intensive and characteristic (*7*, *8*) preening activities. Even the vapors from the effluent were repellent: wetted mouthparts of larvae previously attacked or alerted were usually avoided just short of actual contact by the approaching ants. Tests with lycosid spiders, caged singly and starved for several days before being offered individual larvae, gave comparable results. The spiders pounced on the larvae, but desisted and began cleaning themselves as soon as they were dabbed with effluent. Only one of eight larvae tested received visible (and eventually fatal) injury from the bite of a spider.

The two pinenes are in themselves "obnoxious" to arthropods. Droplets of chromatographically purified α- and β-pinene, applied to the abdomen of decapitated cockroach nymphs (*Periplaneta americana*), elicited prompt scratching with the hind legs (*9*), and capillary tubes filled with either terpene and held close to the proboscises of tethered flies (*Lucilia cuprina*) induced reflex-cleaning of the proboscis (*10*). Pieces of filter paper (2 by 2 mm) impregnated with either pinene and placed in the midst of ants (*Pogonomyrmex occidentalis*) feeding at a bait (crushed grasshopper thorax) beside the entrance to their natural nest, induced quick dispersal of even those ants which had merely come into proximity with the papers. Ants directly contacted cleaned themselves vigorously. No comparable effects were elicited with papers impregnated with resin acids alone (*11*). Papers impregnated with oral effluent, or with an approximate replicate of the effluent (*12*), also had a dispersing effect. Moreover, the effectiveness of such papers always outlasted that of counterparts soaked in pinenes alone, indicating that the viscous matrix of resin acids has a retarding effect on the evaporative loss of pinenes. The resin acids may therefore act only physically, as viscid topical contaminants, and as fixatives for the pinenes. Interestingly, α- and β-pinene are also known from the defensive spray of certain termites (*13*). This fluid, a glandular product seemingly produced by the termites themselves, is also resinous in character, but the chemistry of the resinous base is unknown.

Despite its proven effectiveness, the chemical defense of *Neodiprion* has its shortcomings. A number of enemies successfully parasitize the larvae, or prey upon them, both before and after the larvae have spun their cocoons (*2*, *14*), and these enemies must have ways of tolerating or circumventing the defense.

The utilization by an animal of an unaltered product of exogenous origin has implications of interest. The resin of *Pinus* is to be viewed as a chemical defense of the tree itself. It has repellent qualities and serves for wound healing, and hence must contribute in a number of ways toward reducing the vulnerability of the plant. What *Neodiprion* has evolutionarily achieved is to "crash" through the chemical defenses of its host, without detoxifying or otherwise inactivating the weaponry involved. It simply appropriates intact the resin of the plant, thereby obviating the need for metabolic production of an alternative defensive agent of its own. One wonders to what extent the defensive enteric discharges of animals generally derive their effectiveness from unaltered dietary components. In fact, the whole question of transmission along food chains of nonnutritive substances (*15*), and of the use to which these substances are put as they are relayed with or without alteration from one link to another in a chain, is worthy of increased consideration.

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5. These lateral extensions of branch resin canals are said to end blindly in the base of the needles without merging with the resin canals of the needles [V. Mozheiko, *For.-Chem. Ind. (U.S.S.R.)* **2**, 44 (1933)]. Our finding that branch resin and needle resin differ chemically is in line with this claim. Older larvae also chew sporadically into the bark of twigs, and are sometimes seen with their mouthparts dipped in the resin that bleeds from such injuries, as if drinking from the outflow.
6. The quantitative assays involved gas chromatographic comparisons with standardized solutions of authentic samples of the terpenes.
7. Such cleansing activities, as induced in ants under comparable experimental circumstances, have been described elsewhere (*8*).
8. T. Eisner, J. Meinwald, A. Monro, R. Ghent, *J. Insect Physiol.* **6**, 272 (1961).
9. Such scratch reflexes are a useful criterion for evaluation of irritancy of topically applied materials (*8*).
10. The flies responded by extending the proboscis, emitting a droplet of regurgitate onto the labellum, and wiping the labellar tip against the substrate or other available surface. This cleansing response is also elicited by benzoquinones, phenols, short-chain aliphatic acids, aldehydes, and ketones, and by other "noxious" volatile substances (T. Eisner, unpublished).
11. Pimaric, levopimaric, dehydroabietic and abietic acids were individually tested.
12. The artificial effluent had the following composition: 1 percent α-pinene, 1 percent β-pinene, 68 percent levopimaric acid, 14 percent pimaric acid, 14 percent abietic acid, and 2 percent dehydroabietic acid.
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# Pheromone-Regulated Anemotaxis in Flying Moths

