

# 1

## The odorsphere: the environment for transmission of chemical signals

The scent of flowers does not go against the wind, not sandal, rosebay or jasmine, but the scent of the good goes against the wind; a good man is wafted to all quarters.

SUTTAPITAKA (“basket of discourse”), from Pali canon of Theravada  
 Buddhists, ca. 500–250 BC

Land animals exploit the odorsphere, the world of vapors around them. In any given locale, they move in an odorscape, a landscape of volatiles. Even in fish we speak of odors because neurophysiologically the olfactory system is involved, even though water-soluble stimulants are not necessarily volatile. We expect vertebrates to have taken advantage evolutionarily of the physicochemical characteristics of their environment first to select and then to optimize chemical communication. The chemical communication system of a cold-water fish differs vastly from that of a tropical bat. Despite similar biological functions, each system has been shaped by, and is adapted to, a distinct set of environmental circumstances.

In air, temperature, relative humidity, barometric pressure, and air currents not only modulate the movement of molecules from the source but also affect odor reception once the molecules have arrived near the receptors. The evaporation of an odor from a surface such as animal skin, a scent mark, or vegetation is regulated by air temperature, relative humidity, the porosity of the surface, and other compounds present (Regnier and Goodwin, 1977; Figs. 1.1 and 1.2).

The evolution of chemical communication was probably influenced by such additional factors as adsorption of aerial pheromones to vegetation, or water-borne pheromones to suspended clay. The influence of these environmental features has very likely selected for both the choice of chemical constituents of the signals and the appropriate signal-emission behaviors (Gleeson, 1978).

Chemical signals have several advantages over cues in other sensory modalities. They work in darkness, around obstacles, and may last for a long time, ranging from seconds to months. This enables an animal to communicate with others in its absence, or even with

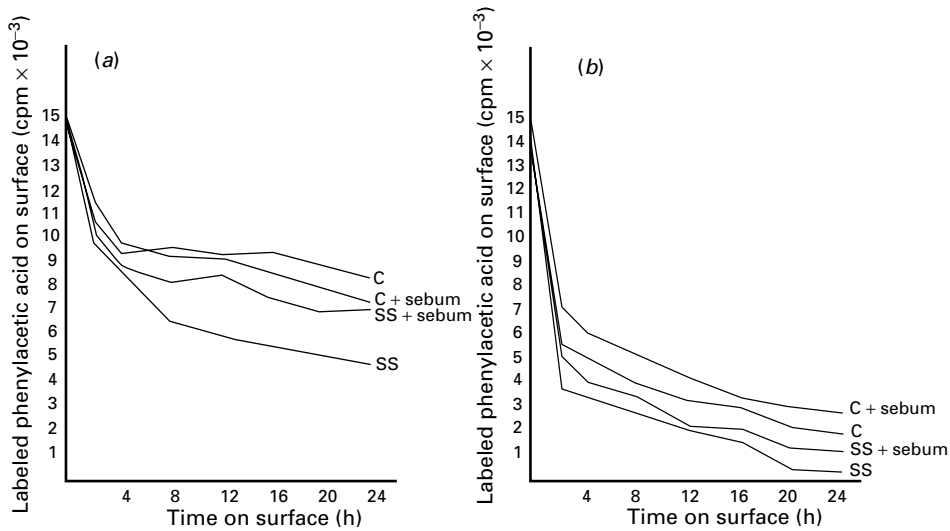


FIGURE 1.1 Effect of relative humidity of air on evaporation of phenylacetic acid from two surfaces in the presence and absence of sebum: stainless steel (SS) and cellulose (C). Relative humidity 0% (a) or 100% (b), both at 20°C. (Adapted from Regnier and Goodwin, 1977.)

