Near-Nest Behavior of a Solitary Mud-Daubing Wasp, *Sceliphron caementarium* (Hymenoptera: Sphecidae)

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*Mud dauber wasps (*Sceliphron *spp.) construct nests by sequential flights to gather mud and return it to their aerial nests. Individual S.* caementarium *differ in the mean time spent in four states of construction: approach, daubing, inspection, and departure. Placing a novel object near nests or replacing a white object by a black one resulted in an increase in individuals' approach times but no change in departure times. Removal of objects or replacing a black object by a white one had no effect. A change in the color of objects near nests elicited increased approach times but did not affect departure. S.* caementarium *appears to memorize three-dimensional objects in the near-nest environment, and changes in the near-nest environment are learned during the approach flight to the nest. The frequency of significant responses to all manipulations decreased with successive visits by the wasps, suggesting habituation to near-nest changes.*

INTRODUCTION

Evans (1966a, b; Evans and West Eberhard, 1970) distinguished three major stages in nest orientation by Hymenoptera: (1) distant orientation, or departure in the correct direction; (2) proximate orientation, or recognition of nest surroundings; and (3) immediate orientation, or finding the nest entrance. Visual stimuli in the form of landmarks are the primary means of proximate orientation

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in bees and wasps (Tinbergen, 1958; Evans, 1966a; von Frisch, 1967, 1971; Evans and West Eberhard, 1970; Michener, 1974; van Iersel and van dem Assem, 1966; van Iersel, 1975). All studies to date on proximate orientation behavior of solitary wasps have been on species that nest in sand or soil (Baerends and Baerends in Tinbergen, 1958; van Beusekom, 1948; Evans 1963; van Iersel and van dem Assem, 1966; van Iersel, 1975; Tinbergen 1932, 1958; Tinbergen and Kruyt, 1938). The present study was undertaken to elucidate the mechanisms of proximate orientation used by a solitary, aerial nesting wasp, *Sceliphron caementarium* (Drury), the black and yellow mud dauber (Hymenoptera, Sphecidae, Sphecinae). The objectives were to discern and categorize the behaviors of *S. caementarium* during construction of their mud nests and to investigate the response of *S. caementarium* to various changes in visual aspects of their immediate nest surroundings.

MATERIALS AND METHODS

S. caementarium has a broad geographic distribution (Krombein *et al.*, 1979) and has been the subject of a substantial body of natural history literature (e.g., Peckham and Peckham, 1898; Rau 1915a, b; 1928; 1935; Rau and Rau, 1916, 1918; Shafer, 1949). These wasps build nests of mud in sheltered sites above ground, commonly selecting buildings, bridges, abandoned autos, and other human constructions for nest placement. A wasp makes repeated trips from a mud source to her nest during its construction. Individual nest cells are built, provisioned with spiders, and sealed in sequence. Each nest cell is usually built by an uninterrupted series of mud collecting trips ($N \approx 30$) in a relatively short time span (usually < 1 h). These periods of concentrated activity were the focus of the present study, which was conducted from June through October 1983 at Washington University's Tyson Research Center near Eureka, St. Louis County, Missouri. Data were collected inside a 2788-m^2 corrugated asbestos, steel-frame warehouse (Building No. 360-2, south). A large opening in one wall granted the wasps continuous access to the building's interior.

The wasps themselves were not marked for individual recognition, so the age and experience of the individuals studied could not be known. Two generations of *S. caementarium* (one diapausing, one not) emerge each season in eastern Missouri. Until mid-July, all wasps were first (diapausing) generation; after mid-July, wasps could have been either first or second generation.

To establish standard patterns of near-nest behavior for *S. caementarium*, 206 observations were made on 13 focal wasps during various stages of nest construction. Nesting behaviors were recorded as four discrete states (Altmann, 1974): (1) approach, or the time from when the mud dauber was in flight approximately 1 m from its nest until it reached the nest; (2) daubing, or the

time spent applying mud to the nest; (3) inspection, or the time spent examining the nest or the interior of a cell; and (4) departure, or the time from when the mud dauber stopped any nest activity until it was approximately 1 m from its nest. During each trip to the nest the amount of time spent in each behavioral state was recorded to the nearest 0.1 s using a series of four stopwatches.

