to the original formulations of learning theory, in which animals were supposed to be incapable of learning outside the context of performing the specific behavior that was being conditioned (16). Tolman (17), however, demonstrated the reality of learning out of context, or latent learning, in rodents: animals allowed to observe or explore in the absence of a food reward, for example, were later able to use information gathered during these episodes in performing tasks rewarded with food. He called this instrumental learning without performance of the relevant response a "cognitive map." Later work, particularly by Olton and his colleagues (18), indicates that at least higher vertebrates can plan behavior to make use of novel and efficient routes on the basis of maplike cognitive representations. The results of my experiments suggest that this ability, which is often considered a basic form of thinking (16), is not limited to vertebrates.

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10. Altitude was measured with a rangefinder for the first departure of each of the ten trained foragers displaced to site B; SD, ±2.3 m; observer-to-bee distance averaged 12.9 m.
11. One possible concern is that the trained foragers might be in the habit of visting the training and release site as part of a single route. This was not possible during training since only one site ever had food during the tenure of a given hive; moreover, foragers could be observed arriving directly from the hive direction, feeding to repletion, and then departing directly for the hive. The possibility is unlikely at other times as well: bees are flower and patch constant [T. D. Seeley, Honeybee Ecology (Princeton Univ. Press, Princeton, NJ, 1985)]. Moreover, care was taken to ensure that the natural flora in the open field site was different from that of the woodland path site; indeed, the latter had no flowers at all. Nor, given the extent of the woods to the northeast, could site A plausibly be imagined to be on a route to a hypothetical second patch, even if bees were in the habit of visiting multiple scattered patches on single trips? Sites C and D lacked flowers of any sort.
12. The unlikely possibility that bees are capable of nonvisual route–based navigation during displacement [J. L. Gould, Am. Sci. 68, 256 (1980)] is ruled out by displacement experiments performed in the absence of prominent landmarks [2; F. Otto, Z. Vergl. Physiol. 42, 303 (1960); J. L. Gould, thesis, Rockefeller University (1975)], in which bees departed as though they had not been displaced, and in the absence of familiar landmarks (7), in which bees were disoriented.
13. Statistics after E. Batschelet in Animal Orientation and Navigation, S. R. Galler et al., Eds. (NASA, Washington, DC, 1972), pp. 61–92. The tip of each mean vector lies at the "center of mass" of the vanishing bearings; a length of r = 1.0 corresponds to perfect clustering, and so the degree to which r < 1 is a measure of the scatter about the mean. (The value of r is normally used in place of SD in circular distributions, since SD can be approximated by taking the inverse cosine of r. There is no standard way of calculating the uncertainty in r). The z test compares the actual distribution to the predicted bearing. Since the first releases are consistent with the map hypothesis rather than the route-specific hypothesis, combining those data with the subsequent releases is justified.
14. P. K. Visscher and T. D. Seeley [Ecology 63, 1790 (1982)] showed, from measurements of dances in natural colonies, that most foraging takes place within about 2500 m of the hive, with a mean of 1700 m. Trips beyond 4000 m are extremely rare.
15. The maximum flight range of bees can be inferred from experiments in which bees were trained as far as possible; H. Knaffl and M. Lindauer [cited in K. von Frisch, The Dance Language and Orientation of Bees (Harvard Univ. Press, Cambridge, MA, 1967)] trained bees to fly as far as 12,000 m. Although unlikely, it is possible that the foragers took longer than normal to get their bearings so that they were out of sight when they became oriented, and their failure to return was a consequence of not having enough "fuel." To control for this possibility, 25 foragers were captured leaving the hive, transported in the dark to site E, fed honey (n = 10) or 2M sucrose solution (n = 15) to repletion, marked, and released; none of these bees returned.
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Memory Constraints and Flower Choice in Pieris rapae

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Darwin hypothesized that flower constancy in insects that feed on nectar results from the need to learn how to extract nectar from a flower of a given species. In laboratory tests, Pieris rapae, the cabbage butterfly, showed flower constancy by continuing to visit flower species with which it had experience. The time required by individuals to find the source of nectar in flowers decreased with successive attempts, the performance following a learning curve. Learning to extract nectar from a second species interfered with the ability to extract nectar from the first. Insects that switch species thus experience a cost in time to learn. These results support recent suggestions on the importance of learning in animal foraging.