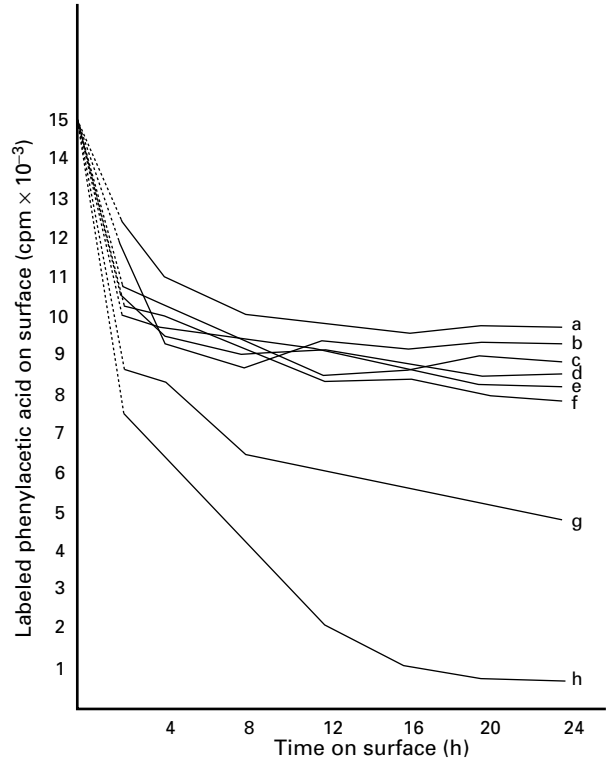


FIGURE 1.2 Effect of surface on evaporation of phenylacetic acid at 0% relative humidity and 20°C. a, montmorillonite; b, mylar plastic; c, glass; d, cellulose; e, kaolinite; f, balsa wood; g, stainless steel; h, platinum. (Adapted from Regnier and Goodwin, 1977.)

itself when returning to a previously scented site. A major disadvantage is a long “fade-out” time that would limit consecutive signals to a slow sequence. In the real world, air or water currents are nearly always present. They transport signals, and the role of diffusion is insignificant because it is too slow.

## 1.1 Air

For the medium air we can distinguish *close-range* from *long-distance* chemical signals. They differ in the behaviors that animals employ to take advantage of physical processes. Sniffing a scent mark, another animal, or potential food at close range is more than a passive receiving. Exhaling moist air onto the focus of attention moistens the surface and liberates more odorant. Thus, sniffing enables an animal to regulate the release of molecules from the substrate. At zero distance, the odor source can be licked to take up non-volatile compounds. An example of long-distance responses is the approach of seabirds to food odors such as dimethyl sulfide over the ocean. Here air currents and water–air interface transport of molecules are important.

Since virtually all communication by terrestrial vertebrates takes place in the air layer near the ground, the chemical ecologist has to understand the properties of that stratum. Volatiles in higher layers of air, however, may attract vultures to carcasses and could possibly serve as cues for migrating birds. Airborne odors are affected by temperature, relative humidity, barometric pressure, air currents, and vegetation, which, in turn, may influence temperature, humidity, and airflow. Complex interactions of these variables create countless unique environmental conditions for communication patterns of diverse species and for various specific purposes.

### 1.1.1 Temperature

The vapor pressure of volatile compounds, measured in atmospheres (or millimeters of mercury), varies with temperature. For example, the vapor pressure of acetone increases from 200 to 400 mmHg with a temperature rise from +20 to +40 °C, and that of *n*-heptane from 100 to 400 mmHg with a temperature change from +40 to +80 °C (e.g. Adams *et al.*, 1970). The half-lives of several acetates decreased by two- to fourfold when the temperature was raised from 20 to 30 °C (McDonough *et al.*, 1989). In temperate latitudes, temperatures can vary from about 40 to 0 °C within 24 hours. Therefore, it is important to know the vapor pressure of a given compound for the ambient temperatures under which a particular animal species operates. Diurnal and nocturnal animals may have selected different signal compounds (or mixtures). Do polar and tropical species differ in their choice of compounds for communication? Have cold-climate

pheromones higher vapor pressures? Do polar and montane animals use behavioral means such as sniffing at close range to optimize chemoreception? Are there environmental temperatures so low that pheromone communication is impractical, or even not feasible? The animal's ability to escape from ambient conditions by burrowing or seeking other shelter has also to be considered.

The sex pheromone of the male pig is adapted to the ambient temperature. The pheromone, a mixture of 5 $\alpha$ -androstenol and 5 $\alpha$ -androstenone, is bound to the protein "pheromaxein" in the saliva. At body temperature (+37 °C) most binding is lost after 72 hours. In direct encounters with females, ample pheromone is given off. At +4 °C, however, the binding of the pheromone to the protein is unchanged over 168 hours. Pigs deposit the frothy saliva in the environment during their breeding season in autumn and winter. At the prevailing low temperatures, the pheromone is released only slowly over a longer time (Booth, 1987).