*Abstract*. *Certain male moths flying upwind toward a scent-producing female appear to be guided anemotactically by optomotor reactions to the ground pattern. Loss of the odor stimulus changes the anemotactic angle from into wind to across wind with left-right reversals.*

For some years it has been generally held that insects steer toward a distant odor source not chemotactically but anemotactically, by turning into the wind when they receive an odor stimulus (*1*). In flying insects this anemotactic orientation has been assumed to depend on optomotor reactions to the apparent movement of the ground pattern. However, as far as sex pheromones are concerned, no experimental evidence for optomotor anemotaxis exists, and a chemotactic guidance mechanism has recently been proposed

(2). We now report new evidence on optomotor anemotaxis in male moths stimulated by wind-borne female sex pheromones.

Experiments were carried out in a wind tunnel (3) 1.8 m long, 1.2 m wide, and 1.5 m high with diffused "daylight" fluorescent top lighting giving about 300 lux at floor level and with a carpet of alternate black and orange transverse stripes 0.15 m wide, which could be moved in either direction along the tunnel. The main experiments were done on *Plodia interpunctella* at 25°C in wind speeds of 0.17 to 0.22 m $sec^{-1}$ during the 7th to 10th hours of the insects' photophase (12 hours light and 12 hours dark; LD 12 : 12).

Two "calling" females were placed in the middle of the upwind end of the tunnel 0.1 m above the floor. A male released into the downwind end of the wind-borne pheromone plume took off and flew upwind toward its source in a series of diminishing, irregular zigzags while the floor stripes were stationary. If the floor stripes were now moved downwind thus increasing the apparent ground speed of the flier, it reduced its airspeed accordingly and was consequently carried downwind at the same height while still facing upwind and zigzagging. In this way males could be entirely prevented from approaching the females.

Quantitative results were obtained by noting the displacement of single males from the moment they crossed an imaginary transverse line midway along the tunnel until they crossed another imaginary transverse line either 0.55 m upwind or 0.55 m downwind, (i) when the floor stripes were stationary and (ii) when they were moved in a downwind direction. Such tests were repeated as long as a male continued to fly, up to a maximum of 16 successive tests (eight of each kind) in one unbroken flight (4). The results of 319 tests made during 47 flights by 14 individual males of *P. interpunctella* are summarized in Table 1. We infer that the males moving upwind toward a source of female scent were responding to the visible ground pattern, as use of optomotor anemotaxis would require (5).

Similar results were obtained with *Anagasta kühniella* and *Cadra cautella*. The optomotor response was so strong that it was possible to take the male upwind beyond the source of the pheromone, by moving the floor stripes upwind and thereby reducing the male's apparent ground speed. It has been reported (6) that *Drosophila* flying toward a source of fermenting fruit odor can likewise be driven to and fro in a wind tunnel by moving the floor pattern.

Table 1. Frequency of movements upwind and downwind by pheromone-stimulated flying males of *Plodia interpunctella* when the transverse stripes on the floor of the wind tunnel were either stationary or moving with the wind away from the odor source.

| Floor stripes | Frequency of movement (No.) | |
|---|---|---|
| | Upwind | Downwind |
| Stationary | 151 | 15 |
| Moving downwind | 0 | 153 |

It has also been reported, for various flying insects including *Drosophila* (6) and *A. kühniella* (7), that, when the insect emerges from an odor plume either laterally or by overshooting the source and the odor stimulus therefore ceases, the insect then turns into a crosswind track which reverses at intervals between left and right. But again, quantitative evidence has been lacking. Moreover, this behavior is usually referred to as "casting" or even simply as "searching" and is not identified explicitly as anemotactic.

