Nesting Behavior and Bionomics of a Solitary Ground-Nesting Wasp, *Ammophila dysmica* (Hymenoptera: Sphecidae): Influence of Parasite Pressure[1]

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ABSTRACT The nesting behavior and bionomics of *Ammophila dysmica* Menke were studied 1982–86 in the Sierra Nevada Mountains, Nevada County, Calif. The wasp is univoltine and protandrous. Females dig and provision nests from 0900 to 1900 hours PDT, with peaks in the late morning and late afternoon. *A. dysmica* excavates a shallow, unicellular nest and provisions it with one or two lepidopteran caterpillars. The time required to capture provisions varies seasonally, apparently in response to changes in availability of prey. Mortality factors for immatures included predation by ants, *Formica* spp., nest-raiding by conspecific females, and cleptoparasitism by the sarcophagid, *Hilarella hilarella* Zedterstedt, and the chrysidid, *Argochrysis armilla* Bohart. Partial life budgets are presented for 1983–86. The intensity of nest cleaning increases when cleptoparasites are detected; nest cleaning is somewhat effective in removing the larvae of *H. hilarella* but not the eggs of *A. armilla*. Specific features of nest-site selection, nest construction, cleaning, and defense, the sequence of activities in the nesting cycle, and the elaboration of a multilayered nest closure incorporating a discrete layer of arthropod carrion are discussed as possible responses to parasite pressure.

KEY WORDS Insecta, *Ammophila dysmica,* Sphecidae, cleptoparasite

ALMOST ALL ASPECTS of the complex nesting behavior of the solitary fossorial Hymenoptera, from nest construction to prey transport to nest concealment, have been interpreted as antiparasite adaptations (Evans 1957, 1963, 1966a,b, 1977, Alcock 1974, 1975, Brockmann 1985, Hager & Kurczewski 1985). However, data supporting such interpretations are scant. Solitary nest-making wasps, like gall-forming, leaf-mining, wood-boring, and other insect groups, leave behind a semipermanent record of their activities and those of their natural enemies. The nest may thus be used to assess directly both the ecological impact of parasites and the role of host behavior in modifying that impact.

The behavior of species of the Holarctic genus *Ammophila* has long been studied. Early naturalists described intricate nesting behavior (Fabre 1915, Rau & Rau 1918) and tool-using habits (Peckham & Peckham 1898). Pioneering comparative ethologists studied these wasps' ability to orient spatially and to learn and integrate neurally a complex series of sign stimuli (Baerends 1941). More recently, *Ammophila* spp. have been shown to exemplify several stages of ethoclines through which today's eusocial wasps (Evans 1958, Evans & Eberhard 1970) and tool-using sphecids (Brockmann 1985) may have evolved. The nesting behavior of several North American species is reviewed by Evans (1959) and Powell (1964).

Ammophila dysmica Menke occurs over much of the United States west of the Rocky Mountains, primarily at elevations >1,200 m (Menke 1965). With the exception of two fragmentary observations on provisioning females (Evans 1970), the biology of this species is unknown. The goals of the present study were to describe the nesting behavior and bionomics of *A. dysmica* and to evaluate the role of parasite pressure in shaping these characteristics. This study is part of a larger investigation of the behavioral ecology of *A. dysmica* and its principal cleptoparasite, *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae).

Materials and Methods

The study was undertaken at the University of California's Sagehen Creek Field Station in Nevada County, Calif., in the Sierra Nevada Mountains during 1983 (5 July–28 August), 1984 (30 June–21 August), and 1986 (22 June–4 August); supplementary observations were made in 1982 and 1985. The field station's weather-monitoring equipment provided daily temperature information. The study site was 1 km south of the station on a broad ridgetop, elevation 2,000 m. *A. dysmica* nested there as isolated individuals as well as in several aggregations. The area's flora was influenced by a 1960 fire which deforested much of the site, but left mixed stands of white fir, *Abies concolor* (Gord. & Glend.) Lindl., Jeffrey pine, *Pinus jeffreyi* Grev. & Balf., and lodgepole pine, *Pinus contorta* Dougl. *murrayana* Grev. & Balf., standing over the site's northern and western peripheries. The burned areas were dominated by the shrubby tobacco bush, *Ceano-*

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thus velutinus Dougl. ex Hook, and the less common currant, *Ribes cereum* Dougl., squaw carpet, *Ceanothus prostratus* Benth., and a large number of small pine and fir saplings. Open areas were sparsely covered by *Sitanion hystrix* (Nutt.) J. G. Sm., the dominant grass on the site.

Many solitary fossorial Hymenoptera cohabited the site with *A. dysmica*, including five other species of *Ammophila: Ammophila azteca* Cameron, *Ammophila marshi* Menke, *Ammophila procera* Dahlbom, *Ammophila regina* Menke, and *Ammophila stangei* Menke.

Nesting activity was observed daily, weather permitting, from the initiation of wasp activity at 0900 hours until 1800 hours PDT. On hot days when wasp activity extended later than 1800 hours, observations were continued until no wasps were present.

During 1983–84, female *A. dysmica* were captured and individually marked on the dorsum of the thorax with Testors brand enamel paint. The position of nests was marked by numbered nails driven into the ground around the nest. During nest excavations at the end of the season, the material used to seal the nest tunnel, the living cell contents, and the remains of the nest provisions were collected. For rearing, cell contents were maintained at room temperature for 4 mo, then chilled at 6 ± 2°C for 5 mo to simulate overwintering, and finally placed in a greenhouse in which temperatures cycled daily from ca. 18 to 35°C. The durations of developmental stages were estimated in the field by excavating cells of known age and examining the contents.

Voucher specimens of *A. dysmica* and its predators and cleptoparasites have been deposited in the Essig Museum, University of California, Berkeley.

To identify the lepidopteran caterpillar prey of *A. dysmica*, caterpillars were collected in the field, reared in the laboratory to pupation on their natural plant host, and in some cases chilled to obtain adult emergence.

Quantitative data describing the duration of nesting activities are summarized with a mean, standard deviation, range, and sample size. Two-sample *t* and Wilcoxon tests (the latter test statistic is reported as t_s and was corrected for ties of rank [Sokal & Rohlf 1981]) were used to compare means. Frequency distribution data are analyzed with likelihood-ratio *G* tests (Sokal & Rohlf 1981).