Temperature may significantly affect *chemoreception*. For instance, electrical responses to amylacetate delivered to olfactory receptors of a tortoise, *Gopherus polyphemus*, were little affected by air temperatures between 20 and 30 °C at the nares but changed considerably above and below that range. Up to +35 °C and down to +10 °C, the olfactory response was a "monotonic slowly decreasing function of temperature" (Tucker, 1963; see also Grundvig *et al.*, 1967).

### 1.1.2 Humidity

The higher the humidity, the more odor molecules evaporate from a surface, because they compete with water molecules for surface sites. Dogs track better on moist ground and/or on humid days, and we are all familiar with the smell of a wet dog. This phenomenon has far-reaching consequences for the choice of compounds and communication patterns in humid versus arid climates. Some field studies have demonstrated behavior differences between wet and dry seasons. For example, the blackbuck, *Antilope cervicapra*, ceases to use dungpiles during the monsoon season (Prasad, 1989). Environments with high temperatures and humidity, such as tropical forests, call for range marks with active compounds that are either large molecules (Alberts, 1992a) or contain effective keeper substances that slowly release volatiles.

An animal can control release of odor molecules from body surfaces, especially skin gland areas, up to a point. But in moist air, volatiles from secretions on skin or hair will evaporate more easily. If only intermittent odor emission is desirable, humidity would interfere with the animal's odor release. Glands that produce such intermittent signals, such as alarm odors, appear to be more developed in species or subspecies in drier climates. An example is the metatarsal gland in

the North American deer genus *Odocoileus*. Within one species, the size of the gland, or even its presence or absence, varies with the climate. In populations of white-tailed deer, *Odocoileus virginianus*, the gland becomes smaller (or even absent) from eastern North America to more humid Central America and northern South America. In the western mule deer, *Odocoileus hemionus*, the gland is larger in more arid environments. Finally, comparing the two species, the mule deer of the more arid western North America has a larger metatarsal gland than the white-tailed deer of the more humid east (Müller-Schwarze, 1987). Similarly, of two species of the Indian gerbil genus *Tatera*, the one in a drier climate has a ventral gland, while it is smaller or absent from the species of a more humid environment (Prakash and Idris, 1982; Kumari and Prakash, 1983).

It is important to measure humidity exactly where an animal operates. In a meadow on a summer afternoon, the relative humidity can be over 90% at 5 cm above ground, but only 60% at 60 cm (Geiger, 1965). The implications of this would be different for a deer or a rodent. Furthermore, a species like a deer beds down on the moister ground but applies scent marks on branches in a higher, drier layer of air. The rodent, by comparison, experiences a higher and stable level of humidity in its burrow or cave. Humidity is high in stands of plants, and different plants offer different conditions. For instance, forest edges promote precipitation from fog. East-facing forest edges are in the wind and rain shadow and, therefore, experience less humidity.

Mammalian odor *reception* is modulated by relative humidity. For instance, neotropical bats (*Carollia perspicillata* and *Phyllostomus discolor*) are less able to approach an experimental banana odor correctly if the humidity is lowered from the normal 75% to under 60%. The sensory impairment results from drying out of the nasal mucosa in low humidity (Laska *et al.*, 1986).

It is well known that dogs track better in humid air. Rodents find buried seeds better in wet soil. This is important in arid climates. After rains, yellow pine chipmunks, *Tamias amoenus*, and deer mice, *Peromyscus maniculatus* found experimentally buried seeds of Jeffrey pine, *Pinus jeffreyi*, and antelope bitterbrush, *Purshia tridentata*, better than in dry soil. The recovered number of seeds increased 27- and 15-fold, respectively. In wet soil, seeds take up water rapidly and emanate volatile organic compounds that the rodents exploit. By extension, variations in humidity in arid environments may have profound effects on olfaction-dependent behaviors such as finding food, social interactions, preying, and predator avoidance (Vander Wall 1998).

