

midline and parafascicular nuclei, produced analgesia and concomitant release of enkephalin-like substances in human patients (17). Third, pharmacological evidence indicates that both the medial thalamus and anterior cingulate gyrus have a high affinity for binding opiates (6, 18) and that iontophoretic application of morphine to the medial thalamus as well as the parafascicular nucleus produces analgesia (19). Finally, although neurosurgical interruption of cingulate gyrus connections does not abolish the sensation of pain, it does eliminate its noxious aspects (5). Similarly, lesions in the medial thalamus and intralaminar nuclei also relieve the affective response to pain (20). Furthermore, other afferents to the anterior cingulate gyrus may also be involved in pain-related activity, for example, the amygdala and insula have a high affinity for binding opiates (18). Besides this direct evidence implicating the anterior cingulate gyrus and its thalamic and cortical afferents in pain-related activity, the anterior cortex may also be involved in reflex responses to painful stimuli. Thus, pupillary dilation, piloerection, and some forms of shrill vocalization can be produced by stimulating the anterior but not the posterior cingulate gyrus (1).

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30 October 1978

## Honey Caches Help Female Paper Wasps (*Polistes annularis*) Survive Texas Winters

**Abstract.** *Polistes annularis* females store honey in their nests in autumn. They return to their nests on warm winter days, eat honey, and defend it from non-sisters. Honey deprivation decreases numbers surviving the winter; females that do survive without honey build smaller spring nests.

*Polistes annularis* exhibits a newly discovered behavior, winter honey caching. Previously, only large perennial colonies of social insects have been reported to make and store honey for use as food during periods of drought or cold weather (1, 2). Females of *P. annularis* abandon their nests after caching winter stores of honey and retreat to hibernacula in more protected places. On warm winter days females leave hibernacula, return to natal nests, and feed on their honey. At this time they will defend it against non-sisters. Dependence on honey stored overwinter has a decisive impact on the social biology of *P. annularis*, for it necessitates proximity of hibernacula to nests and continued contact and cooperation between sisters. This facilitates springtime recognition of sisters who cooperate in building new nests near the natal nest.

Although winter honey caching is previously unreported in polistine wasps, honey manufacture and storage of small droplets in the nest in cells occupied by eggs or small larvae is common (2-5). Honey droplets have been seen in nests at all seasons, as long as the wasps are on the nests.

Winter honey caching was observed in a population of *P. annularis* along a 15-m high limestone cliff overlooking a reservoir, Lake Travis, 26 miles west of Austin, Texas. Nests were extraordinarily common along this particular west-facing cliff; more than 1000 nests were found along a 200-m section. In 1976, 40 nests were observed, and all autumn reproductive males and females were marked with enamel (6). Reproductive females were distinguished from workers by their lack of wing wear (7). Honey first began to appear in quantity in empty cells in September. By November, all

nests still occupied had some honey, and most had all cell walls coated with a thick layer of honey similar in taste to that of honeybees, but much more viscous. In November, females began entering a crack in the cliff and abandoned mud cliff swallow nests, searching for places to hibernate. When nights were cooler than 5°C, wasps spent them in hibernacula, returning to their nests on sunny warm days. On the nest they fed on honey and repelled all intruders not marked as sisters. Commonest among intruders were other wasps from the same population, often bearing marks indicating that they were born on other nests. These were fought off vigorously and chased (8). In addition, other insects tried to steal honey. Several *Vespula* sp. were successful, although they were chased off immediately when discovered. Three low nests were knocked down by a raccoon that shredded them in the process of consuming honey.

Only a small amount of honey loss was endured by *P. annularis* and several factors appeared to be contributory. Most of the nests are inaccessible to mammals in that they cannot walk up overhanging rock faces. Wasps defend the nests on warm days so that other insects have little chance of stealing successfully. Nest predation by birds for honey does not occur (9).

Winter visits to the study site revealed conditions necessary for females to leave their hibernacula. Females returned to their nests on days that reached at least 21°C with at least 110 minutes of sun, and on overcast days when the temperature was at least 26°C. Warm days as defined above were counted for every 15-day period in November through February for the past 13 years (10). Each of the 15-day periods examined had a mean

Table 1. Kendall  $\tau$  correlations with and without honey for traits that may be influenced by female condition. Two-tailed probabilities are given (\*,  $P < .05$ ; \*\*\*,  $P < .001$ ).

