Prey preferences in three species of *Polistes* found in Michigan: *P. fuscatus*, *P. dominulus* and *P. metricus*.

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ABSTRACT

Many wasp species may specialize in a specific type of prey, while others have are known as caterpillar generalists. In this study, we examined the prey preferences of three Michigan, Polistes wasps, P. metricus,P. fuscatus, and P. dominulus. Soft-bodied prey was attained by sweep netting and their physical attributes were measured using the freeware program ImageJ. Wasp colonies were given pairwise choice tests between two immobilized arthropods, for two hours, three times a week. We did not find evidence that Polistes specialize on lepidopteron prey. ($p = 0.19$) We did find that the lepidopteron prey that were selected were significantly shorter ($p=0.031$) and thinner ($p= 0.041$) than those that were rejected. Futhermore, we found that P.metricus attacked significantly less often than P. dominulus and P. fuscatus. ($p= 0.028$) This could be due to P. metricus having fewer adult wasps per nest (risk reduction).

INTRODUCTION

Predators are often specialized for the exploitation of a limited number of prey species due to competitive interactions with other predators, as well as evolutionary arms races with prey species. Due to these interactions, predators often must have unique adaptations to efficiently capture and consume prey and to overcome prey defenses. However, some “generalist” predators retain the ability to utilize a wide range of prey, with varying characteristics, while other “specialist” predators utilize only a few prey species that are similar.

Wasps (Hymenoptera) are important predators of invertebrates that include both specialists and generalists. Some wasps are extreme specialists that prey only on one or a few species, such as the cicada killer, and the digger wasp, *Clypeadon laticinctus*. (Alexander, 1985)

Other groups, such as the Pompilidae, specialize on one type of prey (spiders in this case). Finally, other groups are much more generalist in their diet, attacking insects of many orders, utilizing nectar, and even scavenging from vertebrate carcasses. (Akre *et al*, 1980)

The paper wasp genus *Polistes* attacks a number of different soft-bodied prey, but appears to specialize on lepidopteron larvae (caterpillars; Prezoto *et al.* 1994, Giannotti *et al.* 1995, Rabb & Lawson, 1957; Rabb, 1960 Kasper *et al*. 2004). The *Polistes* genus contains at least 203 species, found throughout the world and in a wide diversity of ecological contexts. Polistes has also been studied extensively as a prominent model system for understanding cooperation and altruism (Reeve, 1996).

Three species of *Polistes* occur in Michigan and were included in this study. *P.* fuscatus is found throughout Michigan and is a temperate climate specialist. *P.* metricus is a larger more southern species, whose range extends north to the southern parts of Michigan. *P.* dominulus is an invasive species that was accidentally introduced into Massachusetts in the late 70's and has spread eastward to Michigan subsequently (Eickwort, 1978).

In this study, we examined the prey preferences of Polistes wasps. We tests the prey preferences of the three local species of Polistes using pair wise choice tests between immobilized prey to determine whether the three species of *Polistes* in Michigan specialized on caterpillars, versus other soft bodied prey, whether Polistes wasps preferred certain sizes of caterpillar prey, and whether certain traits such as lack of defensive hairs or certain colors were associated with attacks

METHODS

Research Sites and Colony Recruitment

We built 120 plywood nest boxes that were approximately 8 inches in each dimension. Half inch wire hardware cloth was stapled across the opening of the box in order to restrict vertebrate predation, but allowing wasps to freely move in and out of the boxes. The tops of the boxes were easily removable for nest observations. These boxes were then bolted to 6 foot long metal fence poles that were then secured in the ground.

We attempted to establish three study populations in the Lower Peninsula of Michigan. These sites included the Ed Lowe Foundation's Red Rock facility (ELF) near Cassopolis, MI, the Pierce Cedar Creek Institute (PCCI) near Hastings, MI, and sites in the Pere Marquette State Forest near Baldwin, MI (BAL). We placed 32 boxes at BAL in two groups, another 32 boxes at ELF in two groups and the remaining 56 boxes at PCCI in 4 groups. Initially all boxes were spaced approximately 10 meters apart. However, boxes at PCCI were moved closer together in order to facilitate observation of choice tests.

To increase the number of study colonies, we located additional colonies on nearby buildings and manmade structures at PCCI and attempted to relocate them into nest boxes. We captured the adult wasps with an aerial net and removed the nest from its original substrate. We then glued the nest into the empty nest box using Elmer's multipurpose glue. Finally, we enclosed the wasps in the box with their nest overnight, releasing them the next morning.

Prey Collection and Measurement

Potential prey were collected by sweep netting large sections of grassy fields. We then selected soft bodied arthropods (e.g. lepidopteran larvae, coleopteran larvae, hemipterans, orthopterans, and spiders) as possible prey items. They prey were then numbered and photographed on a uniform grid for later measurement.