During experiments a wasp's "baseline" behavior was established by timing the four discrete states of nesting behavior for five consecutive visits. Manipulations to the near-nest environment were then made while the wasp was away from the nest collecting mud. The mud dauber's reaction to alterations in the nest surroundings was assessed during subsequent approaches and departures. If the duration of approach or departure was equal to or greater than two standard deviations from the baseline control mean for that wasp ($P < 0.05$), a positive response was scored.

Experiment 1 tested the behavior of 11 wasps after 422 changes in three-dimensional near-nest objects. Object changes were placement or removal of cans. All cans used in this study were 10 cm high × 6.5 cm in diameter, identical in appearance, and subjected to the same cleansing and deodorizing treatment, which consisted of hand-washing and removing labels, machine-washing, soaking in bleach water, and hand-drying.

Construction paper, cut to appropriate size and secured with paperclips, was used to modify the appearance of cans that were placed near nests prior to bouts of cell construction. In Experiment 2, responses of nine wasps to 235 exchanges of black and white cans were observed and recorded. In Experiment 3, 11 wasps' responses to 273 color changes were tested by exchanging green, blue, red, and yellow cans.

Both descriptive statistics and statistical tests were performed using the Statistical Analysis System (SAS). ANOVA for unbalanced design was performed separately for each experiment to test for the effects of experimental treatment. However, most of the data were analyzed using categorical models that could analyze the data with more simultaneous factors without compromising the assumptions of the test.

RESULTS

Undisturbed Behaviors

The mean time spent in each of the four different states of nesting behavior differed significantly among the 13 focal wasps: approach ($F = 15.16$), daubing ($F = 28.39$), inspection ($F = 13.76$), and departure ($F = 28.66$) (for all, ANOVA, df = 12,199; $P < 0.0001$). The wasps spent the most time daubing mud (25.9 ± 15.5 s), followed by approach (14.7 ± 10.1 s), departure (7.0 ±

8.3 s), and inspection (5.4 ± 1.0 s). An a posteriori test revealed daubing to be significantly different from approach, inspection, and departure; approach was found to be significantly different from daubing, inspection, and departure; while inspection and departure were found to be significantly different from approach and daubing but not from each other (Scheffe's test, df = 15, P < 0.05).

Experiments

The effect of each experiment (placement–removal, black–white, color change) on the wasps' approach and departure times was assessed using a paired t test, comparing the first visit during the control series to the first visit during trial 1 of a particular manipulation. Within each experiment the contribution of various factors (trial number, type of manipulation, and visit number within a trial) to approach and departure responses was analyzed by multiple contingency table.

Placement and Removal of Cans. The placement of a can in the wasps' near-nest environment elicited a significant increase in approach time (paired t test, df = 9, P < 0.05), but the removal of a can did not. There was no significant change in departure times after placement or removal. Can placement elicited a higher percentage of responses than did removal during both approach and departure (Fig. 1A). In factor analysis of the placement–removal experiment, type of manipulation was the only significant factor (Table I), and type was significant only during the first visit. However, visit was significant (P < 0.05) for the placement treatment when visits were analyzed independently.

Black and White Cans. There was a significant increase in approach times after the replacement of a white can by a black can (paired t test, df = 8, P < 0.05) but not after the replacement of black by white. There was no significant change in the departure times after a manipulation. Black caused a higher percentage of responses than white during both approach and departure (Fig. 1B). Visit was a significant factor only during approach (Table I). When black and white were analyzed independently, visit remained significant (P < 0.01) only for black during approach.