IN 1876, DARWIN (1, P. 419) MADE THE following suggestions about the well-known flower species constancy of certain insects:

That insects should visit the flowers of the same species for as long as they can, is of great significance to the plant, as it favors cross-fertilization of distinct individuals of the same species; but no one will suppose that insects act in this manner for the good of the plant. The cause probably lies in insects being thus enabled to work quicker; they have just learned how to stand in the best position on the flower, and how far and in what direction to insert their probosides.

As pointed out by Waser (2), this hypothesis implies that a limited memory capacity can be one cause of floral constancy: were the insect able to recall nectar extraction methods of more than one species, there would be less need for constancy (3). Despite recent emphasis on the potential role of learning in animal foraging (4), this hypothesis has received little empirical attention. I present here results for Pieris rapae, the cabbage butterfly, that support Darwin's hypothesis: (i) the insect displayed flower constancy, (ii) the insect learned how to extract nectar from

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flowers, (iii) learning a second species interfered with recall of the first, and (iv) experience with a flower species influenced choice between species.

Recent field observations suggest that some butterfly species, including P. rapae, exhibit the constancy reported for certain bee species (5). This possibility was tested with Bateman's procedure (6) in which the insect is given a binary choice with equal quantitites of both species. The identities of the first and second species used are recorded; constant insects will feed from the same species on both visits irrespective of their initial preference. Both preference and constancy influenced choice in P. rapae: most butterflies initially fed from Vicia cracca in test 1 and from Lotus corniculatus in test 2 (Table 1). Thus, initial preference depended on the identities of the test species, but in both tests, butterflies continued to feed from the species they initially fed from, demonstrating constancy.

To determine if butterflies exhibit the kind of learning hypothesized by Darwin as an explanation for constancy, caged, individually marked butterflies were given flowers and their behavior was observed. When butterflies first land on a flower, they search the sepals and corolla with their probos-

Table 1. Tests of constancy. Frequencies of initial and second feedings of butterflies given binary choices. Tests 1 and 2, χ^2 with Yates's correction (6), $P < 0.001$.

First feeding	Second feeding		
	V. cracca	L. corniculatus	C. rotundifolia
	Test 1		
V. cracca	67	5	
L. corniculatus	7	21	
	Test 2		
C. rotundifolia		8	24
L. corniculatus		68	0

cides, eventually finding the source of the nectar. I term the time elapsed from landing to finding the nectar "discovery time"; it does not include the time to actually drink the nectar or to move between flowers. Discovery times on both *Campanula rotundifolia* and *L. corniculatus* improved with successive attempts in most butterflies as exemplified by the curves in Fig. 1 (7). Initial times varied among butterflies as among bees (3), but the discovery times of most butterflies followed a classic learning curve (8). These curves are well fit by a power law (9). Such learning occurs in some bees (3); to my knowledge, this is the first demonstration of it in the Lepidoptera (10).

Exceptions to these patterns are two butterflies on *C. rotundifolia* that gave up their search before contacting nectar, and two on
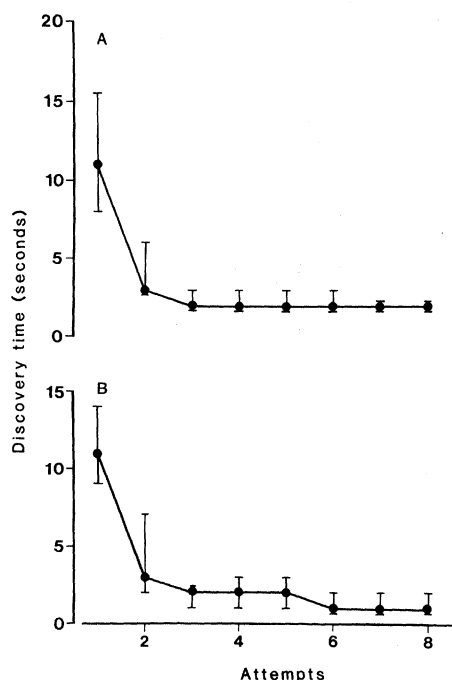

Fig. 1. Discovery times for butterflies given either (A) *C. rotundifolia* (*n* = 24) or (B) *L. corniculatus* (*n* = 18). Data shown are medians and first and third quartiles.