In order to establish quantitatively that casting is indeed anemotactic, we released males of *C. cautella* singly within a longitudinal corridor 0.15 m wide marked down the center of the floor of the tunnel, in a wind of about 0.22 m $sec^{-1}$ and over stationary floor stripes. At a point 1.0 m upwind of the release point and 0.07 to 0.1 m above the floor of the corridor, one pair of forceps carrying the extruded abdominal tip of a virgin *C. cautella* female and a second pair of empty, control forceps were held separately at the tips of two narrow rods projecting in from an aperture in the tunnel wall. When a flying male, stimulated by the pheromone, had advanced upwind along the central corridor to a point 0.45 m downwind of the two pairs of forceps, one of them was swung rapidly upward so that any odor emanating from its tip passed down the tunnel about 0.7 m above the male. For the next 3 seconds a count was made of the number of times the male flew out of the central corridor to either side. The male was then taken back, still flying, to the downwind end of the tunnel (by moving the floor stripes that way) and the same procedure was repeated, and this time the other pair of forceps was removed.

Each male was thus scored for lateral excursions from an upwind track over the same length of time and the same stretch of tunnel, once in the continued presence of the pheromone and once immediately after it had disappeared, the changes in the insect's visual field being the same in each case. The sequence of treatments was reversed for successive males. The paired treatments were given to the same 14 individual males in two successive series. In each series the results differed significantly between the two treatments ($P < .01$, Wilcoxon matched-pairs, signed-ranks test). The males flew out of the central corridor a total of 109 times when the odor source was removed and only 31 times when it remained upwind of them. After odor removal the males' tracks quickly shifted to an angle of about 90° to the wind and reversed left and right at lengthening time intervals (Fig. 1).

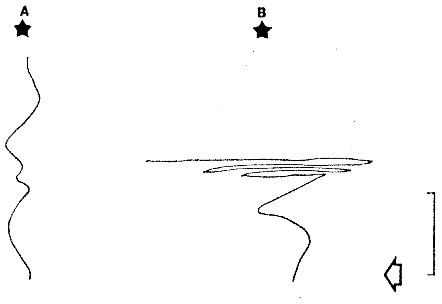

Fig. 1. Two 3-second flight tracks (based on videotape records) of the same male *Cadra cautella* after its arrival by upwind flight at a point 0.50 m from a source of female scent. (A) The source remained throughout in the upwind position marked by the star. (B) The source was removed as soon as the male reached the level of the arrowhead so that the male entered unscented air after traveling approximately 0.15 m further upwind. The scale is 0.15 m.

To check whether this 90° casting could have been guided along the transverse floor stripes rather than anemotactically, the experiment was repeated with the use of a floor bearing white spots 0.10 m in diameter with centers 0.20 m apart on a black ground and aligned in rows in two directions only, at 30° and 60° to the tunnel axis. The results were substantially the same; altogether 200 excursions were made from the corridor when the odor source was removed and 48 when it remained. In only 1 out of 60 pairs of treatments with 12 moths did the male make more excursions with the odor still present than when it had gone. The flight tracks again became transverse after pheromone removal (8), and we infer that the effective orienting stimulus was not the floor pattern itself but its apparent movement caused by the wind.

It thus appears that sudden cessation of a strong odor stimulus resets the moth's anemotactic angle, causing the moth's course to deviate from the upwind direction until the zigzags of its track become perpendicular to the wind. In addition, the intervals between the successive track reversals to right and left of the wind line increase as time passes. In practice, flight paths remain more or less upwind only when the wind is uniformly permeated with the odor (*6, 7*). With an odor plume from a small source the stimulation is discontinuous within the plume as well as between it and the surrounding air (*2, 6, 7*), and the typical flight track consists of irregular zigzags obliquely upwind along the plume (Fig. 1A) (*2, 7*). These left-right reversals, also, could be anemotactic reversals if we postulate that the anemotactic angle is variable, being some function of the odor stimulation. Such a system would give a strong impression of chemotaxis.