Stem	With honey	Without honey
Wasps (No.) marked in autumn $\times$ No. overwintered	$\tau = 0.36^*$	$\tau = 0.29$
Wasps (No.) overwintered $\times$ No. new nests formed	$\tau = 0.70^{***}$	$\tau = 0.11$
Foundresses (No.) $\times$ nest size, 25 April	$\tau = 0.47^{***}$	$\tau = 0.37^*$

of more than five warm days. Lowest was the first half of February (mean  $\pm$  S.D.,  $5 \pm 3.5$ ); highest was the first half of November ( $8 \pm 3$ ) (10). Overall there was an average of 50 warm days between 1 November and 28 February. Thus, each year there usually exists ample opportunity for wasps to feed on honey after hibernating.

There are several ways that the wasps could use honey on warm winter days. They could gorge on each warm day, using up the honey as quickly as possible, or they could ration it through the winter, thus making the honey last as long as possible. The rationing behavior may be construed as altruism on the part of nest-mates, for it would require them to eat less than maximum in order to leave

some for next time. Since the wasps are sisters, inclusive fitness arguments could explain such behavior in that many other cooperative behaviors exist between sisters (3, 11, 12). However, the first possibility seems more likely, since the wasps can store food as fat. Wasps are able to hibernate in areas much colder than Texas, areas with much longer winters where no warm days occur (13, 14). They store fat in their abdomens, and can live at cool temperatures without eating for months (14, 15). In view of this form of alternative storage, and the possibilities, though small, that their nests will be destroyed, or that cold weather will prevent feeding on honey for a time, it seems likely that the best strategy is to convert honey into fat as quickly as pos-

sible through the winter, until the honey is gone (16).

Other populations of *P. annularis* have not been examined for honey caches. It is unlikely that caching honey is restricted to this population, yet requirements for honey usage may not be met everywhere *P. annularis* occurs. Proximity of nests to hibernacula is essential. Warm days during the winter are necessary for the use of honey. A cliff or other inaccessible place may be necessary to protect the honey from other organisms that may steal it if it is near the ground, or in trees that can be climbed. *Polistes annularis* often nests in large groups; other cliff populations and hibernacula have been observed (13, 17). Increase in winter survival by honey cachers can result in strong preferences for returning to the parental nest site (18). This will result in highly clumped populations of nests, as is common for *P. annularis* (19).

In March, females emerged from hibernacula and returned to natal nests. They had mated sometime in late winter. In the spring of 1977, 178 nests were built on the cliff face area comprising the study population. Of these, 106 were initiated by females that had been marked the previous autumn. Nests were initiated by one to six females near natal nests. They were later joined by additional sisters. Rarely a non-sister joined; presumed cousins (determined by the proximity of their parental nest) were the commonest non-sisters joining. Some individuals remained on the natal nest much longer than others before choosing a new nest. Once they are on a new nest, females do not switch nests. Foundress associations ranged from 1 to 9, averaging 3.4.

To test the effect of honey storage on overwintering females, 14 of 33 nests with honey in November were knocked down while females were first in hibernacula. All nests knocked contained substantial amounts of honey. Since knocking was done while females were in hibernacula, they did not suffer any physical disturbance incidental to having their nests knocked. Females without nests emerged on warm days, and returned to the sites of their nests, and it is likely that the only effect of removing the nest was the deprivation of honey. A number of parameters that may distinguish females with honey from those without were examined. If honey were necessary to survival, the condition of females without it should be lower than that of females with it. Condition was measured in three ways: (i) ability to survive the winter, (ii) ability to form new nests, and (iii) size of new nests after 2