Rodent species differ in their ability to smell buried seeds: those from arid climates perform better than species from mesic climates. Specifically, Panamint kangaroo rats, *Dipodomys panamintinus*, from arid and semiarid areas of the Great Basin Desert in North America were the only species that found deep caches

of seeds under dry conditions. By contrast, chipmunks from more humid eastern North America performed the poorest in finding buried sunflower seeds under dry conditions (Vander Wall *et al.*, 2003). Like the much-studied pesticides, volatiles adsorb to soil particles and desorb from these particles when the moisture exceeds the thickness of a monomolecular layer, increasing the vapor pressure; this, in turn, facilitates finding buried seeds (Vander Wall, 2003). Furthermore, rodents, use memory as well as odors to find buried seed caches. As moisture favors searching by smell, pilfering occurs more often after rains (Vander Wall, 2000).

### 1.1.3 Barometric pressure

Hyperbaric pressure may intensify odors or render odoriferous some “odorless” gases such as methane. Professional divers, experimentally exposed to hyperbaric pressures, detected odors of krypton and methane when sniffing these during the decompression phase of a dive. The threshold for krypton was 2 ATA (atmosphere absolute), and 100% positive responses occurred at 6 ATA. For methane, the threshold was 3 ATA (100%: 13 ATA). The thresholds of individuals differed by as much as a factor of three (Laffort and Gortan, 1987).

### 1.1.4 Air currents

Odors travel in moving air. During their long evolutionary history, animals have adapted to detecting chemical signals from downwind. Many animals integrate chemotaxis with photo-, anemo-, or rheotaxis (Vickers, 2000). Several natural history accounts of large mammals report movements into the wind and presumably toward rain and fresh forage. According to French Camel Corps reports, dromedaries are said to detect water pools and fresh pasture from 40–60 km away. These animals turn into wind blowing from rain clouds and will head into that direction if permitted by the rider (Gauthier-Pilters, 1974). African water buffalo, elephant, and zebra are assumed to “smell rain” and migrate there (Daly, 1988). Arabian oryx, *Oryx leucoryx*, are reported to do the same over distances of about 50 km. One female was documented to have traveled 150 km to an area of fresh rain (Daly, 1988).

#### *Factors affecting currents*

##### *Turbulent flow*

The air flow in the microclimate of an animal’s home range usually is more complicated than basic laminar flow (which does not even exist over large

distances and open areas). Fluctuations in air velocity cause turbulence, and stationary objects may create such fluctuations. The air is almost always *turbulent*, and intact parcels of air laden with odor molecules travel in random fashion (Geiger, 1965). The multidirectional turbulence is superimposed on the horizontal wind flow pattern. *Mechanical* turbulence is caused by wind, and *thermal* or *convective* turbulence by heated air rising. The plume from a smokestack loops up and down on a hot day. Such a “looping plume” is shaped by thermal up- and downdrafts, which account for more vertical displacement than the small-scale mechanical turbulence (Thibodeaux, 1979). Clearings in dense forest experience eddies spinning off from the general flow over the treetops, while a sparse stand of trees has a more laminar air flow. Small eddies are typical for the air directly above the air–soil interface (Thibodeaux, 1979). Eddy diffusion varies in space and time: it is less intense and more variable near the ground, and the greatest mixing of air occurs during midday while at night the air is more stable. An exception is the thin layer of air that adheres to the ground, walls, or vegetation. Processes here follow the laws of molecular physics, and not those of eddy diffusion (Geiger, 1965). In most atmospheric odor movements, however, turbulence swamps molecular diffusion. Among insects, turbulent air flow around obstacles such as trees influences the response of a predatory beetle, *Rhizophagus grandis*, to the odor of their prey, bark beetles (Wyatt *et al.*, 1993).

The more stable the air, the higher the concentrations of odor that can be carried over long distances. This, in turn, increases potential communication distances. However, unstable air conditions disperse the odor molecules more “sideways,” with a wider “cone;” consequently more individuals can be reached, although the signal is attenuated over a shorter distance. “Parcels” of odor-containing air travel straight, but subsequent parcels travel at different angles, as the wind direction changes over time (David *et al.*, 1982). Fluctuations in speed and direction (“meandering”) expose an organism that is fixed in place to changes in odor concentration, including zero levels. This amounts to an on–off effect that, in turn, counteracts habituation of the animal’s chemical senses.