This anemotactic hypothesis does not exclude some role for chemoklinokinetic or even chemotactic responses, although evidence for the latter is scant (*9*). An experiment reported by Farkas and Shorey (*2*) suggested that *Pectinophora gossypiella* males can follow a pheromone trail in stationary air, but it seems to us inconclusive since the males had in every case taken off into the odor plume while the wind was still blowing. The possibility is therefore not excluded that their flight direction had been set anemotactically before the wind stopped. When they entered clean stationary air, after being exposed to odor-bearing wind and then to clean wind [condition 3 of Farkas and Shorey (*2*)], they diverged from the central axis of the tunnel, instead of staying close to it as they did when a stationary odor plume was there. This does not necessarily mean that the odor trail guided them chemotactically, for they would be expected to deviate when they entered the clean wind if *P. gossypiella*, like the other moths above, starts casting when the odor disappears from the wind.

Quoting unpublished experiments by Meyer on males of *Plodia interpunctella* with crossed-over antennae, Shorey (*10*) suggests a chemotropotactic mechanism of guidance along an odor plume. Since removing one antenna would likewise be expected to prevent tropotactic orientation, we have performed this operation on 14 male *P. interpunctella* and released them downwind of a calling female. Ten took off and flew in zigzags upwind to the female in a manner indistinguishable from that of intact males; the other four failed to respond at all.

We are led to conclude that, although the mechanism of odor-regulated optomotor anemotaxis remains largely unanalyzed, it is still the most plausible guidance mechanism for the male moths studied so far.

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4. Males that crossed the upwind line were brought back to the midline for the next test by moving the stripes in that direction. Those that crossed the downwind line returned upwind spontaneously when the stripes were stationary.
5. On the few occasions when a male continued to fly for many seconds in the tunnel with no wind or odor plume, it was observed to orient itself with stripe movement and fly at about the same speed and to turn around accordingly through 180° whenever the stripe movement was reversed. Visually, this is equivalent to orienting into wind.
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# Behavioral Thermoregulation in Lizards: Importance of Associated Costs

Abstract. *The Puerto Rican lizard* Anolis cristatellus *behaviorally regulates body temperature in an open habitat but passively tolerates lower and more variable temperatures in an adjacent forest where basking sites are few and distant. Thermoregulation may be adaptive only when costs resulting from associated losses of time and energy are low.*

Many lizards behaviorally regulate body temperatures within a narrow range by shuttling between sun and shade or hot and cold microenvironments to alter heat flux (*1*), by modifying posture to alter surface areas exposed to heat sources or sinks (*2*), and by regulating activity times (*3*). When costs resulting from associated losses of time and energy (*4*) are substantial, thermoregulation to optimal levels is impractical (*5, 6*); indeed, some lizards rarely thermoregulate (*7, 8*). In theory one could predict the amount of thermoregulation that would maximize net benefits within a habitat by measuring the costs and benefits of achieving specific body temperatures. In practice I estimate a correlate of certain costs and demonstrate that a tropical Puerto Rican lizard, *Anolis cristatellus* (*9*), thermoregulates less carefully in habitats where this cost is great.

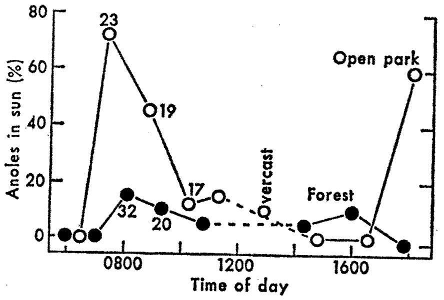

Fig. 1. Percentage of *A. cristatellus* perched in full sun during a day. Anoles in partial sun were counted as being half in sun, half in shade. Open circles indicate lizards in the open park and closed circles indicate lizards in the forest; $N =$ 10 for all samples unless noted.

To study the effect of habitat on thermoregulation and body temperature, I monitored *A. cristatellus* in two adjacent lowland habitats (shaded forest and open park) during a full day (*10*). To index the cost to lizards of raising body temperature by shuttling between sun and shade, I measured the shortest transit distance from an anole perched in partial sun or in shade to a patch of full sun on a contiguous perch (*11*) and included a category "no way" (NW), indicating