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Pheromonal Divergence between Populations of the Salamander *Plethodon vehiculum* in British Columbia

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1). This suggests that occasionally a sloughing skin lodges around the body so tightly that normal crawling movements are inadequate to release it. Typically, shed skins in the sea water tank have most of their length compressed tightly into a compact mass, indicating that they frequently tend to lodge about the snake. Ecdysis was never witnessed in the large tank, so I was not able to determine the frequency of knotting among shedding individuals.

Knotting behavior has been observed in two species of sea snakes (*P. platurus*, *Laticauda semifasciata*), and is suggested to serve in the removal of ectoparasites and in escape from predation, as well as to assist in shedding (Mays and Nickerson, 1968; Pickwell, 1971; Zann et al., 1975). Pickwell (1971) did not observe this behavior among terrestrial or amphibious sea snakes that he also kept in the laboratory. Therefore, he speculates that the "knotting reflex," characteristic of *Pelamis*, evolved as a substitute for contact with a solid substrate. In the central Philippines, where the snakes that I observed were collected, *A. granulatus* occurs in shallow water habitats and typically among mangroves where the substrate is muddy (Voris and Glodek, 1980). The entire manner in which *A. granulatus* sheds its skin seems advantageous in low friction environments, and the occasional requirement for knot formation is perhaps important in this context. While the use of knots to remove objects from the body has obvious utility in low friction aquatic habitats, the behavior is not unique to aquatic species. Both knotting and gaping behaviors are reported to assist skin shedding in certain terrestrial snakes as well (Griehl, 1984; Hudson, 1947). The behavior of sequentially adducting and abducting the ribs may occur only in file snakes, however, which have very supple bodies.

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PHEROMONAL DIVERGENCE BETWEEN POPULATIONS OF THE SALAMANDER *PLETHODON VEHICULUM* IN BRITISH COLUMBIA.—Lungless salamanders of the family Plethodontidae form a morphologically conservative group, in which speciation is to a great extent uncoupled from structural change (Wake et al., 1983; Larson, 1984). The factors influencing reproductive isolation between populations are poorly understood, but recent studies by Dawley (1984, 1986, 1987) indicate that, at least in some cases, chemical signals play a role. Many aspects of salamander behavior, including courtship and territoriality, appear mediated through pheromones. Chemical signals are known to contain information on species, sex, reproductive condition, and familiarity in several species of plethodontid salamanders (e.g., Madison, 1975, 1977; Tristram, 1977; Jaeger and Gergits, 1979; Dawley, 1984, 1986, 1987; Simon and Madison, 1984; Jaeger et al., 1986;

Horne and Jaeger, 1988). In courtship, pheromones are thought to play an important role in mate attraction and recognition, persuasion of the female to mate by the male, and coordination of movements of the sexes for successful spermatophore transfer (Arnold, 1976; Arnold and Houck, 1982). The pheromones involved may originate from specialized glands usually present only in males, or general epidermal odors may be used (Arnold, 1976).

Potentially, pheromonal divergence between populations could arise through sexual selection (Arnold and Houck, 1982), through pleiotropic effects associated with other changes that have evolved in isolation, or as a pre-mating isolating mechanism through reinforcement upon secondary contact between previously separated populations (Dawley, 1987). Due to their high susceptibility to the rigors of the physical environment and especially to moisture conditions (Maiorana, 1976, 1977; Feder, 1983), plethodontid salamanders in general are poor dispersers, and populations within species tend to form genetically distinct demes (Larson and Highton, 1978; Larson et al., 1984; Larson, 1984). The examination of pheromonal divergence between populations with varying degrees of geographic isolation may elucidate processes responsible for reproductive isolation.

I investigated the responses of the western red-backed salamander, *Plethodon vehiculum*, toward odors of conspecific individuals of the opposite sex from different populations in two-choice laboratory tests. The range of *P. vehiculum* extends along the Pacific rim from southern Oregon to southern British Columbia, including Vancouver Island (Storm and Brodie, 1970). Vancouver Island has been geographically isolated from mainland North America since the retreat of the ice sheets during the latest glacial period, approx. 12,000 yr ago. My objectives were to examine whether pheromonal differences exist between populations of *P. vehiculum* from Vancouver Island and from the mainland, and to compare the magnitude of this divergence to that between two Vancouver Island populations. I also make inferences, based on the patterns of responses by the salamanders toward odors, on the mechanisms responsible for the observed differences.