### *Mountains*

In the mountains, differential heating during the day causes upslope winds, which move up both sides of a valley, and upvalley winds that blow along the valley. During the night, the directions reverse to downslope and downvalley winds (Geiger, 1965; Fig. 1.3).

### *Large areas*

Pressing problems of air pollution have spawned experiments and models of odor dispersion over larger areas. Strom (1976) and Beaman (1988)



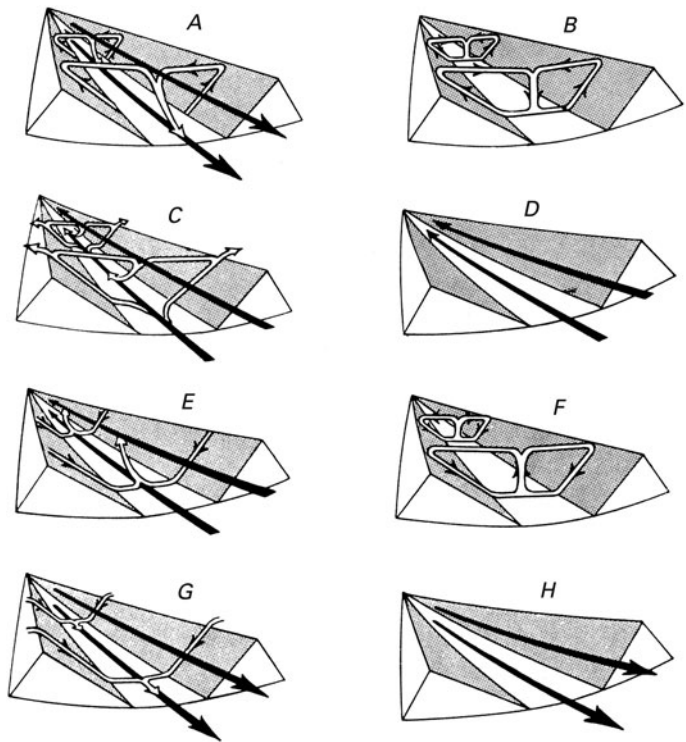


FIGURE 1.3 Changes of wind directions in a valley during 24 hours (from A [night] to H [night again]). Black arrows indicate valley winds and white arrows indicate slope winds. (From Geiger, 1965.)

analyzed transport of stack effluents. Beaman concluded that models of gas dispersion downstream from a source such as a factory predict the actual gas distribution better in rural than in urban areas.

*Fluctuations in concentration in eddies*

The changes in odor concentration during transport depend on eddy size. Large eddies carry small puffs of odor intact, with little concentration change over time (and distance). Eddies smaller than the puff let the puff grow slowly and concentration decreases, but slowly. Puffs of about the same size as eddies are torn apart, and concentration decreases rapidly. Mixtures of compounds of different molecular sizes will retain their relative concentrations in turbulent flows. Therefore, odor mixtures such as those from plants can contain compounds of high and low molecular weights, even though their separate diffusion rates would be different.

How have animals adapted their communication patterns to prevailing wind patterns? Air flows may be variable, as over slopes, valleys, wood slopes, and forest edges; continuous and strong, as on grasslands, tundra, or the Antarctic;