Results

Seasonality. *A. dysmica* is univoltine and protandrous; male emergence preceded female emergence in 1982 and 1983. In 1983 males were abundant when observations were begun on 5 July, whereas the first females were not observed until 9 July. Nesting in 1983 extended from 10 July to 9 August. Individuals of both sexes and a number of completed nests were already present when observations were begun on 30 June of both 1984 and 1985, and 22 June 1986. In 1984 nest construction continued until 27 July. Between-year differences in the timing of nesting activity appeared to be related to the time of snow-pack disappearance; snow remained in several patches on the site into the second week of July in 1983 but was completely absent on 30 June 1984, 30 June 1985, and 22 June 1986.

General Maintenance Behaviors: Feeding, Behavioral Thermoregulation, and Sleep. Upon becoming active at ca. 0900 hours, *A. dysmica* began foraging for nectar, and nectar feeding continued intermittently throughout the day. *Calyptridium umbellatum* (Torr.) Greene was the major early-season nectar source; *Hackelia californica* (Gray) Jtn. also flowered early and was an additional source. *Monardella odoratissima* Benth. ssp. *pallida* (Heller) Epl. flowered later and became the major late-season nectar source.

Behavioral thermoregulation was commonly observed and took two forms: during cool periods during early morning, late afternoon, or partly cloudy weather, wasps pressed their bodies to the sun-warmed ground, with their legs splayed horizontally and lifted in alternate, irregular groups off the soil surface; and during the hot midday females interrupted digging activities to fly up off the hot soil surface and rest in grass clumps or other nearby vegetation.

Male and female *A. dysmica* spent the time between ca. 1800 and 0900 hours "sleeping" on exposed vegetation, including various grasses and the sedge, *Carex multicostata* Mkze. Sleeping wasps grasped the long fine stems of these plants firmly with their mandibles and loosely with their legs. Sleeping wasps were unresponsive to visual or tactile stimuli. Wasps slept in mixed-sex and mixed-species groups (including *A. azteca, A. marshi, A. stangei*, and other Hymenoptera) of up to 10 individuals scattered across a plant.

Male Behavior and Mating. Males became increasingly scarce relative to females as the season progressed. They did not participate in any aspect of the nesting activities. Rather, they engaged in general maintenance activities or searched for receptive females. Searching males flew in rapid, low, weaving flights concentrated in nesting aggregations during the morning and in areas of dense nectar resources during the afternoon. Searching males dropped quickly onto females or other males in apparent mating attempts. Individual males searched across entire nesting aggregations and showed no evidence of territorial behavior; although male/male interactions were common, often taking the form of chases and occasional brief grapplings, they generally ended with both males leaving the area of contact.

Unreceptive females quickly rebuffed males. Mating was observed only once. Two males were observed attempting to copulate with a female at 0942 hours on 23 June 1986 in one of the dense

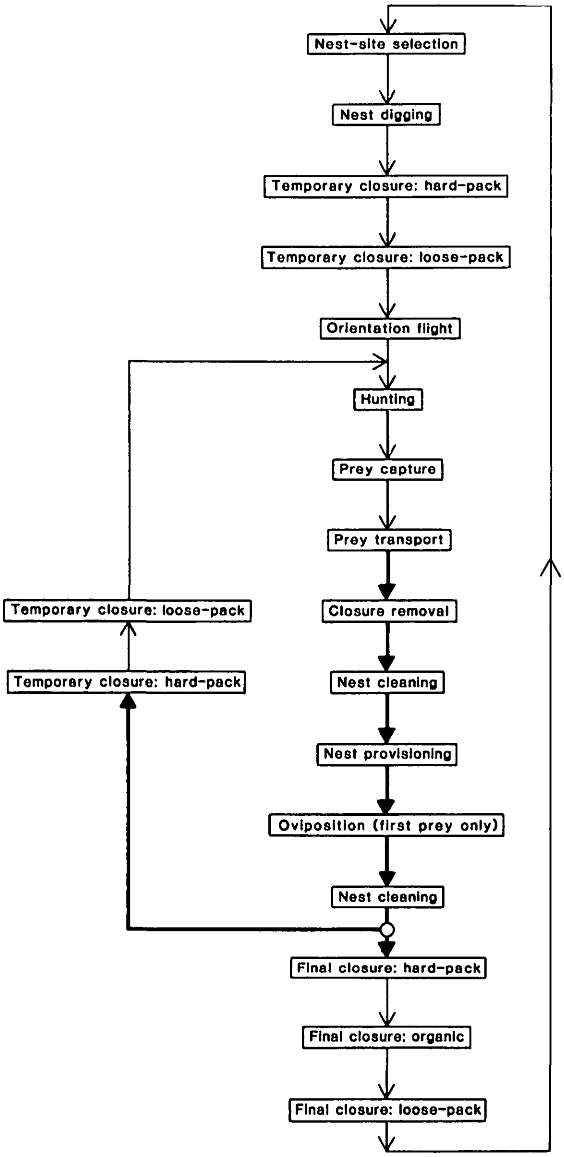

Fig. 1. Nesting activity sequence of *A. dysmica*. Bold arrows connect the steps of the critical activity sequence, which was not interrupted for feeding or sleep, and only rarely for thermoregulation.

nesting aggregations. One had mounted the female, grasping the female's neck with his mandibles, while the other attempted to displace him. The three wasps rolled around on the ground with their wings beating until the female and the first male broke contact with the second male and flew in tandem to a location approximately 15 m away on the periphery of the nesting area. There copulation ensued immediately.

Nesting Behavior

The nesting cycle of *A. dysmica* is outlined (Fig. 1) and described in the following section.