*Materials and methods.*—Reproductive male and female *P. vehiculum* were collected from the forest floor at three localities in southern British Columbia: Goldstream and Mount Douglas on

Vancouver island, and Cultus Lake on the mainland. The habitat between the two Vancouver Island locations (approx. 25 km apart) is discontinuous in terms of its suitability to the salamanders and is broken up by dry, rocky patches, open fields and urban areas. I considered males with SVL >41 mm and females with SVL >43 mm and with eggs (diameter of largest egg > 2.5 mm) visible through the abdominal wall to be reproductive (Peacock and Nussbaum, 1973; Ovaska, 1987). The collections took place in the fall of 1987 (on 1, 6, and 15 Nov. in Goldstream, on 9 Nov. in Mount Douglas, and on 11 Nov. in Cultus Lake), a time of year corresponding to the peak in mating activity of *P. vehiculum* (Ovaska, 1987).

The salamanders were maintained individually in 1 liter glass jars filled with moist moss and were fed weekly with small earthworms. The temperature in the laboratory fluctuated between 8 and 11 C, and the photoperiod was natural for Victoria, British Columbia. The salamanders used as odor donors were kept in captivity for at least 2 wk before the experiments to eliminate confounding effects of odors caused by differences in habitat or diet.

For testing, I transferred the salamanders (odor donors and salamanders to be tested) into individual 15 cm diameter plastic petri dishes, the bottoms of which were lined with sheets of moist filter paper. For the animals used as odor donors, the filter paper was cut into two equal halves to facilitate further handling. The salamanders were given an opportunity to feed to satiation the day before the beginning of the experiment, but they were not fed in the petri dishes. Feces and glandular secretions were allowed to accumulate on the filter paper for 7 d, during which time it was kept saturated with tap water. Odors derived from particular individuals were used one or two times in a given test.

I carried out testing in a 15 cm diameter, glass petri dish, one-half of which was covered with filter paper with the odor of a salamander from one population and the other with that of a salamander from another population. The odors were paired and their sides (left or right) were determined randomly for each trial. I then placed a salamander in the middle of the petri dish and, after a 2 min period of habituation under a small, opaque lid, observed its behavior from behind a blind for 30 min. I recorded the time the salamander spent on each half of the dish (Jaeger and Gergits, 1979) and, to elimi-

nate ambiguity, considered the salamander to be on the side where its snout was located. I also counted the number of times the salamander tapped its snout on each substrate (Trisram, 1977). This behavior (nose-tapping) is thought to enhance chemoreception by facilitating the transport of large, nonvolatile molecules from the substrate along the nasolabial grooves (structures present in all adult plethodontid salamanders and extending from the upper lip to each naris) into the olfactory epithelium of the Jacobson's organ (Brown, 1968). The petri dishes were cleaned between trials by soaking them in a solution of warm water and soap designed for cleaning glassware for a least 1 h.

I gave females from Goldstream a choice between: A) odors of males from Goldstream and Cultus Lake; and B) odors of males from Goldstream and Mount Douglas. Each female performed both tests. Because experience may affect the outcome of the trials, I divided the females randomly into two equal groups, one of which was given Test A first and Test B second, whereas the other group performed them in the reverse order. I also tested males from Goldstream on odors of females from Goldstream vs those of females from Cultus Lake. All the tests were carried out after dark under dim light (2 m from a 60 W red light bulb). I tested 20 individual females and 12 males from Goldstream. The tests for females took place between 2 and 26 Dec. 1987, and those for males between 1 and 18 Jan. 1988.

I used MANOVA (SPSSx User's Guide, 1985) to examine the order of testing on behavior of females. I compared the responses of the salamanders toward different odors using the two-tailed Wilcoxon signed-rank test for paired samples (Sokal and Rohlf, 1981). The level of significance was set at  $\alpha = 0.05$ .

**Results.**—The salamanders usually began moving immediately after the lids confining them were removed and continued movement throughout the observation period. Two females, however, remained inactive and were retested at a later date.

The order of the tests (first or second) for females that were used in two separate tests did not significantly affect the outcome of the trials (odor of Goldstream vs Cultus Lake males: MANOVA with the order of tests as the independent variable and differences between time spent and rate of nose-tapping on the two sub-

strates as the dependent variables, Wilk's lambda = 0.74, hypothetical df = 2,  $P = 0.08$ ; odor of Goldstream vs Mount Douglas males: Wilk's lambda = 0.95, hypothetical df = 2,  $P = 0.07$ ). There was a tendency, however, for females to nose-tap more the first time than the second time they were tested. Because an equal number of randomly chosen females performed each test first, this possible bias should not affect the comparisons.