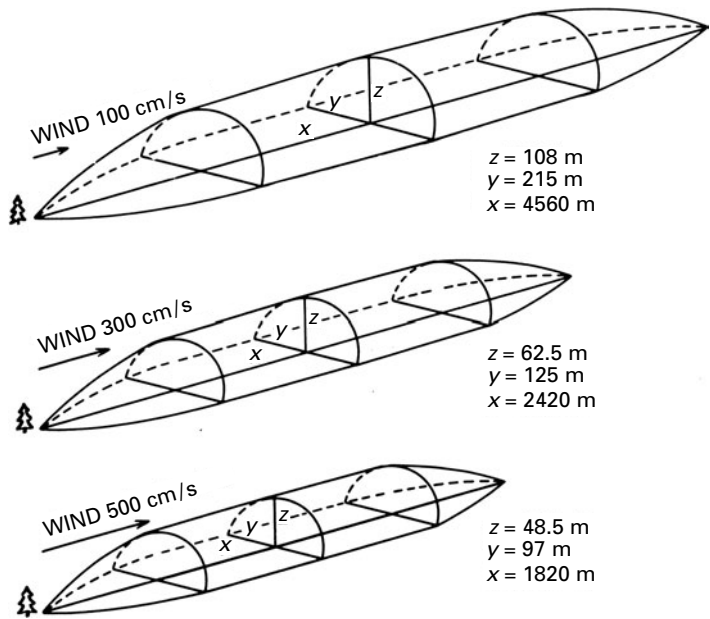


FIGURE 1.4 Active space for different wind speeds. A single female gypsy moth at the tree on the left emits sex attractant. The space where the concentration of pheromone is above threshold (for a searching male) is defined by the dimensions  $x$ ,  $y$ , and  $z$ . The active space shrinks with increasing wind velocity. (From Wilson, 1970.)

minimal, as in woods; or absent, as in caves and burrows. In general, animals are expected to rely on wind only for longer-range attraction to food or conspecifics, avoidance, or warning of conspecifics or predators. Finer details, such as the exact outline of a territory, or the identity of an individual, can be assessed by sniffing scent marks or the animals themselves at close range. In some environments, air flow patterns can be very complex, and we have not even asked how vertebrates exploit these for effective communication. For instance, how do nocturnal downvalley winds and the water current along streams affect odor signals used by beaver? Active at night, beaver probably use these for signal propagation between neighbor colonies. They cannot easily exploit the daytime upvalley wind, because they stay in their lodge during the day.

*Active space*

The biologically significant *active space* where the odor concentration is above threshold is shaped like an overturned boat (Fig. 1.4). (If the molecules were able to spread in all directions, as from an elevated odor source, the active space would assume the shape of a cylinder with pointed ends.)

To calculate the active space, the investigator needs to measure odor emission rate, detection threshold of the animal, and wind speed.

*Plume models*

Pheromone propagation by wind depends on the release rate of the pheromone (or any other odor) and air movements (turbulent dispersion). In wind, the turbulent diffusivity overwhelms the diffusion properties of a volatile compound or mixture itself. Diffusion properties are now properties of wind structure and boundary surfaces, and preferably termed *dispersion coefficients*. Two models have dominated the discussion of insect pheromone propagation. These are the *time-average model* (Sutton, 1953) and the *Gaussian plume model*.

The time-average model considers the average concentration of airborne materials at sites downwind from a point source. The concentration (or density  $D$ ) of a pheromone at any one point with the coordinates  $x$  (downwind direction),  $y$  (horizontal crosswind [transverse] dimension), and  $z$  (vertical dimension) can be estimated with the following formula.

$$D_{xyz} = \frac{2Q}{C_y C_z U x^{2-n}} \exp \left[ -x^{n-2} \left( \frac{y^2}{C_y^2} + \frac{z^2}{C_z^2} \right) \right]$$

where  $Q$  is the release rate;  $U$  the mean wind speed;  $C_y$  and  $C_z$  are horizontal and vertical dispersion coefficients, respectively; and  $n$  a parameter ranging between 0 and 1. Wilson and Bossert (1963) have applied this model to pheromones. Dispersion coefficients are functions of atmospheric turbulence, terrain roughness, and vertical wind speed profile. According to Sutton (1953), with light winds of speeds between 100 and 500 cm/s, neutral atmospheric conditions, and level ground:  $C_y = 0.4 \text{ cm}^{1/8}$ ,  $C_z = 0.2 \text{ cm}^{1/8}$ , and  $n = 0.25$ .

The release rate  $Q$  is doubled to  $2Q$  because odor clouds released on or near the ground are “reflected” by this boundary layer. (For elevated odor sources, only  $Q$  is used because the molecules can disperse in all directions.)

Most pheromone biologists have used the Sutton formula. For elevated odor sources, a more complicated version of the equation exists. However, compared with the concentration differences at different distances from the source, those between elevated and ground-level sources are minuscule (Elkinton *et al.*, 1984).

Now we introduce the sensitivity (perception threshold) of the receiving animal. According to Bossert and Wilson (1963), the downwind maximum distance  $x_{\max}$  (in cm) at which the concentration of an odor remains above threshold is

$$x_{\max} = \left( \frac{2Q}{K \pi C_y C_z U} \right)^{\frac{1}{2} - n}$$