Length and width measurements of the prey were made using the freeware program ImageJ (National Institutes of Health). Width was calculated by taking an average of an anterior, posterior, and a median measurement. Each arthropod was also given a piliousness score, where 1 was no-visible hairs, 2 was moderate hair, and 3 was very hairy. Predominate color of the prey was also assessed.

Prey Choice Tests

Colonies were presented with pairwise choice tests that offered two different immobilized invertebrates. The week before data were collected, mealworms were left under each nest daily in attempt to teach the colony prey location. During choice tests, the prey were pinned down on Styrofoam and placed in a single Petri dish. The Petri dish was then placed on a wire platform located 3-4 inches underneath the nest boxes. Tests were performed for 2 hours, during which, we checked nests every 10 minutes to see if either prey had been attacked and to make sure no other predators (e.g. jumping spiders, and ants) were attacking the prey. When an attack was observed, the Petri dish was removed once the wasp finished attacking. We performed tests three times a week, every other day to avoid colony satiation.

Statistical Analyses

All statistical analyses were conducted in SPSS version 14 (SPSS, Inc 2006). Comparisons based on count data were made using Chi-square tests. Means were compared with unequal variances t-tests as warranted by F-tests. We also examined these comparisons with non-parametric tests but only reported the t-tests.

RESULTS

Initially, a total of 32 wasp colonies occupied boxes at our three sites, including 22 *P. metricus* nests, 7 *P. fuscatus*, and 3 *P. dominulus*. All but one of the colonies at ELF were *P. metricus* and the other was *P. fuscatus*. All three colonies at BAL were *P. fuscatus*. The colonies at PCCI were a mixture of *P. fuscatus* and *P. dominulus* and included only one *P. metricus*. (Appendix 1) Because of the low recruitment at BAL, we removed the site from our study. In an attempt to get more colonies at PCCI, we successfully transplanted 3 additional *P. fuscatus* nests and 2 additional *P. dominulus* nests into boxes that had previously been established on nearby buildings.

We conducted a total of 213 choice trials, including 64 trials for *P. dominulus*, 74 for *P. fuscatus*, and 79 for *P. metricus*. The wasps did not attack either prey item in 178 of the trials, they attacked and consumed both items in 2 of the trials, and they only attacked one of the prey items in 33 of the trials. These 33 trials provide the best information concerning the prey preferences, though the two trials in which both prey items were attacked provide some useful information concerning which prey items were considered suitable prey. The other 178 trials provide no useful information concerning prey preferences. Successful prey choice trials occurred throughout the summer, though there did appear to be a slight increase in the number of successful trials after mid July (Figure 1).

We did not find evidence that *Polistes* preferred lepidopteran larvae to other prey. In trials in which *Polistes* were presented with the choice of either a caterpillar or something else, and in which they attacked only one item, they attacked the caterpillar twice as often as the alternative, but this was not a significant difference (Figure 2; χ^2=1.714, df=1, p=0.19). We did not have a sufficient number of trials to examine whether *Polistes* attacked different non-

lepidopteran groups at different rates, with only 1 to 6 successful observations for each of the other prey groups that we used (Figure 3).

The lepidopteran prey that *Polistes* rejected were significantly larger than the lepidopteran prey they rejected. When all trials are combined in which one of the prey items was a caterpillar, and in which at least one of the prey items was attacked, caterpillars that were rejected tended to be longer than ones that were attacked (Figure 4a; Mean length: 14.04 vs 10.16 mm; Unequal Variances t-test: t=2.305, df=21.326, p=0.031), and wider than ones that were attacked (Figure 4b; Mean width: 2.579 vs 1.813 mm; Unequal Variances t-test: t=2.106, df=18.439, p=0.049).

P. metricus attacked the prey significantly less often than the other two species (Figure 5; χ^2=7.15, df=2, p=0.028). *P. fuscatus* and *P. dominulus* attacked prey in 28% and 27.3% of trials respectively while P. metricus only attacked prey in 8.2% of trials. Such a difference could be explained by differences in the number of foragers, or the number of brood requiring food, however, there were no significant differences in colony sizes between the three species in either the number of adult wasps to forage (Figure 6a; Mean number of wasps: *dominulus*=2.4, *fuscatus*=1.7, *metricus*=1.0; χ^2=2.519, df=2, p=0.284) or the number of brood (Figure 6b; Mean number of brood: *dominulus*=3.4, *fuscatus*=4.3, *metricus*=6.1; χ^2=2.518, df=2, p=0.284).

DISCUSSION

We did not find evidence that *Polistes* specialize on lepidopteron prey. While they chose caterpillars in two-thirds of the trials, the difference was not significant given our small sample size. The larger number of attacks on caterpillars is in the predicted direction however, and a larger number of trials might produce significance. Even with the small sample size, the

relatively high percentage of attacks on non-lepidopteron prey is much higher than the rates reported in previous studies. One difference between those studies and the current one is that we immobilized prey for the prey choice test while previous studies identified prey items from free-foraging wasps. This is both a weakness and a strength of out study. It is a weakness because it probably did cause us to overestimate the wasps' preference for non-lepidopteron prey by reducing the ability of prey such as grasshoppers to effectively escape. However, it does provide insight into the reasons that Polistes specialize on caterpillars – they can't capture other items even though they find them palatable.