L. corniculatus whose performance was erratic. These butterflies initially approached the flowers from the back of the corolla and contacted nectar. They were rewarded for this incorrect approach and were apparently unable to learn (within eight attempts) an approach that more reliably gave them nectar.

To test for interference of this learning by the learning of a second species (11), individually marked butterflies were divided into two groups. Individuals of both groups were given *C. rotundifolia* to learn until a minimum of five and a maximum of ten successive discovery times did not exceed 3 seconds each. Butterflies of group 1 were then given *L. corniculatus* to learn until discovery times did not exceed 2 seconds each. Individuals of group 2 were given no flowers for 20 minutes, the maximum time required by individuals of group 1 to notice and reach criterion on *L. corniculatus*. Individuals of both groups were then tested on *C. rotundifolia*. Butterflies that fed on *L. corniculatus* had to relearn *C. rotundifolia*, whereas those without flowers during the same time period did not have to relearn: final learning times and initial test times on the two rounds of *C. rotundifolia* were significantly different for group 1 butterflies but not for group 2 (Fig. 2) (12). This result suggests that interference has occurred, although it is possible that discovery times of group 2 were shortened by hunger. This possibility is weakened by the observation that those butterflies in group 1 that had the option of feeding on *L. corniculatus* but did not choose to do so, possibly because they were not sufficiently hungry, have final and test discovery times similar to butterflies not given *L. corniculatus* ($\overline{X} \pm$ SEM: final, 2.2 ± 0.14; test, 3.13 ± 0.73; $n = 15$).

These results on interference support Darwin's hypothesis for the two test flower species: switching has a cost in time to learn. This potentially translates into both an energetic cost (13), as this butterfly when adult depends on nectar for 56 percent of its energy budget (14), and a possible increased risk of predation (15).

It is necessary for Darwin's hypothesis that butterflies choose to visit those flowers they have learned to handle, the choice resulting either from increased preference (16) or the formation of a search image for those flowers (17). As a test, I gave caged butterflies either *L. corniculatus* or *V. cracca* for 24 hours. In subsequent choice tests in which both species of flowers were available, a significant number of butterflies chose the species they had received previously: 80 percent experienced with *V. cracca* and 73 percent from *L. corniculatus* (*n* = 15 each, $P < 0.025$, χ^2 with Yates's correction).
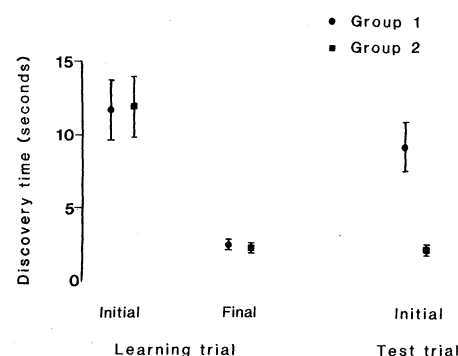

Fig. 2. Test of interference of learning. Group 1 (*n* = 17), exposed to *L. corniculatus* between learning and test trials with *C. rotundifolia*, and group 2 (*n* = 20), exposed to no flowers during a similar period, were used to evaluate the difference between final and test times: group 1, $P < 0.01$, paired *t* tests; group 2, NS (12).

Implied in Darwin's hypothesis is a fifth condition: that the cost of learning nectar extraction exceeds other costs associated with specialization [for example, increased travel time between flowers, (2, 3)]. These costs doubtless vary among habitats differing in resource concentration and for insects in various physiological states; such variation may in part explain observations of inconstant insects (18). A complete explanation of flower choice will unite studies of learning and of these important ecological variables.

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31°C. Butterflies were introduced individually into a 45 by 45 by 45 cm cage containing eight equal-sized inflorescences of the two test species in water vials arranged in a 4 by 4 alternating array. Sample sizes were 42 for test 1 and 37 for test 2.

