Table 2. $\delta^{15}N$ values for the uptake of $^{15}NO_2$ and ^{15}NO in isolated cuticular membranes (CM) and matrix (MX) of spruce needles and cuticular membranes isolated after fumigating the trees (CM*). Exposure concentrations are the same as in Table 1. $\delta^{15}N$ values are given as means with 95 % confidence intervals in parentheses

Chamber	$\delta^{15}N_{CM}$[‰]	$\delta^{15}N_{MX}$[‰]	$\delta^{15}N_{CM^*}$[‰]
1	10.3	6.8	12.5
	(−1.42−22.06)	(1.20−12.38)	(8.9−16.1)
4	363.3	463.8	468.0
	(355.1−371.4)	(424.0−503.5)	(449.2−486.7)

and there is a significant difference between CM and MX, indicating a preferential fixing of NO_x to the polymer matrix in this object.

The purpose of this study was also to explain the influence of the isolation process on the uptake of $^{15}NO_x$. Therefore, spruce trees were exposed in chamber 1 and 5 and the CM was isolated after exposure (Table 2). The uptake into the cuticle of a leaf in vivo is significantly higher than the uptake in the isolated cuticle in case of *P. abies*. Therefore, it is supposed that the isolation procedure has an effect on the uptake capacity of the cuticle.

It may be concluded that NO_x is taken up by plant cuticles during exposure to real atmospheric concentrations. Since, as mentioned above, 100 % NO_2 leads to a higher water permeability of the cuticle, it remains to be investigated, if real atmospheric concentrations of NO_x also impede important functions of the cuticle such as the protection from water loss or permeability for other substances.

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Ants that Go with the Flow: a New Method of Orientation by Mass Communication

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Ants use a variety of cues to assist in orientation outside their nests. These include pheromones [1], visual landmarks [2], forest canopy patterns [3], and the sun [4]; sometimes several cues are used in combination [4, 5]. Workers of the Southeast Asian ant *Pheidologeton diversus* orient along chemical trails [6], raiding in columns and swarms from a stable trunk trail [7]. Food is retrieved singly or by groups. Experiments reported here demonstrate that laden ants alter their course on trails according to the directions taken by laden nestmates. This is the first documented case of social insects using the direction of movement of nestmates as an orientation cue. This orientation mechanism assures a nestbound flow of food at trail junctions and is crucial in coordinating mass responses to disturbances, and thus represents a new form of mass communication [8].

Previous studies showed that when a column of seeds from a canary-food mix was laid so that it extended from an active trail, ants advanced along the column and quickly began to retrieve the seeds [9]. In the study reported here, a seed column 1.5 to 2.0 cm wide and 1.5 to 4.5 m long was laid in a loop from one point on a trunk trail to another. Groups of ants advanced along both ends of the column as soon as workers found the seeds (Fig. 1A). Eventually ants circled the whole loop. In five experiments [10], ants kept closely to the seed column, and the results were clear-cut. The original transport directions used by ants moving along either side of the loop (Fig. 1A) were maintained after the troops met at the top of the loop. Thus seeds were carried away from the place where the troops had met (the "transition area"; Fig. 1B). Few laden ants moved in directions opposite to those shown in Fig. 1B, and any that did soon reversed course. Within the transition area itself (which was roughly 2 to 8 cm long), the direction of food transport was inconsistent.

Typically, numerous unladen ants walked by each point on the loop in both directions within any given min-

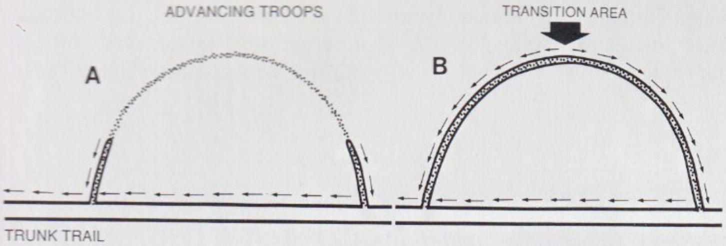

Fig. 1. The pattern of worker advance and food transport on a column of seeds laid in a loop connecting two points along a trunk trail. The trunk trail crosses the bottom of the drawing. The seeds are indicated by dots; the location of ants is indicated by the narrow bordered columns; the direction in which seeds are transported is indicated by the small arrows. See text

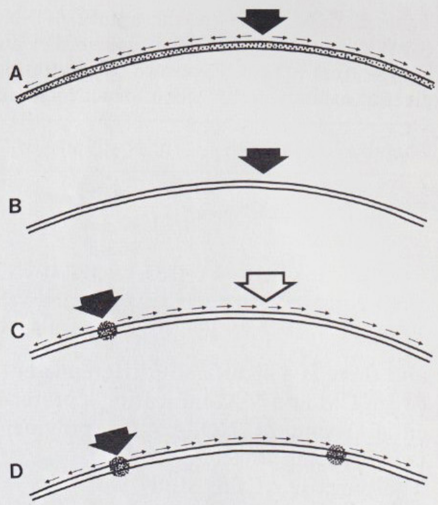

Fig. 2. Experiments using the seed column arrangement diagrammed in Fig. 1. Here only the portion of the seed column near the transition area is presented. Symbols as in Fig. 1. Large black arrows indicate the current transition area; large open arrows indicate the previous transition area. See text