We also found that *Polistes* wasps preferred to attack smaller caterpillars. This may have to do with the time it takes to process larger prey. In most cases, a caterpillar is too big to take to the nest in one trip and must be cut into pieces. Prey items that are too large may be difficult to cut and may take more processing time, exposing the wasps to additional risk. It's also possible that larger caterpillars are difficult to cut into pieces that make efficient loads for carrying in flight. These are both hypotheses that need to be addressed in future studies.

Finally, we found that *Polistes metricus* attacked prey items significantly less often than the other two species. Two possible explanations for such a reduced rate of attack include responses to larval food demands and risk reduction. The first explanation is need based behavior and suggests that foraging should increase when the number of brood increases due to their increased energetic requirements. This explanation does not appear to fit our data however, because metricus had more brood per nest than either of the other two species (though the difference was not significant). The second possibility is related to risk reduction. As stated previously, foraging is risky, and wasps should reduce their foraging time when there are fewer foragers on the nest because the loss of one forager represents a greater loss to the nest. In partular, when

there is only one wasp, the loss of that forager would mean the death of the nest. We did find that *P. metricus* nests tended to have fewer foragers than *P. dominulus* or *P. fuscatus*, consistent with this idea, but again, the differences in colony size were not significant.

ACKOWLEDMENTS

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FIGURE CAPTIONS

Figure 1. The number of prey choice trials attempted each day and the number of successful trials in which one or more prey items were attacked by *Polistes*. Trials were conducted from 6/16 to 7/22, 2009.

Figure 2. The number of trials in which *Polistes* preferred either lepidopteran or non-lepidopteran prey. These data are based on trials in which one choice was a lepidopteran prey item, the other was a non-lepidopteran prey item, and only one prey item was attacked.

Figure 3. A summary of the number of times *Polistes* attacked and rejected non-lepidopteran prey. These data include all attacks on non-lepidopteran prey, regardless of what the alternative prey item was, or whether both prey items were attacked.

Figure 4. (a) The mean length (± standard error) of lepidopteran prey that were attacked and rejected by *Polistes*. (b) The mean width (± standard error) of lepidopteran prey that were attacked and rejected by *Polistes*. These data are based on trials in which a prey item was attacked and one of the prey items was a lepidopteran.

Figure 5. The number of trials in which colonies of each of the three *Polistes* species attacked at least one of the prey items or failed to attack the prey items.

Figure 6.Colony size on a representative date (July 9th) during the middle of the period when trials were conducted: (a) Number of adult wasps, (b) number of larvae and pupae.