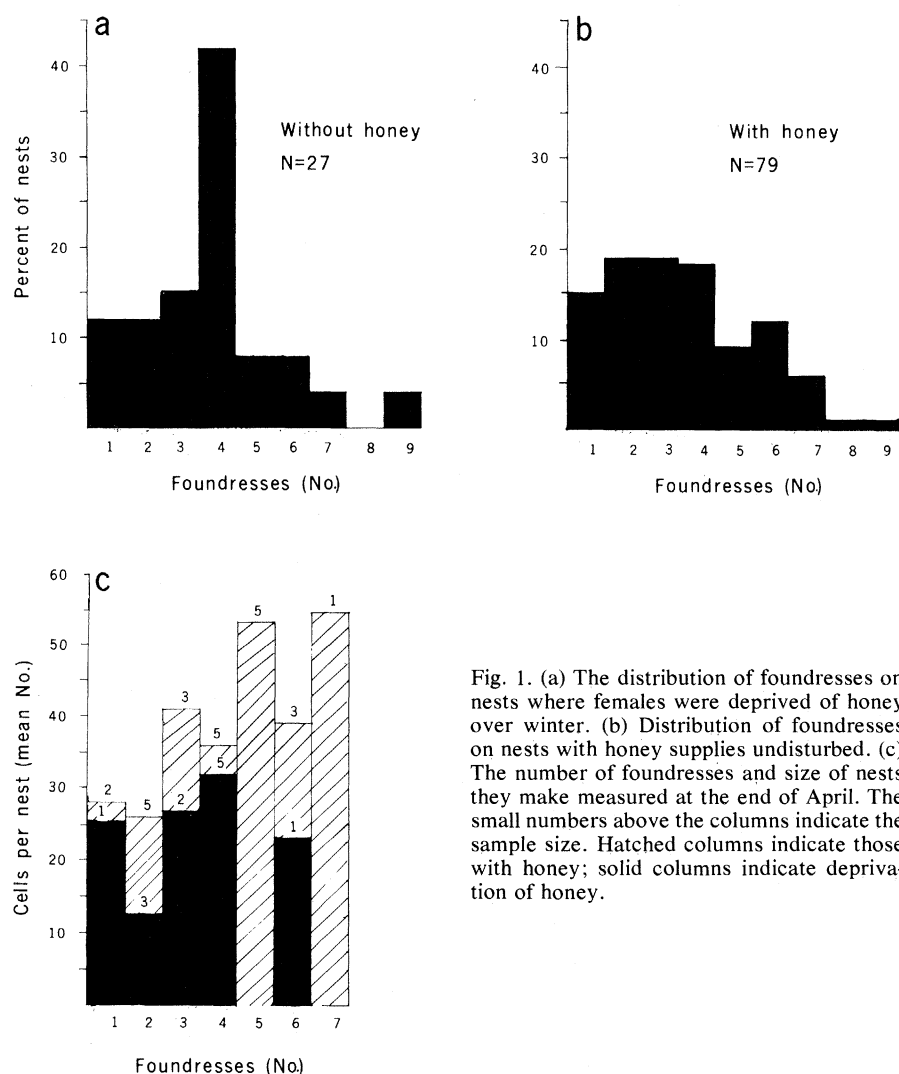


Fig. 1. (a) The distribution of foundresses on nests where females were deprived of honey over winter. (b) Distribution of foundresses on nests with honey supplies undisturbed. (c) The number of foundresses and size of nests they make measured at the end of April. The small numbers above the columns indicate the sample size. Hatched columns indicate those with honey; solid columns indicate deprivation of honey.

months. Since deficits in stored fat can be compensated for by honey, wasps without honey might be expected to be more variable relative to these indices of quality. Since sisters hibernate together and may control temperature fluctuations in the hibernaculum to some extent, winter survivorship was compared between nests that initially had the same number of females, with and without honey. It was possible to form 11 such pairs of equal numbers. Significantly more females survived the winter from nests with honey (Wilcoxon rank sum test,  $P < .01$ ,  $N = 11$ ).

If females without honey are in poorer condition, they will be expected to form larger foundress associations if larger foundress associations represent groups of females unable to form their own nests. With honey, the mean number of foundresses per nest was 3.64; females from nests without honey formed associations averaging 3.70. These means are not significantly different. The distribution of foundress number from nests with honey was not different from that found from nests without honey (Fig. 1, a and b) (Kolmogorov-Smirnov test,  $\chi^2 = 1.81$ , d.f. = 2; not significant).

A comparison of nest size just before workers emerge at the end of April, 2 months after nest initiation, was made to ascertain whether females without honey built smaller nests. Comparisons were made by pairs for one, two, three, four, and six foundresses. Females who did not have honey over winter built smaller spring nests (Wilcoxon rank sum test,  $P < .025$ ,  $N = 14$ ) (Fig. 1c).

To compare variability in quality between females with honey and without, Kendall tau correlations were calculated between variables that should be highly correlated if females are all of the same quality. The number marked in autumn was correlated with the number surviving the winter, the number surviving the winter was correlated with the number of new nests formed, and the number of foundresses was correlated with the number of cells in the nest after 2 months (Table 1). Differences in correlations between individuals that overwintered with honey as opposed to those without were significant. All three correlations were significant for wasps with honey, while only the correlation of foundress number and number of cells was significant in wasps without honey, and that one barely so (Table 1). It is clear that in all situations where the condition of the wasps could affect the outcome of the correlation, it is much lower for those without honey.

