



## Intraspecific Vertical Stratification as a Mate-Finding Mechanism in Tropical Cockroaches

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1,25(OH)<sub>2</sub>D<sub>3</sub> in the central amygdaloid nucleus, in the bed nucleus of the stria terminalis, and in the anterior thalamus are located within projection fields of the stria terminalis, of which they seem to form a subsystem. An analogy to relationships between other steroid hormones and brain-endocrines is suggested (Fig. 2), and 1,25(OH)<sub>2</sub>D<sub>3</sub>-related peptidergic messengers and links to the portal system in the median eminence and to pituitary secretion can be expected. The finding of 1,25(OH)<sub>2</sub>D<sub>3</sub> in the brain, the previous demonstration of 1,25(OH)<sub>2</sub>D<sub>3</sub> in the pituitary (1, 2), and the effects of this hormone on thyroid-stimulating hormone secretion (12) suggest central modulation of calcium homeostasis involving a brain-pituitary-thyroid axis (Fig. 2). The possibility of a brain-intestine link in endocrine regulation must also be considered, since 1,25(OH)<sub>2</sub>D<sub>3</sub> apparently acts on structures in the amygdala, which, when lesioned or electrically stimulated, produce changes in gastric motility and secretion (13).

Vitamin D-inducible calcium-binding protein has been found not only in many peripheral target tissues for 1,25(OH)<sub>2</sub>D<sub>3</sub> but also in cell bodies, dendrites, and axons of Purkinje cells of chicken brain (14). We did not observe a concentration of radioactivity in these cells in our present studies (Fig. 1f). Although a correspondence between 1,25(OH)<sub>2</sub>D<sub>3</sub> target cells and cells containing vitamin D-dependent calcium-binding protein seems to exist—at least in some tissues—such a correspondence needs to be established through the use of our autoradiography-immunohistochemistry technique (15). This technique permits the simultaneous visualization of radioactivity and antibodies in the same preparation. Clinical reports indicate the importance of vitamin D action for normal brain function. In humans, retardation of mental growth has been observed in both vitamin D hypervitaminosis and hypovitaminosis (16). The frequency of epileptic seizures was reduced after vitamin D treatment, and this effect was unrelated to changes in serum calcium and magnesium (17). In hypoparathyroidism and pseudohypoparathyroidism, conditions in which 1,25(OH)<sub>2</sub>D<sub>3</sub> serum levels are low, seizures are a frequent symptom (18). Facilitated by the present anatomical data, the nature of the effects can now be studied and it can be clarified to which degree general or local actions of the hormone are involved.

1,25(OH)<sub>2</sub>D<sub>3</sub> may act to maintain normal brain functions by providing normal serum calcium and phosphate levels. In addition, it may selectively affect specif-

ic neuronal populations with changes in metabolism, neuritic growth, alterations of sensitivity thresholds, and changes in production and secretion of certain aminergic-peptidergic messengers, as has been demonstrated for other steroid hormones.

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dorsal thalamus; 3600 to 8500 in area postrema and vicinity; 6800 to 7200 in spinal cord lamina II; and 2000 to 3500 in epithelial crypt cells of duodenum. These data are preliminary and need to be verified statistically with larger numbers of animals. Competition experiments with 25-OH-D<sub>3</sub> show results similar to those with <sup>3</sup>H-labeled 1,25(OH)<sub>2</sub>D<sub>3</sub> alone. In competition experiments with 1,25(OH)<sub>2</sub>D<sub>3</sub>, no nuclear concentration of radioactivity is obtained.

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## Intraspecific Vertical Stratification as a Mate-Finding Mechanism in Tropical Cockroaches

**Abstract.** *Cockroaches in a tropical forest stratify vertically both inter- and intraspecifically along micrometeorological gradients. At night, low wind speeds and unstable atmospheric conditions result in efficient vertical mixing of the air near the ground. Convective ascent of warm air imparts directionality to the pheromone-dispersion process. The occurrence of males at greater heights than pheromone-emitting conspecific females appears to be a mate-finding strategy.*

For airborne chemicals to be effective signals in communication, their release and reception must correlate with favorable micrometeorological conditions. To maximize their efficiency in finding pheromone-emitting females, males should occupy ranges above, overlapping, or below the females' vertical ranges, depending upon the prevailing atmospheric conditions. Since meteorological patterns exhibit circadian cycles, they cou-

ple the orientation behavior to specific times during the day or night. If, for example, buoyant (I) atmospheric conditions prevail at night, males should occupy perches at greater heights than females. Conversely, under stable (I) atmospheric conditions with temperature inversion, males should overlap with the vertical distribution of the females or range below them.

