a few centimeters of male clusters, the males always become highly agitated, rapidly moving the antennae and palps, and generally disperse in a matter of seconds. While I have at times observed that actual contact between female abdominal glands and male antennae is required to dislodge the most persistent male from the pupa, the repulsive quality of the mated female seems certain. I have observed males of another pupal mating species, *H. charitonia*, to behave in the same way. These responses of "pupa-sitting" males are not consistent with Crane's conclusions on the basis of her observations of males courting mature mated females—that is, that the "odor has no apparent effect on the courting male" (*5, 8*).

Given that the "stink club" odor is transferred from the male to the female at mating and that the odor of mated females lasts for weeks (*5*) and even months (*9*), it is likely that (i) a large amount of the substance or its precursor is transferred at mating and (ii) special structures are involved in transfer and storage.

While no storage organ is known, the yellow abdominal gland of the female is a possible candidate. In fact, this gland enlarges and its color intensifies after mating, indicating that it may be filled up during copulation. Moreover, Eltringham's early study (*10*) of the structure of *Heliconius* abdominal glands provides the probable answer as to how the transfer occurs. Inside the male clasper Eltringham found and described a pouch lined with glands. It appears that the female's "stink club" would fit neatly into this pouch during mating.

The understanding of why these complex behavioral and morphological traits have coevolved between the sexes of *H. erato* is relevant to elucidating the nature of selection pressures that act on courtship behaviors (*11*). With respect to the *H. erato* system described here, two evolutionary questions emerge. (i) Why should males pay attention to antiaphrodisiac pheromones, especially if, as in *Euphydryas* butterflies and other insects (*1*), males that mate after the first mating gain sperm precedence? (ii) Why should the female sex "cooperate" by evolving structures for receiving and disseminating the pheromone?

The answers to these questions present no problem if the prevention of further matings is in the interest of both male and female parents. The female may be accepting assistance from the male in reducing time-wasting future courtship and avoiding the possible injury (*12*) attendant on subsequent matings. Males that respond to the pheromone and restrain from extended courtship of mated females or prolonged perching on male pupae may also avoid wasting considerable time and energy.

However, the fact that additional spermatophores probably increase female fecundity (*13*) suggests that monogamy may not be in the interests of the female, and may be enforced by her mate. If so, the "stink clubs" must have evolved in the context of other unknown functions, and it is more difficult to understand why subsequently courting males respond to the pheromone. One possible scenario involves the evolutionary derivation of the pheromone. Male *H. erato* assemble on young conspecific pupae of both sexes, and also sometimes (in insectaries) on pupae of *H. melpomene*, the males of which are not attracted to pupae. As the pupae develop, those of *H. melpomene* and *erato* females receive further attention, which continues during and after eclosion. This results in the mating of female *erato* (usually before the wings are fully expanded) but in general *melpomene* of both sexes may be dislodged from their grip on the pupal cases and killed by falling. Conversely, male *erato* pupae become either repellent or unattractive some time before emergence, and the adults are not harassed while expanding their wings. This suggests that there is a male identification pheromone that is effective in late *erato* pupae and that protects teneral males by repelling other males. The possession by males of such a compound could have constituted a preadaptation for rendering females repellent to other males, and the pheromone could thus have acquired a dual function. Males would therefore be subjected to complex selection pressures in their responses to and synthesis of repellent pheromones, with the possible result that they would be deterred from mating with nonvirgin females with which it would be in their interest to mate. One further piece of circumstantial evidence supports this hypothesis. I have already referred to the detectable difference between the odors of mated female *H. e. adanus* and *H. e. chestertonii*. The fact that the only observed case of intraspecific harassment of an eclosing male *erato* occurred between these two races (Fig. 1C) suggests interracial variation in the hypothesized male identification pheromone.

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6. Female pupae of *H. erato* attract males which then sit on the pupae until eclosion (Fig. 1B). Mating usually occurs on the pupal case as the female emerges. Thus, even though the adult color pattern of *H. e. chestertonii* (blue-black and yellow) differs greatly from that of *H. e. adanus* (black and red), interracial matings were easily obtained when these races were mixed.
7. In spite of the distinctive odor of the parent types, it was nevertheless difficult to distinguish hybrid odor from either parent after a few minutes of sniffing.
8. It should be pointed out that Crane was apparently unaware of the pupal mating behavior in *H. erato* and conducted all of her experiments on fully eclosed individuals.
9. Female *H. erato* mated only once still have perceptible odor after 3 months in the laboratory.
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13. Evidence for the nutritional role of spermatophores is as follows. Females mated to males fed solutions of ^{14}C amino acid produced ^{14}C-labeled eggs. (There was no significant difference in the number of counts per minute between fertilized and unfertilized eggs, indicating that eggs are labeled independently of the sperm by other components of the spermatophore.) Moreover, after several days most of the label exists in the female hemolymph (L. E. Gilbert, in preparation).
14. I thank K. Brown, who obtained the *chestertonii* stocks, and the National Science Foundation for support of my more general work on *Heliconius* that made such "side projects" possible. Support was also provided by the University of Texas, Austin (B.S.S.G. RR-07091-06). I thank B. Barth, B. Cade, C. Norris, M. C. Singer, J. Strassman, and, in particular, D. Otte, all of whom read the manuscript and made numerous improvements.