FIGURE 1

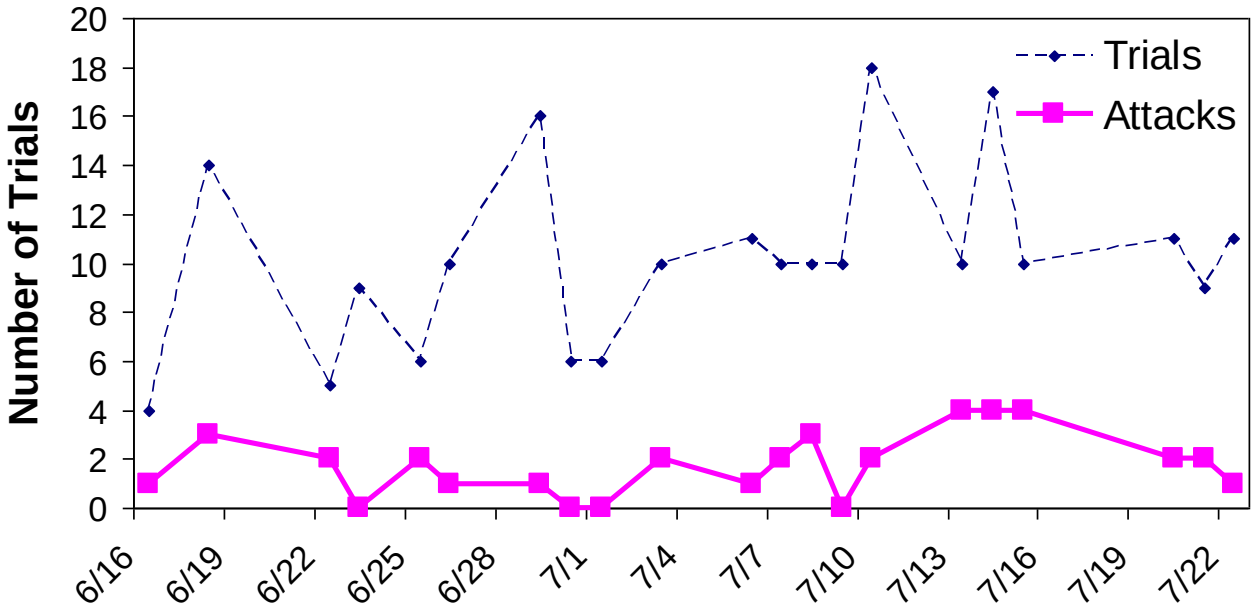

Number of Trials
20
18
16
14
12
10
8
6
4
2
0
6/16
6/19
6/22
6/25
6/28
7/1
7/4
7/7
7/10
7/13
7/16
7/19
7/22
Trials
Attacks