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Bacterioplankton: A Sink for Carbon in a Coastal Marine Plankton Community

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Recent determinations of high production rates (up to 30 percent of primary production in surface waters) implicate free-living marine bacterioplankton as a link in a "microbial loop" that supplements phytoplankton as food for herbivores. An enclosed water column of 300 cubic meters was used to test the microbial loop hypothesis by following the fate of carbon-14–labeled bacterioplankton for over 50 days. Only 2 percent of the label initially fixed from carbon-14–labeled glucose by bacteria was present in larger organisms after 13 days, at which time about 20 percent of the total label added remained in the particulate fraction. Most of the label appeared to pass directly from particles smaller than 1 micrometer (heterotrophic bacterioplankton and some bacteriovores) to respired labeled carbon dioxide or to regenerated dissolved organic carbon-14. Secondary (and, by implication, primary) production by organisms smaller than 1 micrometer may not be an important food source in marine food chains. Bacterioplankton can be a sink for carbon in planktonic food webs and may serve principally as agents of nutrient regeneration rather than as food.

UNTIL RECENTLY, BACTERIA WERE viewed as relatively minor components of marine plankton communities (*1*). That view is now being revised as a result of new discoveries by marine microbiologists. Free-living heterotrophic bacterioplankton less than 1 μm in diameter may constitute up to 20 percent of the carbon biomass in marine coastal waters (*2–4*). With gross growth efficiencies of over 50 percent (*5*) and rapid growth rates often surpassing two divisions per day (*6*), bacterioplankton are potentially important biomass producers (*2, 7*). This discovery has prompted the hypothesis that bacterioplankton could be an important source of nutri-

tion at the base of plankton food webs, supplementing phytoplankton in the diets of microzooplankton (*3, 8*). However, researchers have concluded that heterotrophic microflagellates 2 to 10 μm long are the principal predators of bacterioplankton because larger grazers are not capable of efficient removal of micrometer-sized prey (*9, 10*). It is believed that these small bacteriovores are grazed in turn only by ciliates or the smallest juvenile stages of other planktonic forms. Thus the large bacterial production may enter the classical marine metazoan food chain only via the protozoa (*2, 8*) and not directly.

Bacterioplankton and their predators form the hypothetical "microbial loop" that returns to the main food chain energy lost as dissolved organic matter (DOM) (*2, 3, 8*). Although bacteria appear to scavenge DOM released by phytoplankton (*2, 5, 6*) and herbivores (*2, 11*) with great efficiency, the extent to which bacterial production is a salvage pathway supplementing primary

production as food for herbivores remains uncertain. This speculation about the trophic structure of microbial food webs has been termed the link versus sink question (*5, 12*). Are bacteria a source of carbon for higher organisms, or are they mainly the terminal group in a detrital food chain?

We report the results of a large-scale experiment designed to examine the fate of bacterial production in a representative coastal marine plankton community. Most studies of production and grazing by marine and freshwater plankton have been performed in containers at most a few liters in volume (*13*). Such experiments are easy to replicate, but sampling, surface-volume effects, and containment lead to serious artifacts that affect the various components of
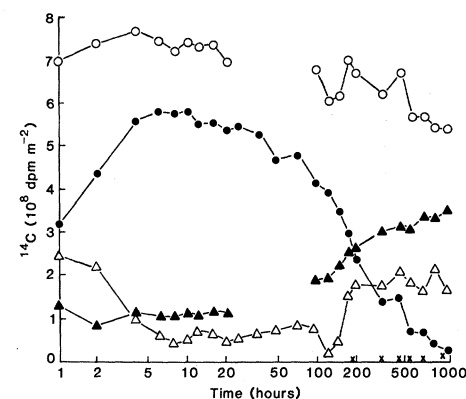

Fig. 1. Partitioning of labeled carbon initially fixed by bacterioplankton from [^{14}C]glucose inoculated throughout the enclosed 15-m water column. The dissolved label was initially removed from solution by bacterioplankton; it later reappeared in solution as dissolved organic and inorganic carbon. Total water column content of ^{14}C label was estimated by integrating data from six depths (2.5, 5, 7.5, 10, 12.5, and 15 m) and by pumping out a collecting cone at the bottom of the enclosure. Symbols: (○), total label; (●), ^{14}C-labeled POC; (△), ^{14}C-labeled DOC; (▲), ^{14}CO$_2$; and (×), sediment. Breaks in lines indicate missing samples. The experiment began at noon on 12 May 1983.

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