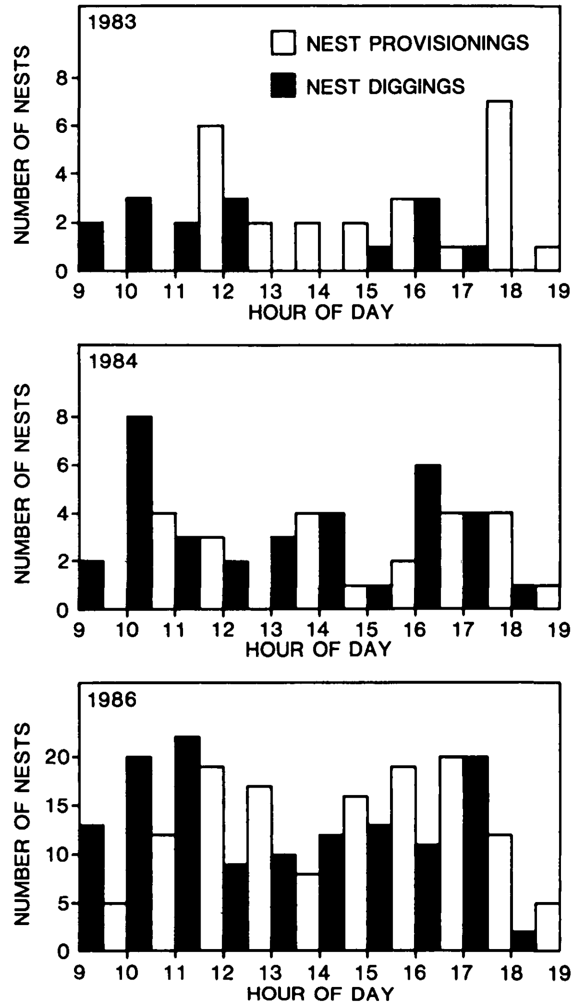

Fig. 2. Hourly distribution of nest diggings and provisionings by *A. dysmica* during 1983, 1984, and 1986.

Daily Activity Patterns. Nest digging and provisioning were observed between 0900 and 1900 hours (Fig. 2). Between-year differences in daily activity patterns were not significant for either activity ($G = 0.40$, df $= 4$, $P > 0.9$; and $G = 1.24$, df $= 4$, $P > 0.5$, respectively). The combined data from 1983, 1984, and 1986 show that hourly levels of digging activity were not constant from 0900 to 1800 hours ($G = 16.02$; df $= 8$; $P < 0.005$). Rather, in each of the 3 yr, activity decreased during the hot early afternoon. The distribution of provisioning events was similarly bimodal ($G = 24.02$; df $=$ 8; $P < 0.005$). Although similar in shape, the distributions of digging and provisioning events differed in temporal location ($t_s = 2.80$; $n_1 = 181$; $n_2 =$ 180; $P < 0.005$); diggings occurred earlier (Fig. 2), even though provisioning generally occurred on a day after the day of excavation.

Nest-site Selection. I summarize here my more extensive observations. Wasps appeared to excavate nests in the area from which they had emerged.

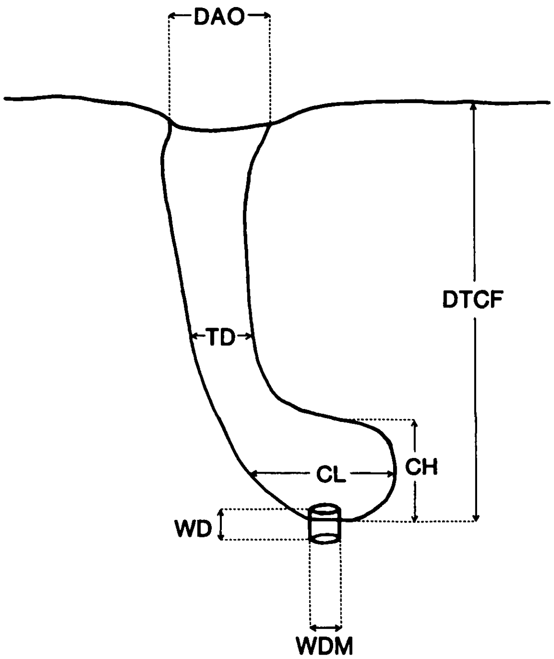

Fig. 3. Cross-section of an *A. dysmica* nest (drawn from a photograph). DAO, diameter at opening; TD, tunnel diameter; DTCF, depth to cell floor; CH, cell height; CL, cell length; WD, well depth; WDM, well diameter. Cell width (CW), not shown, was measured perpendicular to cell length at the cell midpoint.

Digging occurred in friable soil in open, level, bare areas. While digging, females detected and discriminated between a number of insect intruders, including several predators and parasites. In response to some natural enemies, wasps permanently abandoned sites at which they had been digging. The mean number of *A. armilla* cleptoparasites attending nest-sites that were subsequently abandoned was significantly greater than the number attending sites where nests were completed.

Nest Digging and Architecture. Digging wasps (n = 188) dislodged soil by biting with their mandibles while vibrating their bodies. The vibration, audible as a loud buzz, was transmitted to the ground by the mandibles, allowing the wasps to penetrate hard earth. Wasps initiating digging raked the loosened soil away with the front legs, but within 1–2 min began carrying soil away in bundles held between the head and front legs. Excavated soil was generally discarded in flight but sometimes while on foot. Flights varied greatly in length but averaged ca. 10 cm. Nest excavation required an average of 63.48 ± 35.62 min (range, 20–231; n = 102).

A. dysmica excavated shallow, unicellular nests whose only unusual feature was a small, cylindrical well in the center of the cell floor (Fig. 3). Nest dimensions are presented in Table 1.

Table 1. Dimensions of *A. dysmica* nests

Nest feature[a]	n	$\bar{x}$ ± SD (mm)	Range (mm)
Tunnel diameter at opening (DAO)	14	8.9 ± 0.8	8–10
Depth to cell floor (DTCF)	44	49.3 ± 8.7	37–70
Tunnel diameter (TD)	12	5.7 ± 0.7	4.5–7
Cell length (CL)	76	19.0 ± 2.1	14–24
Cell width (CW)	72	10.2 ± 1.1	8–12
Cell height (CH)	12	10.0 ± 1.9	8–14
Well depth (WD)	9	4.6 ± 1.9	1–6.5
Well diameter (WDM)	8	4.9 ± 0.8	4–6.5

[a] See Fig. 3 legend for explanation of nest features measured.