FIGURE 2

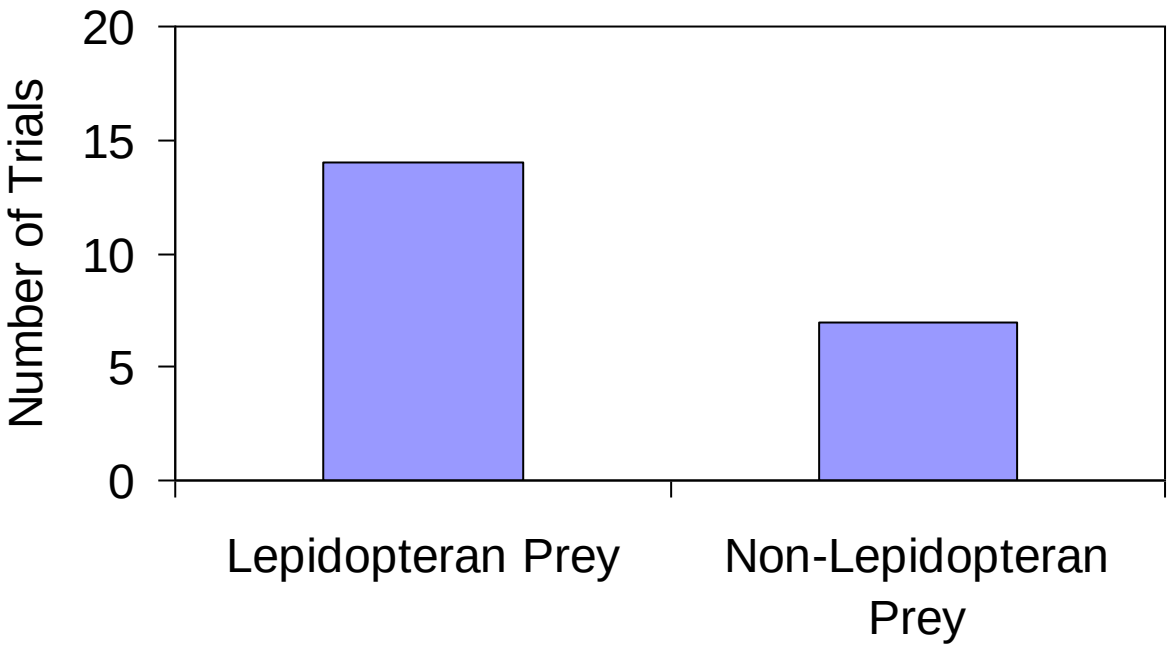

20
15
10
5
0
Number of Trials
Lepidopteran Prey
Non-Lepidopteran Prey

FIGURE 3

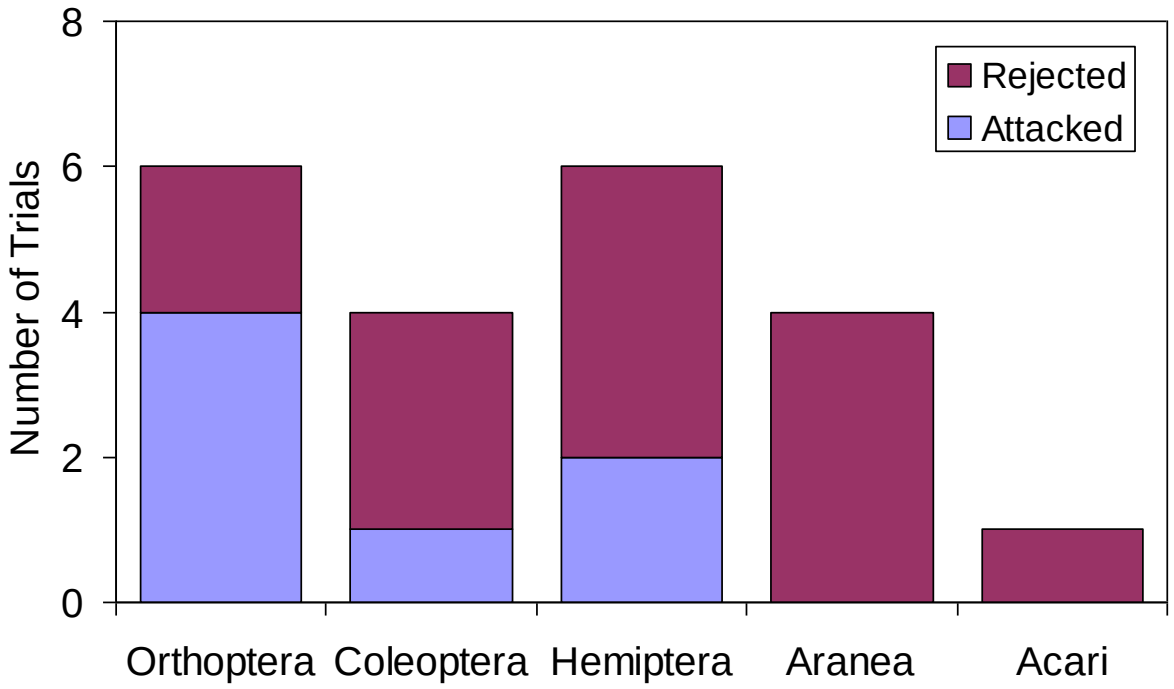
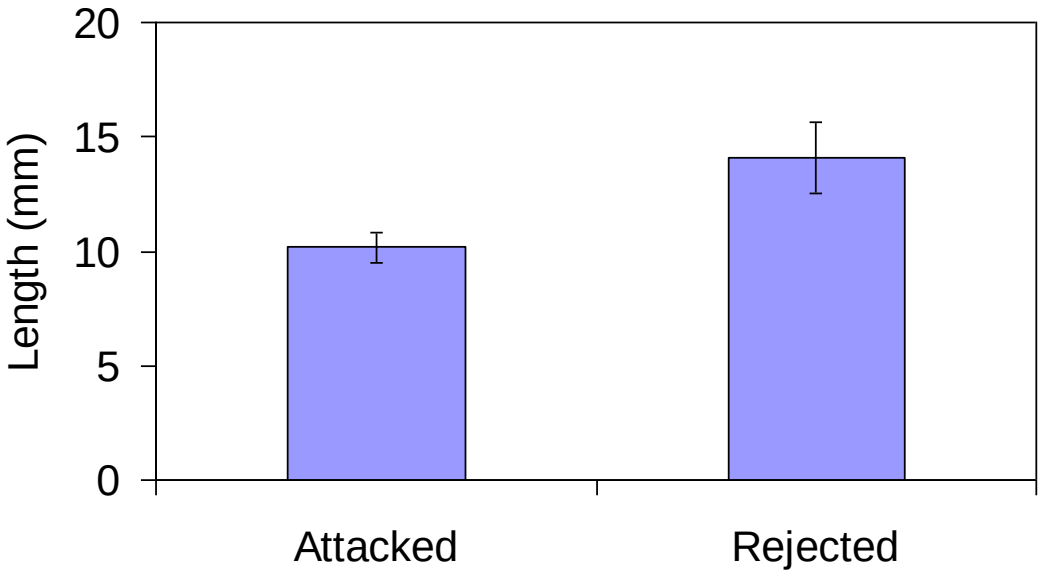

8
6
4
2
0
Number of Trials
Rejected
Attacked
Orthoptera
Coleoptera
Hemiptera
Aranea
Acari

FIGURE 4

(a)


20
15
10
5
0
Length (mm)
Attacked
Rejected

(b)