Dispersion models (2) describe plumes

with center lines parallel to the ground and remaining at the height of the point source. The vertical and horizontal profiles of the plumes at any point along this line correspond to Gaussian distributions (3). These models predict that the optimal vertical distribution for males should completely overlap the range of pheromone-emitting females.

With increased interest in behavioral and biological control and management of forest insects, it is important to describe the transport mechanisms which operate in olfactory communication. I report spatial distribution data for forest

cockroaches with micrometeorological profiles and show that height stratification is an important mechanism in the mate-finding process.

I found that the cockroach community at Finca La Selva in Costa Rica (4) stratified vertically both inter- and intraspecifically (Fig. 1A). Interspecific separation may be a mechanism of resource partitioning or the result of habitat selection for temperature, humidity, wind, food, or other conditions (5). Height-specific or species-specific predation may force individuals of the prey species to occupy different vertical ranges from

those normally preferred in the absence of predation (6).

Intraspecific separation (Fig. 1A) is more difficult to explain. Resource partitioning due to sexual dimorphism is likely to occur in several species (for example, *Epilampra involucris* and *Hyporhynchoda reflexa*), where the females are either larger than the males or are wingless. However, this mechanism does not account for the consistent occurrence of males higher than conspecific females regardless of the morphology or size of the sexes. I hypothesized that sexual stratification enhanced the efficiency of males in orienting to pheromone-emitting females (7). This may be the case when temperature lapse profiles result in convective ascent of air (and airborne chemicals) near the ground.

Contrary to what is expected in the canopy and above the forest, daytime temperature inversion is followed by nighttime temperature lapse within 2 m above the ground (Fig. 1B) (8). The wind profile (Fig. 1C) is similar to results obtained by other researchers (9), but the wind speeds recorded in the tropical forest at night are at least an order of magnitude smaller than those reported from other forest types.

The interaction of vertical thermal gradients and mechanical aspects of the wind profile is described by the Richardson number,  $R_i$  (10). It is a measure of the stability of the atmosphere near the ground. In the present study, temperature lapse and low wind speeds near the ground at night result in large negative  $R_i$  values. Free convection (1) predominates close to the ground; buoyant air of relatively low density moves vertically into denser, cooler air resulting in efficient vertical mixing. Higher above the ground free convection and wind-generated eddies coexist to form a hybrid turbulence regime called mixed convection.

The driving force of the nighttime thermal convection is directly proportional to the difference in temperature between the two mixing layers of air. As air rises, its temperature excess over that of its new environment increases, and therefore the buoyant driving force increases. Hence, a convective plume will accelerate upward until slowed by entrainment (mixing) or until it meets a layer of stable air. The observed temperature differences decrease per unit distance of ascent (Fig. 1B). Therefore, both entrainment and stability at higher levels decrease the rate of upward movement of the plume.