Temporary Closure. Wasps (n = 151) closed their nests temporarily before leaving to hunt. Searching around their nests for a pebble with which to plug the tunnel, wasps sized pebbles by grasping them with the mandibles. If pebbles carried to the nest were too large or too small, they were tried and discarded. After a plug was in place at a depth of 13–25 mm, the tunnel was filled by adding pebbles, dirt clods, and loose dirt, which was bitten off the tunnel walls above the plug. Females firmly packed this material into place as it was added, by vibrating their bodies while pressing either the anterior surface of their heads or a pebble held by the mandibles onto the closure. Pebbles used to pack the plug material were usually incorporated into the closure, but were occasionally removed and discarded. After rounds of packing material into place, wasps often rose vertically in a hovering flight and then descended while slowly rotating, so as to spin around one or more times. The significance of this "helicoptering," which was occasionally also exhibited by digging wasps, is unclear. Helicoptering appeared to be unrelated to thermoregulatory flights off the hot soil surface, for the behavior was exhibited at all hours in sunny or cloudy weather, and was occasionally interspersed with attempts to increase body temperatures by hugging the ground. Wasps switched from this "hard-pack" to the "loose-pack" phase of closure when the tunnel was approximately half-filled. The loose-pack phase consisted of dropping pebbles or dirt clods into the nest until the closure reached the soil surface. The duration of the entire temporary closure averaged 5.04 ± 2.45 min (range, 1.43–16.00; n = 84).

Orientation Flight. Temporary closure was followed by a low, slow, weaving flight in the form of an irregular spiral centered on the nest and gradually widening to 1.5–2.5 m. Orientation was brief, requiring an average of 48.1 ± 30.8 s (range, 10–136; n = 22).

Hunting. Upon completing nest construction, wasps began a search for provisions, interrupted only by occasional visits to flowers and by nightfall. *A. dysmica* hunted for lepidopteran caterpillar prey primarily on the shrubby, 1- to 2-m-tall *C. velutinus*, but also on the low-growing (<15 cm) *C. prostratus*. Wasps searched on the branches, twigs, foliage, and inflorescences of the lower half of *C. velutinus* and the entire *C. prostratus* plant, as well as below the plants' canopies on the leaf litter. Hunting wasps walked quickly, their antennae tapping the substrate. The most commonly taken prey items were the ultimate, or rarely the penultimate, instars of a complex of geometrid caterpillars. Two of these were reared to adults and identified, the frequently provisioned *Drepanulatrix foeminaria* (Guenée) and the much less common *Itame quadrilinearia* (Packard). A pierid caterpillar was found in one nest, the only instance of nest-provisioning with a nongeometrid.

The actual capture of prey was observed only once. A wasp was discovered on the ground below a *C. velutinus* shrub attempting to grasp a lashing geometrid final instar. After several unsuccessful attempts the wasp grasped the caterpillar with her legs and mandibles and stung the venter of one of the thoracic segments. Without releasing her hold the female then moved towards the caudal end of the caterpillar, inserting her sting in one of the anterior and one of the posterior abdominal segments. The caterpillar was immobilized within a few seconds of the final sting. Caterpillars were partially paralyzed by the wasp's sting.

The duration of the hunt, measured as the time between the temporary nest closure and the return of the wasp with prey, assuming wasps could hunt only between 0900 and 1830 hours, averaged 10.35 ± 8.48 h (range, 0.20–41.68 h; $n = 128$) during 1983–86. In 1986, the only year in which the sample was large enough to be examined for seasonal trends, regression analysis revealed a positive relationship between the duration of the hunt and the date (22 June = day 1, 20 July = day 29) on which the hunt began ($r = 0.246$; slope = 0.261 ± 0.098 h/d; df = 111; $P < 0.01$) (Fig. 4). Increasing hunting time appeared to be a reflection of decreasing prey abundance rather than either a general physiological decline associated with wasp aging or a seasonal trend in temperatures. A physiological decline associated with aging was not apparent in a regression of the time required to excavate nests upon season date ($r = 0.118$; slope = 0.490 ± 0.407 min/d; df = 90; $P > 0.25$), nor was there a significant relationship between temperature maxima and season date ($r = 0.041$; slope = −0.023 ± 0.104; df = 28; $P > 0.25$). The observed temporal variation in prey availability may be a contributing factor to the variable patterns of nest provisioning exhibited by *A. dysmica*.

Nest Inspections. Wasps were unable to complete the provisioning of 87 of 119 (73.1%) nests on the day of nest excavation. Before recommencing the provisioning hunt for a nest dug on a previous day, wasps often inspected their nests. Nest inspections were highly variable. Some consisted simply of briefly antennating the closure and slowly walking or flying around the nest, whereas others were more extensive, the female removing the nest closure, entering and cleaning the nest (see following), and replacing a temporary closure. All forms of inspection intermediate to these were also observed. Inspections occurred most frequently between 0900 and 1030 hours.

Prey Transport, Nest Provisioning, and Nest Cleaning. The general behavior of wasps engaged in the sequence of activities beginning with prey transport and ending with the firm packing of the nest closure (Fig. 1, bold arrows) differed markedly from that exhibited at other stages of the nesting cycle. Wasps were unusually highly active, performing all tasks with great rapidity. Furthermore, unlike other nesting activities, this critical activity sequence was never interrupted for feeding or sleep, and only rarely for thermoregulation.

Paralyzed caterpillars were grasped with the mandibles only and carried to the nest on foot. Progress was sometimes aided by beating the wings and was often accompanied by a pronounced up-and-down waving motion of the abdomen. Caterpillars were held venter up and usually head first. Wasps released the caterpillars at the lip of the nest to remove the temporary closure in 10–20 digging motions. Removal of the closure was rapid, requiring an average of 39.3 ± 32.7 s (range, 8–183; $n = 42$); the median time was 27.5 s. Some wasps then entered the nest to perform 2.23 ± 1.78 (range, 1–9; $n = 43$) cleaning trips, removing loose material from the nest in short flights (time required, 29.5 ± 36.3 s; range, 3–148 s; $n = 29$); 19 of 62 (31%) wasps omitted these cleaning trips. Wasps then entered the burrow, turned around in the cell, reemerged partway to grasp the caterpillar, and dragged it into the burrow. The caterpillar was stowed and a single egg affixed to the dorsopleural region of an anterior abdominal segment; storage and oviposition required an average of 34.5 ± 12.2 s (range, 20–72 s; $n = 65$).