Table 1. Data for the directions selected by burdened ants at two distances from the transition area. Burdens were sampled as they crossed marked points on the trail. More burdens passed by points farther from the transition area ($p<0.001$, Student's t-test). Burdens carried toward the transition area were denoted as "heading in the wrong direction"; such mistakes were most frequent near the transition area ($p<0.001$, Chi-square test)

Distance from transition area	Number of burdens passing by in five 1-min intervals ($\bar{X}\pm$S.D.)	% of burdens heading in the wrong direction
150 cm	30.6 ± 5.5	0 ($n=233$)
40 cm	9.0 ± 5.6	10.1 ($n=$ 69)

ute. These ants freely crossed the transition area. Moreover, ants picking up a seed turned around for retrieval if they had not yet reached the transition area ($n=11$), but continued with the same bearing taken previously if they had passed that area ($n=6$).

These observations suggest two hypotheses: The trails laid by the advancing troops are polarized, and this polarization is used by laden ants as an orientation cue (Polarization Hypothesis); burdened workers orient by responding to the movements of other ants, most likely other laden ants (Flow Hypothesis).

The Polarization Hypothesis was disproven with the following experiment ($n=5$). After marking the transition area (Fig. 2A), workers were allowed to remove most seeds until little or no transport occurred (Fig. 2B). Now a seed clump was placed on the loop some distance from the transition area. If laden ants were orienting with respect to a polarized trail, workers taking seeds from the pile should walk in the single direction indicated by the trail at that point; if they were guided by other laden ants, the paucity of such ants should permit them to go in either direction. In fact, numerous seeds were carried in both directions (Fig. 2C). When a new seed column was laid all along the course of the old loop, the transport directions established by the seed pile (Fig. 2C) remained unchanged along the loop thereafter.

As a test of the Flow Hypothesis, a new seed pile was deposited on the established route while retrieval from the old site was brisk ($n=7$). Even though unladen ants arrived at the new pile from both directions, there was no change from the previous transport pattern (e.g., Fig. 2D). Yet if the new pile was replenished while the old one was allowed to dwindle, this pattern eventually shifted so that all seeds were carried with reference to the new pile ($n=4$). Thus laden ants appear to use the courses taken by other porters as orientation cues.

The frequency with which porters initially made directional errors was correlated with distance from the transition area (Table 1). Presumably, this occurred because the number of laden ants passing by on the trail at any given time increased with distance from the transition area (Table 1); thus, workers near the transition area received less information on which direction to choose. Perhaps also for this reason burdened ants moved slowly and more erratically near the transition area [11]. Observations on normal colony trunk trails support the view that laden ants rely on each other for directional information. When I deposited a pile of seeds onto each of four trails with bidirectional worker traffic but little food transport, some ants arriving at the baits carried off seeds in the wrong direction. Indeed, in two cases a few remained outbound for several meters, reaching the end of a trail and milling about before reversing course. When seed piles were placed on trails with vigorous food retrieval, all ants taking seeds headed in the correct direction, after walking, at most, about 5 cm in the wrong direction.

Ants with food sometimes initially took a wrong direction at trail intersections. Errors were much more frequent for trails with light traffic, indicating that the ants were probably guided by the presence of laden workers passing by on the new route.

Results on disturbed trails (such as trails hit by a falling branch) were also instructive. Burdened ants reaching the point of disturbance backtracked, clearing the disturbed area of food [9]. Most nestbound ants meeting the back-

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flow also reversed course. If the backflow proceeded along a heavily-used route, ants soon began to turn around as a result of confronting a continuous flux of laden ants heading in the correct direction. On routes with light traffic, however, the backward surge of ants sometimes continued all the way to the trail's end.

Sometimes workers were forced to alter their course because of physical conflict with the overwhelming numbers of ants moving the opposite way. Yet physical contact between ants was probably not necessary for course shifts to occur. Indeed, a worker often passed laden ants heading the opposite way without reacting, only to reverse course later when no such ants were near. It is conceivable that such workers were responding to returning ants other than those with burdened mandibles (e.g., those with replete crops). In any case, directional changes are apparently not made in response to single incidents of course conflict; rather they are the result of a broad assessment by the workers of traffic patterns. This orientation mechanism therefore represents a new form of mass communication (the transfer of information among groups of individuals [8]). In *P. diversus* this mechanism is crucial to the emergence of complex, coordinated group behavior during trail disturbances and at trail junctions, despite the underlying simplicity of the responses made by individual ants.

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10. Most experiments ($n=17$) were unsuccessful, in that ants began raiding out from the column to form trails that cross-linked various parts of the loop. Burdened ants on these trails moved in differing directions
11. In one experiment, 20.5 ± 10.7 s/5 cm ($\bar{X} \pm$ S.D., $n=12$) for ants working in groups of three to carry seeds at 0.5 m from the transition area, compared to 7.9 ± 1.4 ($n=12$) for similar groups at 1.5 m from that area; $p<0.01$, Mann-Whitney U test