Colored Cans. Approach times were significantly longer after a color change (paired t test, df = 10, P < 0.05). There was no significant difference in the departure times. During approach, blue caused the highest percentage of responses, followed by yellow, green, and red; the descending order of responses during departure was blue, red, green, and yellow (Fig. 1C). None of the factors (trial, color, or visit within a particular trial) was significant in the functional categorical response model (Table I), even when the four colors were analyzed independently.
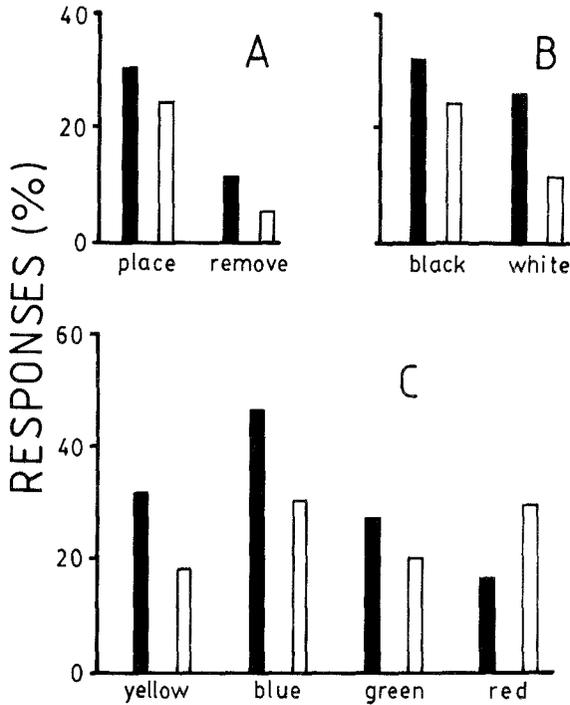
Fig. 1. The percentage of significant responses ($x \geq \bar{X} \pm 2$ SD) during approach (filled bars) and departure (open bars). (A) Placement–removal; (B) black–white; (C) color change.

Table I. Functional Categorical Response Model Examining the Effect of Trial, Type of Manipulation, and Visit on Approach and Departure Response During Placement–Removal, Black–White, and Color-Change Experiments

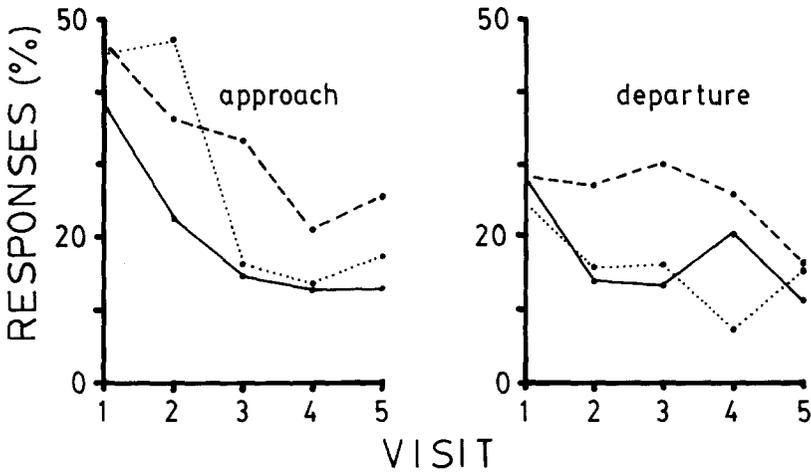|	Placement–removal		Black–white		Color change	
	df	χ^2	df	χ^2	df	χ^2
Approach						
Trial	1	1.94	1	1.13	1	0.12
Type	1	7.02[a]	1	0.00	3	5.75
Visit	6	9.42	4	16.01[a]	4	4.48
Type–visit	6	5.10	4	6.06	12	4.86
Residual	11	6.22	9	6.94	11	5.80
Departure						
Trial	1	0.08	1	0.41	1	0.57
Type	1	7.04[a]	1	2.42	3	1.25
Visit	6	4.87	4	2.88	4	3.25
Type–visit	6	0.74	4	2.83	12	3.20
Residual	11	7.00	9	2.52	11	4.21

[a]$P < 0.01$.

Fig. 2. The percentage of significant responses ($x \geq X \pm 2$ SD) for approach and departure of the first five visits within a trial of wasps exposed to the experimental manipulations. Solid line, placement–removal ($N = 11$); dotted line, black–white ($N = 9$); dashed line, color change ($N = 11$).