Before closing the nest the female performed a variable number of postprovisioning cleaning trips. Females that detected cleptoparasites (as evidenced by the ensuing chase) while opening, cleaning, or provisioning the nest performed a greater number of cleaning trips ($\bar{x} = 12.57 \pm 5.95$; range, 2–30) (time between leaving the nest after oviposition and the initial plugging of the tunnel, 219.6 ± 154.0 s; range, 32–607 s; $n = 18$) than did females not encountering parasites ($\bar{x} = 5.66 \pm 2.98$; range, 0–15) (time required, 89.9 ± 80.1 s; range, 10–412 s; $n = 43$). The two distributions of the number of cleaning trips were significantly different ($t_s = 7.48$; $n_1 = 61$; $n_2 = 21$; $P < 0.001$). Increased attempts to clean the nest were, in 20 of the 21 instances, responses to *A. armilla*, but in none of the 28 nests in which *A. armilla* oviposition was observed were cleaning trips successful in removing parasite eggs, which *A. armilla* glued firmly to the cell walls and ceiling; these nests were invariably parasitized. (In two instances *A. dysmica* did remove from the nest adult *A. armilla*, which had penetrated the nest to oviposit. These parasites were discarded with the debris gathered from the cell.) In the one remaining case the parasite was *Hilarella hilarella* Zedterstedt (Sarcophagidae: Miltogrammini). In contrast to *A. armilla,* in one of the three nests into which *H. hilarella* was observed to larviposit, the cleaning trips did successfully remove the parasites from the cell. I collected four maggots from a pile of material removed from the cell seconds earlier by the resident wasp and reared them in the laboratory, yielding four *H. hilarella* adults. The nest from which the maggots had been ejected contained only an *A. dysmica* cocoon at season's end.

After placing the first provision in the nest, *A. dysmica* females either replaced the temporary closure and proceeded to hunt for another provision, or finished the nest by constructing a final closure (Fig. 1). Direct observations and nest excavations for 1983-86 estimated the proportion of all cells receiving a second provision at 50/229 = 21.8%; the true figure is probably slightly higher due to the imperfect recovery of caterpillar head capsules during excavations.

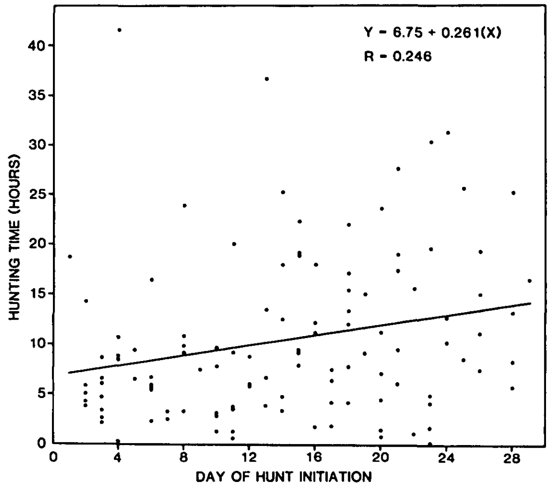

Fig. 4. Linear regression of *A. dysmica* hunting time on the day of hunt initiation (22 June 1986, day 1; 20 July 1986, day 29).

Final Closure. The final closure was trilayered: hard- and loose-packed layers similar to those described were prepared, with the addition of an intervening organic layer. The initial plug was now positioned at or near the bottom of the tunnel, at an average depth of 36.8 ± 4.5 mm (range, 30-44; $n = 11$). The firm-packed material filled the tunnel to within ca. 15 mm of the soil surface and required an average of 9.69 ± 3.65 min (range, 4.25-22.20 min; $n = 47$). Females then made several trips ($\bar{x} = 3.33 \pm 1.29$; range, 1-6; $n = 15$) searching for organic objects, consisting mainly of dead insects but also including seeds and other plant and animal remains (Table 2). The large representation of ants in the organic layer appears to reflect their relative abundance on the site. Females searched within approximately 15 m of the nest by walking with the body tilted forward, head near the ground, antennae tapping the soil. Suitable objects were carried in flight to the nest and packed into the closure. The construction of this organic layer was the most time-consuming step of the final closure, requiring an average of 17.29 ± 16.50 min (range, 1.93-61.80 min; $n = 15$). An average of

Table 2. Composition of the organic layer of the final closure of fourteen *A. dysmica* nests constructed in 1983

Nest	Organic layer contents			
	Formicidae (*n*)	Other Insecta	Plant matter[a]	Other
1	*Formica fusca* L. (s.l.) (1)	Piece of wing	2 small seeds Petal	—
2	—	Piece of integument	Part of a flower Unknown plant part	Bird dropping
3	*F. sibylla* (2) *Formica* sp. (1)	—	Male conifer flower bract	—
4	*Formica* sp. (1)	—	Piece of burned wood	—
5	*Camponotus laevigatus* (F. Smith) (1) *Formica* sp. (1) Undetermined (1)	—	—	—
6	*Formica* sp. (1)	Beetle prothorax	—	Animal dropping (?)
7	*Formica* sp. (1)	Muscoid fly (entire) Asilid fly leg	—	—
8	Undetermined (1)	—	Unknown plant part	—
9	—	12 pieces insect frass	—	—
10	*F. sibylla* (2)	—	Seed capsule 3 fragments plant matter	—
11	*F. sibylla* (1) *Formica* sp. (1)	—	Seed Piece of pitch	—
12	*F. sibylla* (2)	—	—	—
13	*F. sibylla* (3) Undetermined (1)	Heteropteran exuvia	—	—
14	*F. sibylla* (1) *Formica* sp. (1)	Piece of integument	Piece of burned wood Male conifer flower bract	—

[a] It is possible that some of the plant matter listed was present in the soil adjacent to the organic layer rather than being incorporated into the closure by *A. dysmica*.