Visual representations of plumes from point sources of artificial, nonbuoyant

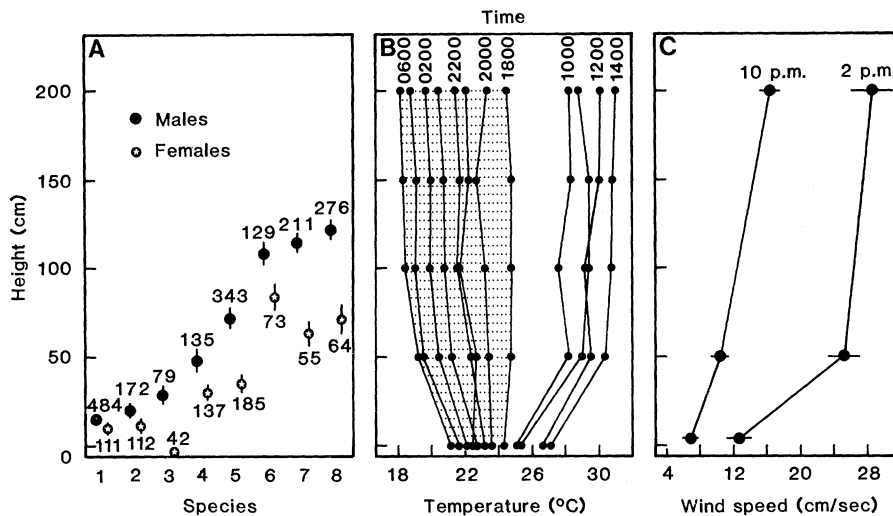


Fig. 1. (A) Height stratification of eight species of cockroaches. Each point represents the mean ( $\pm$  standard error) of  $N$  height measurements (values adjacent to points) which were approximately equally distributed throughout the night. Females of *H. reflexa* remain in the leaf litter at night. The ranges for males and females of the other species overlap considerably: 1, *Epilampra involucris*; 2, *Nesomylacris* sp. near *asteria*; 3, *Hyporhynchoda reflexa*; 4, *Xestoblatta hamata*; 5, *Xestoblatta cantralli*; 6, *Imblattella impar*; 7, *Cariblatta imitans*; and 8, *Imblattella* new sp. "G." (B) Temperature profiles for a typical 24-hour period in the dry season (10 April 1980). Mercury thermometers were positioned at four heights in the understory. Measurements were recorded manually every 2 hours along with climatological conditions. In the rainy season the profiles are similar to those for the dry season but the temperature range is smaller. The patterns are consistent and predictable on a daily basis. The stippled area represents nighttime. (C) Wind profile for day and night conditions in the dry season. Instantaneous readings with an Alnor type 8500 Thermo-anemometer were taken every 15 seconds for 4 minutes at each of three heights, followed by eight additional readings at each height. The sampling order of the three heights was randomized; 96 instantaneous readings taken over 4 days were averaged ( $\pm$  standard error) for each height.

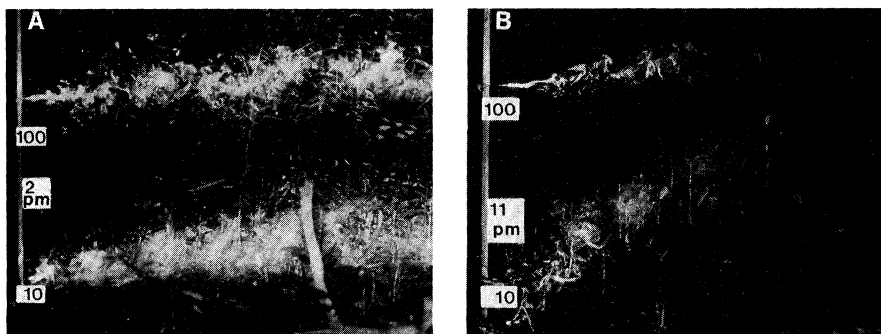


Fig. 2. Titanium tetrachloride was used as point sources for smoke plumes. The photograph (A) was taken at 2 p.m. Note the predominantly horizontal flow at both point sources. The photograph (B) was taken at 11 p.m. Nighttime unstable conditions result in vertical ascent from the lower source (10 cm).

smoke (Fig. 2) show that the vertical component is frequently more significant close to the ground where large temperature differences and low wind speeds predominate. At higher levels the horizontal component accounts for most of the air movement as entrainment, increased wind speeds, and a shift to thermal stability interact to reduce the vertical flow.

If relatively small vertical temperature gradients impart directionality to air movement, then a behavioral response which does not occur under vertically isothermal conditions (that is, subthreshold pheromone concentrations) ought to be elicited in males downwind in a temperature gradient. In isothermal (neutral) conditions the *Periplaneta americana* sex pheromone did not elicit searching in males (11); no courtship responses were observed. However, when temperature was made to decrease with height, and the pheromone was introduced below the males, their locomotion increased significantly (*t*-test,  $P < .01$ ), and the complete courtship sequence was elicited (12). Clearly, the thermal gradient imparts a new directionality to the airflow. The 360° emission angle of Fickian diffusion decreases to a narrow vertical plume in the direction of the males. Hence, more molecules per unit volume of air impinge on the male antennae, and threshold concentrations are more likely to be reached (13).