1 March 1976; revised 13 May 1976

Trajectory of the Mt. St. Augustine 1976 Eruption Ash Cloud

Abstract. *The ash clouds from the 23 January 1976 eruption of Mt. St. Augustine in Alaska drifted over Arizona on 25 January at an altitude of 6 kilometers as deduced from air trajectories and the observation of an unusual cloud.*

A major eruption of Mt. St. Augustine (59.36°N, 153.43°W) occurred on 23 January 1976. The eruption produced two major ash clouds, the first emitted at 0700 A.S.T. (1700 U.T.) and the second at 1630 A.S.T. (0230 24 January U.T.). The event was observed locally and also by the NOAA weather satellite, the weather being unusually clear at the time of the eruptions. The second eruption was photographed by Kienle (*1*) from an altitude of 3.0 km and showed an anvil structure similar to a large thunderstorm, with the anvil platform at 7.9 km and a spike rising to 11.2 km. The lateral points of the anvil showed the bulk of the cloud to be at approximately 6.1 km.

On 25 January Meinel and Meinel observed a cloud of unusual coloring and structure passing over Tucson starting at 1630 M.S.T. and continuing for 2 hours, when darkness prevented further observation. All traces of the cloud had disappeared by sunrise the next morning. We immediately suspected that the cloud was ash, from our previous experience with the observation of clouds from volcanic eruptions (*2*) and because the sky earlier in the day had no sign of water moisture, as evidenced by the lack of contrails from jets traveling along the Los Angeles to Dallas air corridor lying just north of Tucson. The cloud appeared in a perfectly clear blue sky, coming from the northwest and rapidly drifting southeast. By sunset the entire sky to the west of the zenith at Tucson was filled with curiously bluish-gray clouds lying in long windrows parallel to the direction of the flow. We immediately began a photographic sequence of the cloud. A photograph of the cloud at 1704 M.S.T. is shown in Fig. 1.

Previously, the unusual nature of clouds of volcanic origin was indicated by their great height, which is on the order of 19 km (*2*) as deduced from the persistence of sunlight on the cloud stratum after local sunset. We were puzzled when the sunset time on this cloud was only 13 minutes after local sunset, indicating that the geometrical altitude of the cloud was only 1.6 ± 0.5 km above the observer. The altitude of observation was 0.76 km, and the estimated screening height due to mountain ranges at the solar grazing ray was approximately 0.5 ± 0.3 km higher than Tucson. Screening was caused by the mountain ranges near Sonoita, Sonora, Mexico, 208 km from Tucson in the direction of the setting sun. The horizon height from Tucson at the intersection of the grazing ray and local horizontal was therefore 2.86 ± 0.5 km. The portion of the ash cloud on which the sunset time was taken was 2° ± 1° above the horizontal, which added 4.0 ± 2.0 km to the cloud height, indicating that the cloud was at a height above sea level of 6.9 ± 2 km. This height is in reasonable agreement with the altitude of the points of the anvil cloud as observed by Kienle (*1*).

After sunset occurred on the cloud we watched to see whether there was any change in the later glow from the 20-km aerosol stratum, which is often enhanced by volcanic eruptions. Sunset time on a 20-km stratum is approximately 45 minutes after local sunset for a point on the local horizontal. No change was noted for this stratum during the several weeks after the appearance of the cloud, but high-altitude striations faintly resembling the original cloud structure appeared on 19 February. We had an opportunity on 28 February to observe the sunset glows from aircraft altitude over the Atlantic from 42°N, and noted no enhancement, a point also established by Shaw at 65°N.