Table 3. Nest success and immature stage mortality factors of *A. dysmica* based upon nest excavations and direct observations, 1983–86

Mortality factor	Nest outcome	Yr				Total
		1983	1984	1985	1986[a]	
Cleptoparasite mortality	*A. armilla* cocoons/larvae only	5	17	4	37[b]	63
	Both *A. dysmica* & *A. armilla* larvae[c]	4	0	2	0	6
	H. hilarella puparia only	1	2	1	4[d]	8
	Unknown Diptera puparium only	0	1	0	0	1
	Unknown Hymenoptera larva only	0	0	1	0	1
Predator mortality	Empty due to *Formica* spp. predation	2	0	0	2[e]	4
	Empty due to *A. dysmica* raiding	0	1	0	0[a]	1
Unknown mortality factors	Molded cell contents/dead larva	1	7	0	18[f]	25
	Empty cell	1	14[g]	0	18[h]	33
Successful host development	Both *A. dysmica* & *A. armilla* cocoons	1	0	0	1	2
	Both *A. dysmica* cocoon and an unknown Diptera puparium	0	1	0	1	2
	A. dysmica cocoon/larva only	8	37	6	77[i]	128
Total		23	80	14	158	275

[a] Wasps were not individually marked during 1986, making it impossible to distinguish between raiding and resident females. Footnotes explain possible instances of nest raiding.

[b] Caterpillar and host egg in one cell parasitized by *A. armilla* were removed by a wasp which may have been a raiding female. Nest was subsequently reprovisioned.

[c] These nests were excavated before the development of host and parasite larvae was complete; most, if not all, would have produced parasites only.

[d] Initial caterpillar and host egg in an unparasitized temporarily closed nest were removed by a wasp which may have been a raiding female. The nest was parasitized by both *A. armilla* and *H. hilarella* when the second provision was added.

[e] In both nests subterranean ant tunnels led into the cell. One nest had been oviposited in by *A. armilla*. In the other the initial caterpillar and host egg were parasitized by *A. armilla*. An *A. armilla* larva was removed from the cell by a wasp which may have been a raiding female. The nest was then reprovisioned.

[f] Four of these nests had been oviposited in by *A. armilla*.

[g] It is not known if these empty cells had ever been provisioned.

[h] One of these nests was parasitized by *H. hilarella*; 15 d later a wasp, which may have been a raiding female, removed the caterpillar remains and four *H. hilarella* puparia from the cell. Another nest had been parasitized by *A. armilla* and was then emptied by a wasp which may have been a raiding female. The remaining 16 nests were never observed to have been provisioned.

[i] Caterpillar and host egg in one unparasitized nest were removed by a wasp which may have been a raiding female. Nest was subsequently reprovisioned.

22.8 ± 8.0 (range, 10–34; $n = 14$) pebbles, dirt clods, and pine needles were added to the loose-packed layer of the closure, requiring an average of 2.60 ± 1.51 min (range, 1.00–7.65; $n = 30$). Wasps rarely raked a small amount of loose dirt or sand over the closure, but in all cases the burrow remained visible despite being filled to a level even with or just below the soil surface.

On five occasions females returned to completed nests that had been parasitized by *A. armilla*, removed the closure, performed additional cleaning trips, and replaced the closure. In none of these cases were the cleaning trips effective in removing the *A. armilla* eggs.

Immature Stages

The creamy white, sausage-shaped eggs averaged 2.73 ± 0.21 mm long by 0.78 ± 0.03 mm wide ($n = 3$). First instars became active within 2 d and pierced the chorion and the caterpillar integument where they were in contact in order to feed. Swelling larvae burst the chorion on approximately day 3. Larvae grew rapidly, consuming all provisions and spinning cocoons within 7–8 d. Cocoons were surrounded by a diffuse array of threads which attached them to the cell walls; cocoons consisted of an outer translucent envelope and a smaller inner parchment-like capsule. The inner capsule averaged 15.3 ± 1.0 mm long by 4.3 ± 0.3 mm wide for males ($n = 12$) and 16.5 ± 1.4 mm long by 4.8 ± 0.4 mm wide for females ($n = 9$). The outer envelope was identical in length to the inner capsule; the width was difficult to measure due to distortion caused by handling during excavation, but averaged ca. 6.9 ± 0.9 mm (range, 5.5–8.0) ($n = 11$).The inner capsule was coated internally with a smooth, brown, shellac-like material, initially applied by larvae as a colorless liquid. The caudal end of the capsule bore the meconial mass. The creamy yellow prepupae overwintered. Adults voided a meconial mass of many fine white pellets upon emergence.

Mortality Factors

A partial life budget for *A. dysmica* was constructed for 1983–86 (Table 3). The 1983, 1985, and 1986 data were collected from nest aggregations, whereas the 1984 excavations included both aggregated and relatively isolated nests; the percentage of parasitism by *A. armilla* increased with increasing nest density (unpublished data). The impacts of the major mortality factors were relatively constant from year to year.

A. armilla. The principal mortality factor was the facultatively gregarious cleptoparasite, *A. armilla*, which developed in 71 of 275 (25.8%) nests (Table 3). In two of these nests both host and parasite developed successfully. The bionomics and host-locating behavior of this wasp will be presented separately, but the key elements of behavior are summarized here and in Table 4. *A. armilla* located host nests by responding to visual cues provided by nest-digging or provisioning females (unpublished data). Parasites watched nesting females from nearby perches and remained motionless while the host was above ground; parasites flew from perch to perch or to the nest entrance only when the host was in the cell. *A. armilla* learned the location of nests and used landmarks to reorient to these nests in the absence of the female host (unpublished data). In this way parasites could attend nests intermittently while the host hunted for provisions. Thus *A. armilla* located nests during the relatively invulnerable but conspicuous digging stage and then waited for the less conspicuous but more vulnerable provisioning stage, when parasite oviposition generally occurred. The rate of nest parasitism was positively correlated with the number of parasites that discovered the nest during digging (unpublished data). Parasites also commonly dug into nest closures but only rarely reached the cell. *A. armilla* was generally able to elude the defensive attacks of nesting females and return safely to continue watching the nest.