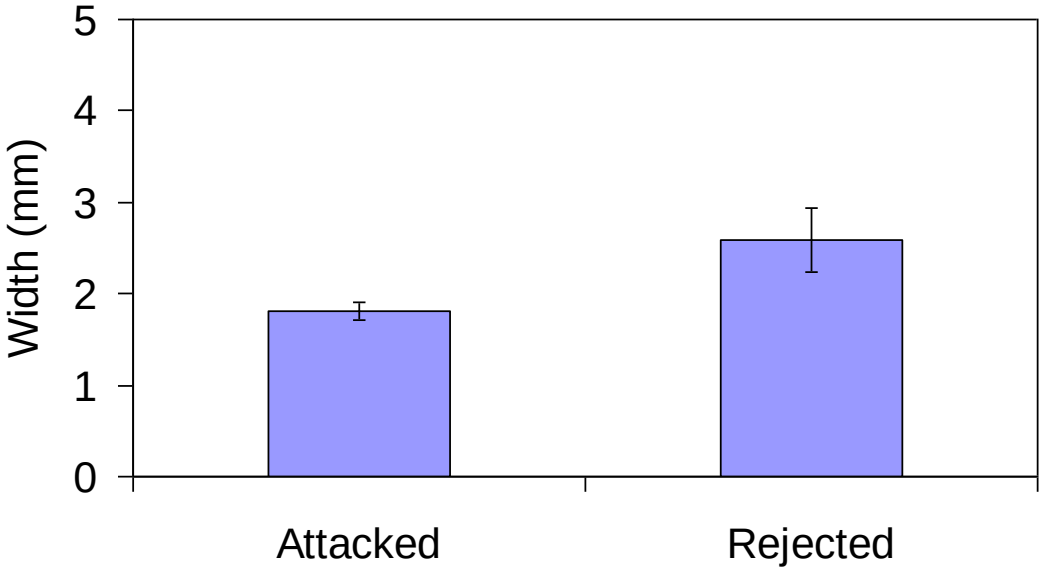

5
4
3
2
1
0
Width (mm)
Attacked
Rejected

FIGURE 5

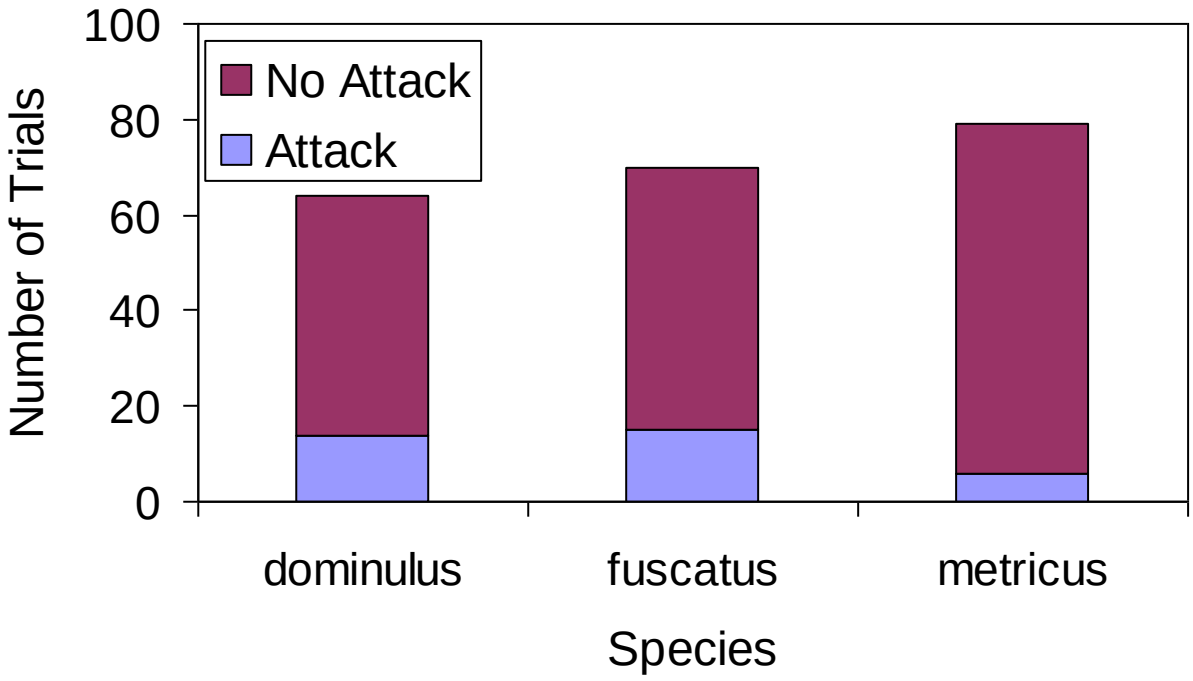
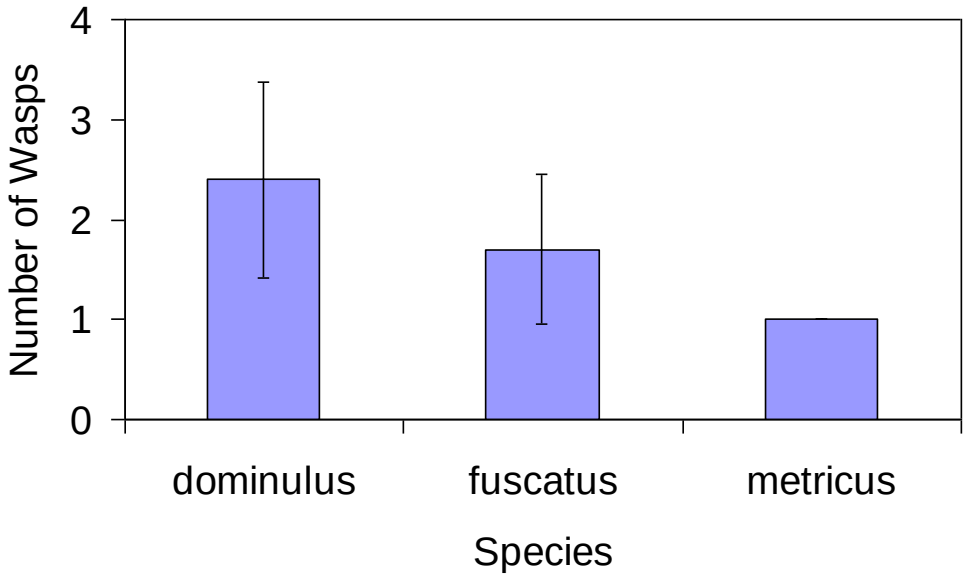
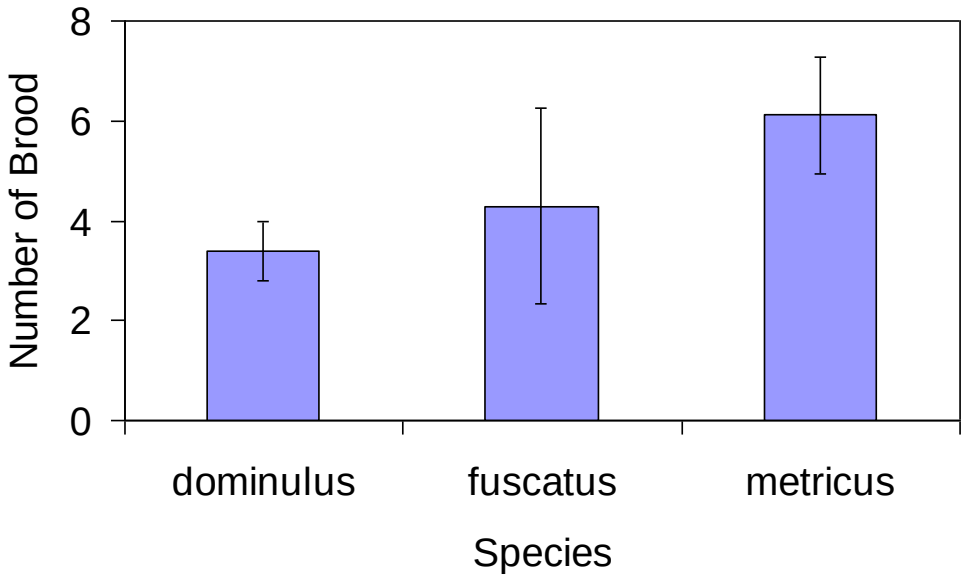