Silverman and Bell (14) found that *P. americana* males tethered on a vertical surface showed gravitational responses to sex pheromone delivered perpendicularly to the vertical surface. Air without pheromone caused the males to run up, whereas air currents with sex pheromones caused them to run down. These data are consistent with my convective model for volatile pheromones.

In conclusion, the vertical distribution data, predictable nocturnal micrometeorological profiles, pheromone dispersion models, male orientation behavior, and laboratory experiments suggest that intraspecific height stratification in these species of cockroaches is a mechanism that enhances the efficiency of the mate-finding process.

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#### References and Notes

1. Stable conditions: temperature inversion, where temperature increases with height above the ground. Unstable conditions: buoyant or temperature lapse profile, where temperature decreases with height above the ground. Free convection: thermals move vertically because of temperature and density gradients; near the ground, this process may occur at low wind speeds. Forced convection: vertical wind shear

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11. A 1 centigrade degree vertical gradient was installed over a vertical distance of 60 cm with resistance wire and two temperature regulators (Yellow Springs Instruments models 71 and 73). A continuous output of the temperatures was provided by a two-channel strip-chart recorder (Esterline-Angus Speed Servo 2). I used  $5 \times 10^{-6}$  µg of synthetic (±)-Periplanone B [M. A. Adams, K. Nakanishi, W. C. Still, E. V. Arnold, J. Clardy, C. J. Persons, *J. Am. Chem. Soc.* 101, 2495 (1979)] adsorbed onto 1-cm<sup>2</sup> Whatman No. 1 filter paper to elicit sexual responses in *P. americana* males in a screen cage above the pheromone source. The test recorded the number of times in 30-second intervals that the males crossed a line bisecting the floor of the cage. Each test was 4 minutes. I performed ten tests in isothermal and ten in temperature lapse conditions.
12. The courtship sequence of *P. americana* proceeds from rapid antennal movement to stilt walking, wing raising, and wing fanning by the male [L. M. Roth and E. R. Willis, *Am. Midl. Nat.* 47, 66 (1952); W. J. Bell, in *The American Cockroach*, W. J. Bell and K. G. Adiyodi, Eds. (Chapman & Hall, London, 1981)].
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## Suprachiasmatic Stimulation Phase Shifts Rodent Circadian Rhythms

**Abstract.** *The integrity of the suprachiasmatic nuclei (SCN) of the hypothalamus is essential to the expression of normal circadian rhythms in rodents. Electrical stimulation of the SCN caused phase shifts and period changes in the freerunning feeding rhythms of rats and activity rhythms of hamsters. The phase response curve for SCN stimulation appears to parallel that for light pulses. These findings strengthen the hypothesis derived from lesion studies that the SCN are the dominant light-entrained oscillators in the rodent circadian system.*

Circadian rhythms synchronized to the solar day are a pervasive feature of mammalian physiology and behavior (1). Until recently little was known about the mechanisms responsible for either endogenous generation or environmental synchronization (entrainment) of these rhythms.

A significant advance was the identification of the hypothalamic suprachiasmatic nuclei (SCN) as structures critical to the generation and entrainment of mammalian circadian rhythms (2). Ablation of the SCN results in the disruption of a variety of behavioral, physiological, and endocrine rhythms in rodents (3). These observations generated the hy-

pothesis that the SCN act as a pacemaker in the mammalian circadian system. The observation of circadian rhythms in spontaneous electrical and metabolic activity in SCN neurons (4) is consistent with this hypothesis.

A pacemaker in a circadian system should regulate both phase and period of circadian oscillations; the available data do not establish that the SCN serve this function. The strongest support for this hypothesis would be provided by evidence that manipulation of spontaneous SCN neural activity modifies these features of circadian rhythms. The first evidence for such a mechanism was the finding that infusion of carbachol near