H. hilarella. The cleptoparasitic fly *H. hilarella* was common on the site and an occasional parasite of *A. dysmica* nests (Table 3). *H. hilarella* frequently attended nest-digging and provisioning females. While the host was above ground the fly perched motionlessly on nearby rocks or vegetation, orienting towards the nest entrance. When the wasp was below in the cell, the fly switched perches, sometimes circling directly over the nest entrance before alighting. These parasites were also attracted to wasps transporting caterpillars and in these instances exhibited a stereotyped tracking behavior: *H. hilarella* flew to a perch ca. 10–25 cm ahead of a prey-transporting wasp and oriented towards the wasp, pivoted on the perch so as to continue pointing at the wasp as it walked by, and flew to a new perch to repeat the cycle when the wasp had travelled ca. 8–15 cm beyond the perch. Flies waited when wasps climbed into vegetation and rested. In this way flies arrived at the nest at the start of provisioning. Larviposition occurred only during nest provisioning while the wasp was ovipositing (one instance), cleaning the cell (one instance), searching for a plug (one instance), or firm-packing the nest (one instance). To larviposit, flies flew to the lip of the nest, spun around to position the tip of their abdomen over the nest, and dropped a cluster of maggots into the burrow. One, two (three instances), four (three instances), five, and six puparia were recovered from single cells. Only *H. hilarella* developed successfully in one nest where both this parasite and *A. armilla* had oviposited.

Table 4. Antiparasite adaptations of a solitary ground-nesting wasp, *A. dysmica*, and counteradaptations of its principal cleptoparasite, *A. armilla*

Host	Parasite
1. Abandons nests under construction in response to parasite detection	1. Remains motionless when host present above ground
2. Constructs an inconspicuous nest	2. Locates nest indirectly by searching for digging hosts
3. Seals nest entrance	3. Digs through plug
4. Executes nest–prey sequence	4. Learns locations of nests. Keeps nests under intermittent surveillance while host hunts
5. Visually locates moving enemies	5. Remains motionless when host present. Enters nest directly behind host. Avoids detection in cell
6. Actively defends nest	6. Possesses thick, highly sculptured integument. Evades host with excellent mobility. Curls into ball when attacked
7. Cleans nest	7. Glues eggs securely to cell walls
8. Constructs organic layer (=false cell?)	8. —
9. Accelerates critical-phase activities	9. —

Ants. Foraging *Formica* spp. ants, mainly *Formica sibylla* W. M. Wheeler, were abundant in the nesting areas. *A. dysmica* actively defended nests and provisions by hovering over ants and dipping down to administer quick bites. Ants were occasionally carried aloft and quickly dropped aside. Wasps sometimes withdrew only temporarily from a nest if unable to drive the ants away, whereas on other occasions the presence of ants caused females to abandon permanently nests under construction. Ant attacks upon nesting females were generally restricted to isolated bites, but twice the ant held on after biting, causing the wasp to fly from the area carrying the ant. Although no clear cases of ant predation of adult *A. dysmica* were observed, one such case was seen for a nest-digging *A. azteca*.

Contacts with ants during prey transport were common; wasps sometimes responded to such contact by ascending nearby vegetation and resting aloft with the caterpillar for several minutes. (Wasps may have climbed vegetation for other reasons as well, such as for thermoregulation or spatial orientation; see Baerends [1941].) Ants stole caterpillars in 6 of 106 (5.7%) provisionings when the wasp with caterpillar was observed before arriving at the nest. *F. sibylla* was responsible for five of these thefts and *Formica integroides* Emery for one. Because wasps transporting prey were generally only observed when they had successfully arrived at or within a few yards of their nests, the actual frequency of robbery by ants may have been much higher.

Provisioned nests were raided by surface-foraging ants (two nests in 1983) before being sealed. Nests with complete closures were also apparently raided by ants whose subterranean galleries intersected the nest (two nests in 1986) (Table 3).

Nest Raiding by Conspecific Females. One instance of nest destruction by an intruding conspecific female was observed in 1984. An unmarked female was observed at a nest that had been provisioned 5 d earlier by a known, marked female. The nest had been opened and the contents, an *A. dysmica* larva feeding on a largely devoured caterpillar, removed. The unmarked female behaved aberrantly, repeatedly stinging the caterpillar and drawing it into the nest only to remove it again immediately. The raiding female finally constructed a temporary closure and departed, leaving the caterpillar and larva lying outside the nest where they were quickly collected by *Formica* spp. ants. The following day, the original marked female was observed placing a final closure on the nest. During the 1986 season *A. dysmica* females were not individually marked, making it impossible to distinguish resident from raiding females. Several possible cases of nest raiding like that described above were observed (see footnotes to Table 3). Raiding females were never observed to appropriate nest contents for their own use; the adaptive significance of nest raiding, if any, is therefore unclear.

Unknown Causes. Mortality of immature *A. dysmica* not obviously associated with insect enemies was observed in 25 of 275 (9.1%) nests (Table 3). Fungi were often associated with these cells, but whether they were pathogens or saprophytes is unknown.

Discussion

Much of the nesting behavior described above appears to enhance the ability of *A. dysmica* to reproduce successfully in an environment cohabited by parasites and predators. The figures in Table 3 reflect the imperfection of these adaptations. These figures do not, however, provide a measure of the potential impact of these and other parasites and predators in the absence of defensive adaptations by the host. Some of the antiparasite adaptations of *A. dysmica* and the counteradaptations of its principal cleptoparasite, *A. armilla*, are presented in Table 4 and discussed in the following paragraphs.

In addition to the basic protection afforded the wasp's progeny by placing them within a nest (Evans 1977), several aspects of nest structure represent passive defenses against parasites and predators. The first of these is the construction of a nest made inconspicuous both by placing a closure on the nest and by carrying excavated dirt away from the nest, thereby avoiding the formation of a visible tumulus. These defenses may reduce nest discovery by a range of natural enemies, including a number of miltogrammine and bombyliid flies (Ristich 1956, Evans 1966a, Endo 1980, Hager & Kurczewski 1985, Spofford et al. 1986, Wcislo 1986) and chrysidid and mutillid wasps (Hicks 1932, Bohart & MacSwain 1940, Batra 1965, Kurczewski 1967), which search for open nests or signs of nest excavations. Two hole-searching parasites that were ineffective parasites of *Ammophila* spp. at Sagehen Creek (never reared from *A. dysmica* nests and only very rarely from *A. azteca* [unpublished data]), the bombyliid, *Exoprosopa dorcadion* Osten Sacken, and the chrysidid, *Ceratochrysis trachypleura* Bohart, may have been prevented from locating many nests. *A. armilla* and *H. hilarella* located inconspicuous nests indirectly by searching for digging or provisioning females; *H. hilarella* also oriented to prey-transporting wasps.