Habituation

The percentage of responses to all manipulations tended to decrease with order of visit (Fig. 2). An ANOVA performed on the first trial of each experiment revealed a significant difference among visits in the approach time for placement–removal ($F = 6.13$; df $= 9,326$; $P < 0.0001$), black–white ($F = 2.38$; df $= 9,139$; $P < 0.05$), and color change ($F = 2.36$; df $= 9,170$; $P < 0.05$). Visit number was not a significant factor affecting departure time. The mean approach time of the first visit was significantly different from the mean control approach time only during the placement–removal experiment based on the Scheffe a posteriori contrasts. Otherwise, mean approach and departure times were not significantly different from control approach and departure times or from each other.

DISCUSSION

A great deal of variability exists among wasps for each nesting behavior state and between the behaviors for all wasps. The approach, or preentering (van Iersel and van dem Assem, 1966), flight varied in part because of the nature of the nests sites. In most instances the wasps landed some distance from their nest and walked to it with their mud load. However, some wasps landed directly on their nest if it was accessible. These observations differ from Shafer's (1949) contention that *S. caementarium* always alights some distance from

its nest. The departure, or preleaving (van Iersel and van dem Assem, 1966), flight for a particular wasp always differed from the approach flight in the route followed and duration. Like the approach, the nature of the departure flight was dependent largely upon the nest location. The mean approach time was longer than the mean departure time for all but 2 of 49 wasps observed. Often a wasp's approach flight was indirect (landing some distance from the nest), while its departure flight was directly from the nest.

Wasps just beginning a nest performed locality studies comparable to those described in the literature for other species of wasps and bees (Peckham and Peckham, 1898, 1905; Rau and Rau, 1918; Tinbergen, 1932; Chmurzynski, 1964; Evans, 1966a; van Iersel and van dem Assem, 1966). A locality study by *S. caementarium* consisted of flying, while facing the nest, either in a zigzag fashion or in ever-decreasing loops during the approach. Locality studies ceased after repeated visits with mud loads. Subsequently, detailed locality studies during approach flights occurred only when a wasp's nest environment had been manipulated. Locality studies during departure flights were rare and brief, consisting of a half-loop.

S. caementarium can discern black and white near-nest objects. Black had a stronger disturbing value than white, which differs from the findings of van Iersel and van dem Assem (1966) in *Bembix rostrata,* a digger wasp. In the social wasp *Polybia occidentalis,* Jeanne (1981) demonstrated that black objects near disturbed nests elicited attack significantly more than similar white objects.

Color-change manipulations caused a significant increase in approach times. Although the factor analysis revealed that no specific color was significant in causing a response, blue elicited the greatest percentage of responses during both approach and departure. We conclude that some differentiation of color was occurring. A color hierarchy was suggested for *B. rostrata* when searching for its nest surroundings (Chmurzynski, 1957). Similarly, Mazokhin-Porshnyakov (cited by Spradbery, 1973) suggested that three social species, *Vespula (Paravespula) vulgaris, Dolichovespula sylvestris,* and *Vespula rufa,* can distinguish green, yellow, and orange. More research into the color vision of wasps is necessary.

Trends documented in this study suggest habituation in *S. caementarium.* The duration of the approach immediately following a manipulation was consistently found to be greater than the control, but it was significantly different only in the first visit of the placement–removal experiment. The percentage of responses during approach diminished by a factor of 2 by the fourth visit following a manipulation.

These results demonstrate that learning of changes in near-nest landmarks by *S. caementarium* takes place during initial exposure to those changes and always during the approach flight. This differs from results of those investigators who suggest that most learning occurs during the departure or preleaving

flight (Tinbergen, 1932; van Iersel and van dem Assem, 1966; van Iersel, 1975). Therefore, the generalized statements purporting the same mechanisms of nest orientation in both ground-nesting and aerial-nest wasps (Evans and West Eberhard, 1970) and solitary wasps as in social bees and wasps (Michener, 1974) require reconsideration.

ACKNOWLEDGMENTS

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