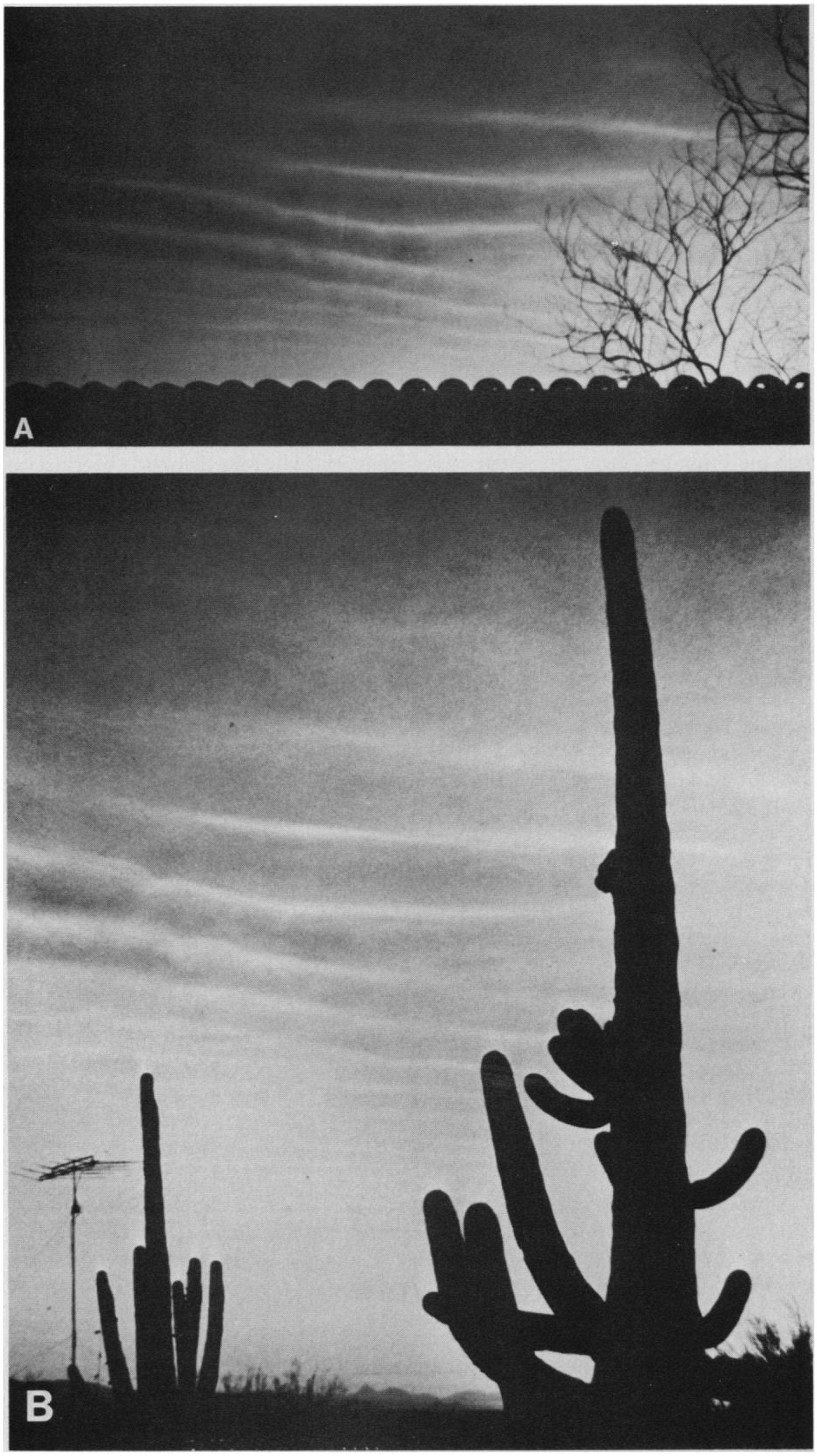

Fig. 1. The St. Augustine ash cloud passing southwest of Tucson, Arizona. Motion of the cloud is parallel to the streamers and toward the left. (A) The sun is below the roof line. (B) The sun is obscured by the lower trunk of the saguaro cactus in the foreground.

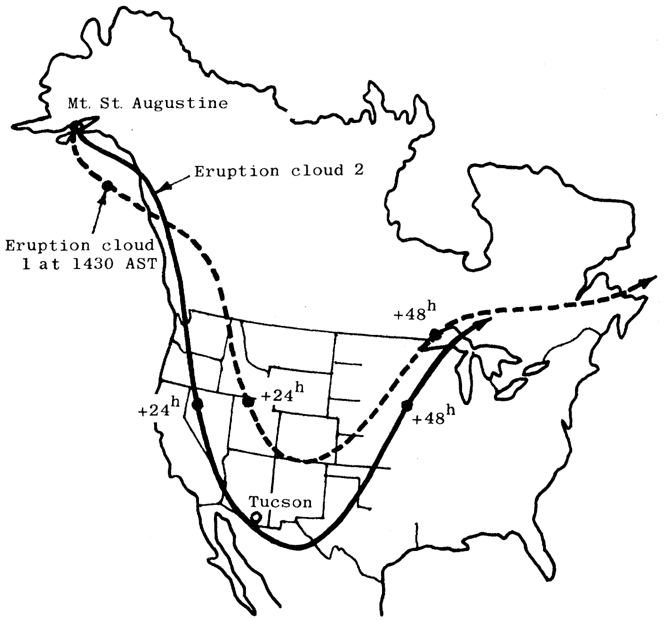

Fig. 2. Trajectory of the two ash clouds from the St. Augustine eruption, deduced from the 300-mbar level meteorological data.