Nest closure not only conceals the nest but is also a physical barrier to parasite and predator penetration. Adult and larval forms of some miltogrammine flies (Peckham 1977, Endo 1980, Hager & Kurczewski 1985, Spofford et al. 1986), adult chrysidids (Hicks 1932, Bohart & MacSwain 1940, Evans & Gillaspy 1964), mutillids (Batra 1965, Evans 1966a), and ants (Hook & Matthews 1980, Peckham & Hook 1980, Matthews et al. 1981) may attempt to dig into closed nests. In addition, as noted for *A. dysmica* and previously for other sphecids (e.g., Brockmann & Dawkins 1979, Parker et al. 1980, Hager & Kurczewski 1986, Alexander 1986), conspecific females may dig into closed nests and either discard or steal the contents. A mutillid wasp, *Sphaerothalma* sp., was observed on one occasion digging into an *A. dysmica* nest closure. *A. armilla*, which easily penetrated the minimal nest closures of *A. azteca* (unpublished data), frequently attempted to dig into temporarily or permanently sealed *A. dysmica* nests, but was observed to penetrate the hard-packed layer only once. Ants were never observed digging in nest closures. Finally, the organic layer of the final nest closure may itself be protective, although how is unclear. The insect carrion may function as a false cell, which may either divert the parasite's eggs into the nest plug, or simply discourage the parasite by making the nest appear to be unsuitable for parasite development. Although sphecid wasps in the genus *Microbembex* use dead arthropods as nest provisions (Evans 1966b), the scavenging of insect carrion for incorporation into a nest closure has not been reported. Further work is required to understand the adaptive basis of this behavior.

The evolution of the order of activities in the nesting cycles of *Ammophila* species may have been shaped by selective pressures imposed by parasites. Several species of *Ammophila*, including *Ammophila boharti* Menke, *Ammophila dolichodera* Kohl, *Ammophila marshi* Menke, *Ammophila novita* (Fernald), and *Ammophila wrightii* (Cresson), exhibit the relatively primitive behavior of digging the nest after the prey has been captured (Hicks 1934; Alcock 1984; Weaving 1984; unpublished data). The evolutionary shift from this prey–

nest sequence to the nest–prey sequence exhibited by *A. dysmica* probably reduces the impact of parasites and predators in two ways. First, the prey is not left exposed while the nest is constructed (Evans 1970, 1977). Second, the step of the nesting cycle that is most conspicuous to parasites, the digging of the nest, is temporally separated from the step of the nesting cycle that is most vulnerable to parasite exploitation, the provisioning of the nest. *A. armilla* has adapted to the nest–prey sequence by keeping the nest under intermittent surveillance throughout the host's hunting period, thereby essentially waiting for the female to return with provisions. Learning the location of the nest is a key component of this prolonged surveillance (unpublished data). Why some *Ammophila* species retain the prey–nest sequence is unclear; different ecological pressures in different habitats may favor alternate behaviors, or the species' evolution may be genetically constrained.

A. dysmica, like many solitary Hymenoptera, actively attacked intruders perceived near the nest (Powell 1964, Batra 1965, Hager & Kurczewski 1985, Spofford et al. 1986), but could detect insects only if they moved. Stationary cleptoparasites observing the nest from nearby perches were therefore effectively invisible. Apparently in response to female nest defense and abandonment, *A. armilla* and *H. hilarella* exhibited convergent nest-attending behaviors: both species remained motionless while the host was above ground, and flew from perch to perch or from perch to nest entrance only while the female was below in the cell. *A. armilla* penetrated nests without being seen by walking directly behind the host wasp as she reentered her nest, or by entering when the female was below ground. *A. armilla* also oviposited without eliciting defensive attacks by the host, even when both wasps were in the cell simultaneously (unpublished data). When *A. armilla* were induced to move in the presence of the host by interactions with conspecifics, including male mating attempts and contact with other females attending the same nest, they were often pursued in flight by the host. The mobility of the parasites usually enabled them to elude these attacks. On the rare occasions when *A. armilla* was caught in or near the nest, the thick, highly sculptured integument and ability to roll into a defensive ball, both of which characterize the subfamily Chrysidinae (Bohart & Kimsey 1982), appeared to protect the parasite from the biting host.

Although forms of nest cleaning occur in diverse groups of solitary Hymenoptera, and the possible role of nest cleaning as an antiparasite defense was suggested long ago (Newcomer 1930, Evans 1957, 1966b), evidence to support such an interpretation has only recently been gathered. Hager & Kurczewski (1986) demonstrated that *Ammophila harti* (Fernald) makes more cleaning trips when cleptoparasitic flies are present. These authors did not look for maggots in the material deposited outside the nest, but suggested that such searches be conducted as part of future studies. The results of the present study parallel those of Hager & Kurczewski (1986) in demonstrating that the intensity of cleaning increases in response to parasite detection. Although the ability of *A. dysmica* to remove *H. hilarella* maggots from the cell was established, equal success did not extend to the removal of *A. armilla* eggs. *A. armilla,* perhaps in response to the host's nest-cleaning behavior, entered nests to glue its eggs securely to the cell walls and ceiling. In fact, this parasite exploited the host's nest-cleaning behavior to penetrate the cell and oviposit.

The critical activity sequence beginning with prey transport and ending with nest closure coincided with the period of greatest vulnerability to ant predators and wasp and fly cleptoparasites. The rapid, uninterrupted execution of this activity sequence may have increased the likelihood of completing a nest before a natural enemy intervened.

In this study I have attempted to understand the nesting behavior of *A. dysmica* through field observations of this wasp and its interaction with a complex of parasites and predators. The interpretations of some aspects of the wasp's behavior, such as nest cleaning and sealing, are directly supported by observational data. Other aspects of behavior, such as the use of arthropod carrion in the nest closure, are less well understood and require further study. In conclusion, however, it may be said that many aspects of the behavioral program of *A. dysmica,* ranging from such basic tasks as nest-site selection to the peculiarities of nest closure, appear to have been shaped by the selective pressures imposed by parasites and predators. The complexity of behavior exhibited by individual species of solitary Hymenoptera and the diversity of behavior patterns expressed within the order appear to make nidifying wasps and bees ideal subjects for studies of the impact of parasites upon the evolution of host behavior.

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