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) (Komolgorov-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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6. 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.
7. 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.
8. 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.
9. 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.
10. 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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16. 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.
17. 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.
18. 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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20. I thank R. Thomas for field assistance, Y. Hiraizumi, L. Lawlor, and W. Mueller for help with data analysis, and L. Gilbert, J. Smiley, J. Waage, and an anonymous reviewer for criticizing the manuscript. This research was supported by grant 5-T32-GM-07126 from the National Institute of General Medical Sciences, National Institutes of Health.

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Carbon Input to the Atmosphere from Forest Fires

Wong (*1*) estimated that forest fires and land-clearing fires release 5.7×10^{15} g of carbon per year into the atmosphere. Natural sinks remove most of this, but 1.5×10^{15} g year^{-1}, 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 experimental 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,

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that is, dead organic matter that accumulates over several decades. Even fires that burn through the tree crowns (which are much less extensive than is commonly believed) consume only foliage and some branch wood ≤ 0.6 cm in diameter. For a well-stocked stand of 60-year-old Douglas fir (*Pseudotsuga menziesii*) on a medium site in the Pacific Northwest (*3*), these components make up only 8 percent of the living phytomass above-ground (*4*). Fires in nonforest vegetation burn larger percentages but from much smaller standing stocks. Thus, one cannot realistically calculate the carbon yield in a single operation based on living phytomass.

Estimates of the mean consumption of living and dead organic matter by wildfires in the United States, made to determine the potential for air pollution, are 2.30×10^3 g m^{-2} (oven dry weight) for the southern 48 states and 2.46×10^3 g m^{-2} for Alaska (*5*). The means for individual states range from 0.7×10^3 g m^{-2} in areas where grassland predominates to 14×10^3 g m^{-2} in the heavily forested Pacific Northwest. The Alaska mean includes boreal forest and nonforest. The gross yield of carbon, calculated as 45 percent of the total dry matter (*6*) reduced by 7.5 percent for unburned particulates, is 0.97×10^3 g m^{-2}. For the temperate and boreal area burned annually worldwide (*1*, table 2), the gross carbon input based on the above figures is 0.11×10^{15} g $year^{-1}$, as compared with Wong's 0.47×10^{15} g $year^{-1}$. Wong may have overlooked prescribed burning of forest debris in the temperate zone for management purposes; however, the gross carbon from this source, calculated as above, would amount to only $\leq 0.02 \times 10^{15}$ g $year^{-1}$, not enough to reduce his overestimate appreciably.

I have not found fuel consumption figures for tropical land-clearing fires, but photographs commonly show much residual large-diameter wood, representing a considerable fraction of the phytomass from before the fire. Therefore, Wong's estimate of carbon input from tropical burning may be as much too high as that for the temperate and boreal zones. It would appear prudent not to depend heavily on the estimate until it can be checked against sample measurements.

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Fahnestock has pointed out the highly complex nature of the wood-burning process and an additional source of CO_2 from prescribed fires for wild-land management. For those working on the problem of the carbon budget and on the modeling and prediction of atmospheric CO_2 increase, the uncertainties in the terms used are well recognized (*1*) although not often stated explicitly. The crux of the carbon cycle is as crude as whether the terrestrial phytomass is a net source of CO_2 or not (*2–4*). A review of the fluctuating estimates of the input of CO_2 from the land phytomass (*4*) indicated a possible concensus in the recent literature toward a significant but much smaller contribution of CO_2 from wood burning. Fahnestock's comments help further this downward revision of the nonfossil CO_2 contribution.

My intent (*5*) was to derive, perhaps in a very speculative way, an upper limit for the CO_2 contribution from nonfossil wood burning. This derivation was based on the amount of phytomass burned and the area burned, both values subject to limitation of unreliable statistics and highly variable burning conditions. My lower estimate of new forest clearings of 7.5×10^{10} m^2 $year^{-1}$ (*5*), based on an increase in the rural population, is probably more reliable than the higher estimate of the Food and Agriculture Organization (United Nations) based on unreliable statistics, also pointed out by Bolin (*1*). This led to a lower net CO_2 input from nonfossil sources of about 18 percent of the fossil fuel CO_2 input (*4*). Using a combustion efficiency of 0.2 based on Fahnestock's comments and my lower estimate of new forest clearings, one obtains a net CO_2 input of 0.17×10^{15} g of carbon per year, slightly smaller than the soil carbon loss in agriculture. Thus, the total net carbon input from nonfossil wood burning and other sources amounts to about 0.6×10^{15} g $year^{-1}$, or about 12 percent of the fossil fuel sources. This lower limit is in line with Stuiver's (*3*) conclusion of a smaller reduction in biomass over the last few decades based on ^{13}C data and with the view of Broecker *et al.* (*6*) of a negligible contribution from wood burning (within the 10 percent uncertainty of their geochemical model).

It is important to obtain more data on the combustion efficiency of forest wood, a highly variable quantity between 0.2 and 0.75, affected by such environmental factors as the intensity of heat, humidity, wind, the duration of burning, and the nature of the woody material. Moreover, the charred remains of the unburned wood after fires may ultimately contribute through decay processes as net CO_2 input to the atmospheric CO_2 reservoir, over a longer time scale and with a similar difficulty in its quantification. Uncertainties in assessing other heterogeneous land carbon add immense difficulty to an understanding of the carbon cycle based on phytomass and soil detritus carbon in our terrestrial environment. The key to our future search for more reliable information on the global carbon cycle lies rather in an examination of the more homogeneous oceanic environment and its interaction with the atmosphere (*4*).

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