The lack of enhancement of the 20-km aerosol layer led us to conclude that either the eruption of St. Augustine was small compared to that at Agung, Irazu, or Fuego, or that the total amount of reactive gases which lead to the enhancement of the 20-km layer through photochemical reactions was smaller. We do not think that the ballistic strength of these four eruptions is important in causing high altitude "ash stratum" effects, as discussed by Meinel and Meinel (*3*). Instead, we believe these effects are influenced by the integral of the SO_2 emission during the lifetime of the activity of each volcano.

Shaw has provided the trajectory of the two principal eruption clouds of St. Augustine, as shown in Fig. 2. This trajectory is based on velocities and directions of the 300-mbar weather maps for the dates involved, and indicates that the second cloud did pass over Tucson. This trajectory would predict passage of the cloud beginning at 0230 M.S.T. on 25 January, whereas it was observed at 1630 M.S.T. The time difference could be explained because the cloud may have been at a different pressure altitude than 300 mbar (9.2 km) and thus traveling at a lower velocity of approximately 94 km/hour.

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4 May 1976

Suckling in Newborn Rats: Eliminated by Nipple Lavage, Reinstated by Pup Saliva

Abstract. *Chemical lavage of the nipples of anesthetized maternal rats virtually eliminated suckling by their 4- to 5-day-old pups. Normal suckling was immediately reinstated, however, by painting a vacuum distillate of the wash or of pup saliva onto the nipples. Thus, a substance necessary to direct and release suckling, possibly rat pup saliva, appears to coat the nipple surface.*

Suckling is the defining behavioral characteristic of Mammalia. Yet, despite its preeminence, little is known about either the factors that control newborn suckling or the means by which these controls recede during the course of ontogeny. To identify these factors we studied suckling in rats. Unlike newborns of other species, which are led to or placed on the nipple (*1*), newborn rats locate and suckle the teat without maternal assistance, even from the first. Also, in contrast with others, infant rats do not suckle objects other than the teat. Thus, suckling in the blind and deaf newborn rat is controlled by a narrow spectrum of stimuli—olfactory, thermal, and tactile—that define the mother and, more particularly, her mammary area.

In seeking the stimuli that release suckling we were guided by the work of Kovach and Kling (*2*) and Tobach and coworkers (*3*) who, by making very young kittens and rats anosmic through bulbectomy, eliminated suckling. Centrally produced olfactory deficits are difficult to interpret, however (*4*), the more so in infant rats whose nervous systems are rapidly maturing and differentiating. Accordingly, in a more direct approach, we determined if removing olfactory cues from the mother's nipples disrupted suckling in normal newborn rats and, in the counter experiment, if cue replacement reinstated suckling. We report that removal of such cues by chemical lavage prevents previsual and preaudial 4- to 5-day-old rats from either finding or attaching to nipples, even when held directly in contact with them. Returning the scent reinstates suckling, as does pup saliva, presumably a source of this vital olfactory cue.

Sprague-Dawley rats were mated and bred in our colony. A litter of 10 to 12 pups and their natural mother were used in each test. At the start of each test session, half the pups from a litter were removed and placed in a warm and moist incubator; this is the deprived group. Four hours later the mother was anesthetized with Equi-thesin (2 ml per kilogram of body weight), a barbiturate-based agent that blocks milk letdown under these test conditions (*5*), and laid supine in a clear Plexiglas trough. The method of Hall *et al.* (*6*) was used to assess suckling behavior. Deprived and nondeprived pups were placed in successive groups of three next to the anesthetized mother. Thus, the full complement of maternal cues were presented to the pup, but in the absence of maternal participation. Number of pups attaching, latency to attach, and general activity were determined during the 5-minute test. After all pups were tested once with this procedure, the mother was removed from the trough and placed on a table. Then, following a protocol similar to that of Drewett *et al.* (*7*), each pup was assigned a different nipple, and gently held and positioned by the experimenter so that its snout was in direct contact with the assigned teat. Latencies to attach were recorded; a 1-minute ceiling was employed. While both methods appear to be sensitive indices of suckling, the method of Hall *et al.* (*6*) (pups on mother) demands that the