of trap designs to minimize shade bias on trap catch depending on the taxa of interest. Deploying a white/white trap with one of the other Malaise trap designs at each site might well largely minimize the bias associated with either trap.

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