Depriving some wasps of honey is a

rather crude way of manipulating the component of their quality or condition determined by adult experience. While the results show that this was detrimental treatment to the wasps overall, there may have been some that were able to survive the loss of honey without ill effects. Perhaps some were able to steal honey from other nests. These would have been other nests in the study, since the two types of nests were intermingled. In addition, females with honey probably had different amounts depending on the number of females, the time that honey gathering was initiated, the nest size, and the number of workers surviving through the honey gathering period.

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- Wasps were marked by placing a plexiglass bucket on a pole over the nest. The wasps attacked the bucket, which contained ether, and hence were anesthetized. They were removed, placed on ice, and marked with Testor's PLA enamel on the thorax. After a quick recovery, they flew off. A different combination of colors was used for each nest. Laboratory and field longevity studies indicated that the ether had no long-term detrimental effects.
- To affirm this, I dissected presumed workers and presumed future queens. The large fat bodies and slightly developed ovaries of future queens always distinguished them from the yellow fat bodies and stringy atrophied ovaries of workers, and the predictions based on wing wear were always correct.
- Sometimes the fights were so intense that both females crashed to the ground and lay there for up to a minute grappling and trying to sting each other. Although no fatalities were observed, there were wasps lying on the ground on their backs, alive and twitching their legs, but apparently unable to move otherwise; these may have been stung.
- P. Rau, *Can. Entomol.* **73**, 196 (1941). Birds are often major predators on polistine nests, usually removing the nest and eating all the larvae. However, in this population of *P. annularis* bird predation was rare except during severe droughts.
- Local climatological data, Austin, Texas, obtained from the National Oceanic and Atmospheric Administration, Environmental Data Service, 1965-1977. These data were taken at a site 26 miles from the study site. The main difference between the two locations was that the study site had cooler nights; warm days and cloud cover were approximately the same for the two locations.
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- K. Eickwort, *Insectes Soc.* **16**, 67 (1969). I kept 15 groups of seven sisters each in a constant temperature room at 8°C for 2 months, interrupted by two warm days on which they were given a mixture of two-thirds brown sugar, one-third hydrolyzed yeast, and water. Under these conditions, only 3 of 105 wasps died during the cold period.
- This hypothesis is supported by the observation that in 1977-1978, honey was gone in early February, while in 1976-1977, honey remained in the nests until March when females permanently came out of hibernacula. This difference would be expected from an examination of the number of days available to feed on honey in the 2 years. In 1976 there were 12 days warm enough for honey feeding in November and December, while in 1977 there were 32 days in the equivalent period. In 1976 the wasps may not have had a chance to finish the honey, while they did in 1977. Which sort of year is more typical? A comparison with the last 13 years indicates that 1976 was the coldest year of all, 12 warm days being 16 days below the mean of 28 warm days for November and December. The number of warm days in 1977 was 4 days above the mean for the period, but is clearly much more typical. Thus honey is usually finished before spring nest founding, but the exact date depends on the number of warm days as well as the initial amount of honey stored.
- The entire reservoir was searched for additional dense populations of *P. annularis*, and only one other colony was found; it had 40 nests. Other cliffs nearby were searched, and only isolated nests were occasionally noted. Perhaps most important is that the cliff is in the shade until 3 p.m.
- Of the 40 nests marked in the fall, all females from seven of them left the area entirely in October. All sisters disappeared on the same day; there were no signs of predation. Since females have to be present to guard honey, migration could be a nest specific phenomenon, occurring before honey storage.
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4 April 1978; revised 28 August 1978

## Carbon Input to the Atmosphere from Forest Fires

Wong (1) estimated that forest fires and land-clearing fires release  $5.7 \times 10^{15}$  g of carbon per year into the atmosphere. Natural sinks remove most of this, but  $1.5 \times 10^{15}$  g year<sup>-1</sup>, almost exclusively due to new tropical clearing, constitutes 22 percent of the net input from all anthropogenic sources. However, Wong calculated the consumption of organic matter by applying a combustion efficiency of 0.75, derived from the experi-

mental burning of felled and partly dried logging debris (2), to total living phytomass, little of which burns. The result is that Wong overestimates by a factor of about 4 the gross carbon input from fires in the temperate and boreal zones. If, as seems likely, his estimates for the tropics are similarly exaggerated, the net carbon input from forest burning is much less significant.

Forest fires consume mainly detritus,