100
80
60
40
20
0
Number of Trials
No Attack
Attack
dominulus
fuscatus
metricus
Species

FIGURE 6

(a)


Number of Wasps
0
1
2
3
4
dominulus
fuscatus
metricus
Species

(b)


Number of Brood
0
2
4
6
8
dominulus
fuscatus
metricus
Species

Appendix 1. A summary of nest box occupation at each of the three study sites. ELF = Ed Lowe Foundation, Cassopolis, MI; PCCI = Pierce Cedar Creek Foundation, Hastings, MI; BAL = Pere Marquette State Forrest, Baldwin, MI. An asterisk in the occupancy column indicates a nest that was transplanted to the box from nearby buildings partway through the season.

Box #	Site	Occupancy/ species
1	ELF	metricus
2	ELF	unoccupied
3	ELF	metricus
4	ELF	metricus
5	ELF	metricus
6	ELF	metricus
7	ELF	metricus
8	ELF	metricus
9	ELF	unoccupied
10	ELF	metricus
11	ELF	unoccupied
12	ELF	metricus
13	ELF	metricus
14	ELF	metricus
15	ELF	unoccupied
16	ELF	metricus
17	ELF	fuscatus
18	ELF	unoccupied
19	ELF	metricus
20	ELF	metricus
21	ELF	unoccupied
22	ELF	unoccupied
23	ELF	unoccupied
24	ELF	unoccupied
25	ELF	metricus
26	ELF	metricus
27	ELF	metricus
28	ELF	unoccupied
29	ELF	metricus
30	ELF	metricus
31	ELF	metricus
32	ELF	metricus
33	PCCI	fuscatus
34	PCCI	dominulus*

35	PCCI	unoccupied
36	PCCI	fuscatus
37	PCCI	fuscatus*
38	PCCI	unoccupied
39	PCCI	fuscatus*
40	PCCI	unoccupied
41	PCCI	unoccupied
42	PCCI	unoccupied
43	PCCI	unoccupied
44	PCCI	unoccupied
45	PCCI	unoccupied
46	PCCI	unoccupied
47	PCCI	unoccupied
48	PCCI	unoccupied
49	PCCI	unoccupied
50	PCCI	dominulus
51	PCCI	unoccupied
52	PCCI	unoccupied
53	PCCI	unoccupied
54	PCCI	unoccupied
55	PCCI	dominulus
56	PCCI	unoccupied
57	PCCI	unoccupied
58	PCCI	unoccupied
59	PCCI	unoccupied
60	PCCI	metricus
61	PCCI	unoccupied
62	PCCI	unoccupied
63	PCCI	unoccupied
64	PCCI	unoccupied
65	PCCI	unoccupied
66	PCCI	dominulus
67	PCCI	unoccupied
68	PCCI	unoccupied
69	PCCI	dominulus*
70	PCCI	unoccupied
71	PCCI	unoccupied
72	PCCI	unoccupied
73	PCCI	unoccupied
74	PCCI	unoccupied
75	PCCI	unoccupied
76	PCCI	unoccupied
77	PCCI	unoccupied
78	PCCI	unoccupied
79	PCCI	unoccupied

80	PCCI	unoccupied
81	PCCI	unoccupied
82	PCCI	unoccupied
83	PCCI	unoccupied
84	PCCI	unoccupied
85	PCCI	unoccupied
86	PCCI	fuscatus
87	PCCI	unoccupied
88	PCCI	fuscatus*
89	BAL	fuscatus
90	BAL	unoccupied
91	BAL	unoccupied
92	BAL	unoccupied
93	BAL	unoccupied
94	BAL	unoccupied
95	BAL	unoccupied
96	BAL	fuscatus
97	BAL	unoccupied
98	BAL	fuscatus
99	BAL	unoccupied
100	BAL	unoccupied
101	BAL	unoccupied
102	BAL	unoccupied
103	BAL	unoccupied
104	BAL	unoccupied
105	BAL	unoccupied
106	BAL	unoccupied
107	BAL	unoccupied
108	BAL	unoccupied
109	BAL	unoccupied
110	BAL	unoccupied
111	BAL	unoccupied
112	BAL	unoccupied
113	BAL	unoccupied
114	BAL	unoccupied
115	BAL	unoccupied
116	BAL	unoccupied
117	BAL	unoccupied
118	BAL	unoccupied
119	BAL	unoccupied
120	BAL	unoccupied

Appendix 2. The number of adult wasps in each colony at each survey date. An asterisk in the box column indicates a nest that was transplanted to the box from nearby buildings partway through the season.

Box	5/12	5/18	5/19	5/26	5/27	5/29	6/3	6/4	6/9	6/18	6/22	6/29	7/9	7/15
1			1		1			1	1	1				
3			1		1			1	1	1				
4			1		1			1	1	1				
5			1		1			1	1	1				
6			1		1			1	1	1				
7			1		1			1	1	1				
8			1		1			1	1	1				
10			1		1			1	1	1				
12			1		1			1	1	1				
13			1		1			1	1	1				
14			1		1			1	1	1				
16			1		1			1	1	1				
17			1		1			1	1	1		1	1	
19			1		1			1	1	1		1	1	
20			1		1			1	1	1		1	1	
25			1		1			1	1	1		1	1	
26			1		1			1	1	1		1	1	
27			1		1			1	1	1		1	1	
29			1		1			1	1	1		1	1	
30			1		1			1	1	1		1	1	
31			1		1			1	1	1		1	1	
32			3		3			3	3	3		3	1	
33		1		1			1				1			3
34*		0		0			0				1			7
36		1		1			1				1			1
37*		0		0			0				0			1
39*		0		0			0				0			3
50		0		1			1				1			2
55		0		1			1				1			5
60		1		1			1				1			0
66		0		1			1				1			1
69*		0		0			0				1			3
86		1		1			1				1			4
88*		0		0			0				0			1
89	1					1								
96	1					1								
98	1					1								

Appendix 3. The number of larvae and pupae in each colony at each survey date. We did not include pupae in the survey counts on 6/29, 7/9 or 7/15. An asterisk in the box column indicates a nest that was transplanted to the box from nearby buildings partway through the season.

Box	5/12	5/18	5/19	5/26	5/27	5/29	6/3	6/4	6/9	6/18	6/22	6/29	7/9	7/15
1			0		0			0	4	8				
3			0		0			0	3	11				
4			0		0			0	5	11				
5			0		0			0	7	15				
6			0		0			0	3	10				
7			0		0			0	3	8				
8			0		0			0	2	7				
10			0		0			0	5	10				
12			0		0			1	5	7				
13			0		0			2	7	14				
14			0		0			0	4	10				
16			0		0			1	7	14				
17			0		0			4	10	19		18	15	
19			0		1			0	0	0		1	2	
20			0		1			0	5	10		8	9	
25			0		1			0	3	7		3	2	
26			0		1			0	4	12		8	4	
27			0		1			0	3	12		5	6	
29			0		1			0	2	11		7	4	
30			0		1			0	0	8		7	6	
31			0		1			0	7	12		15	12	
32			0		3			2	14	22		16	10	
33		3		0			0				13			4
34*		0		0			0				0			0
36		0		0			0				9			0
37*		0		0			0				0			0
39*		0		0			0				0			4
50		0		0			0				0			0
55		0		0			0				12			0
60		0		0			0				8			3
66		0		0			0				16			0
69*		0		0			0				22			2
86		0		0			0				13			1
88*		0		0			0				0			6
89	0					0								
96	0					0								
98	0					0								