Females spent an equal amount of time on substrates with the odor of males from Goldstream and Cultus Lake (Wilcoxon signed-rank test,  $T = 103$ , n (no. of untied pairs) = 20,  $P < 0.94$ ) and also on substrates with the odor of males from Goldstream and Mount Douglas ( $T = 91.5$ , n = 20,  $P < 0.60$ ). The rate of nose-tapping, however, was greater on substrates soiled by Cultus Lake males than by Goldstream males (Wilcoxon signed-rank test, Fig. 1). The rate of nose-tapping did not differ when the females were given a choice between odors of males from Goldstream and from Mount Douglas (Wilcoxon signed-rank test, Fig. 1). The behavior of males, when simultaneously presented with odors of females from Goldstream and from Cultus Lake, was similar to that of females: the time spent on the two substrates did not differ (Wilcoxon signed-rank test,  $T = 34$ , n = 12,  $P < 0.37$ ), but males nose-tapped more on substrates with odors of Cultus Lake females than on those of females from their own population (Wilcoxon signed-rank test, Fig. 2).

**Discussion.**—Both male and female *P. vehiculum* from Goldstream, Vancouver Island, discriminated between odors of conspecific individuals of the opposite sex from their own population and those from Cultus Lake, mainland British Columbia. I conclude that pheromonal divergence has taken place between the Vancouver Island and the mainland populations. In contrast, I detected no evidence that females from Goldstream discriminated between odors of males from the two Vancouver Island localities.

The behavior the salamanders showed toward odors involved differential rates of nose-tapping, rather than unequal amounts of time spent on the substrates with different odors. Most individuals spent a large proportion of the observation period moving around the periphery of the dish and nose-tapping on the vertical sides that were uncovered by filter paper. The time devoted to these apparent escape activities

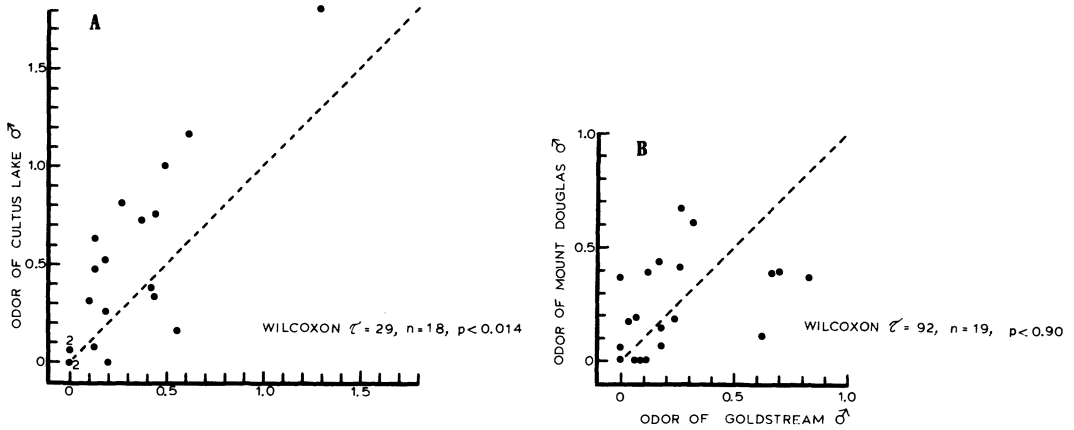


Fig. 1. Rate of nose-tapping per min for reproductive females from Goldstream when simultaneously presented with odors of males from Goldstream, Vancouver Island, and from Cultus Lake, mainland British Columbia (A), and from Goldstream and Mount Douglas, Vancouver Island (B). Broken line represents hypothetical break-even points. Circles represent responses by individual females. Numbers by circles indicate multiple points.

could have masked any differences in timing caused by responses toward the odors.

The rates of nose-tapping can not easily be linked with odor preferences, although Trisram (1977) was able to associate increased rates with attraction, based on frequency of other

behaviors, in experiments involving *P. cinereus*. Both male and female *P. vehiculum* nose-tapped more on substrates with odors of conspecific individuals of the opposite sex from Cultus Lake than from their own Vancouver Island population. The salamanders may have been attracted to odors of strangers. Potentially at least, inbreeding depression may pose a serious problem for terrestrial plethodontids with low vagility and generally poor dispersal abilities (Madison, 1975, 1977). Unfortunately, observations of mate choice by *P. vehiculum*, which would allow the linking of the results of the odor tests with preferences, are lacking due the reluctance of these salamanders to mate in captivity. Instead of indicating attraction, *P. vehiculum* may have exhibited increased rates of nose-tapping toward odors that deviated somewhat from the familiar and thus required more investigation. Novel stimuli are known to elicit increased olfactory interest in the lizard *Sceloporus jarrovi*, which exhibits greater rates of substrate licking toward unfamiliar than familiar odors (DeFazio et al., 1977).

Reproductive condition is likely to affect the behavior of salamanders toward odors of potential mates (Dawley, 1986, 1987). *Plethodon vehiculum* used in this experiment were collected and tested during the peak mating season in the fall (Ovaska, 1987). The collections took place soon after the first heavy rains in the fall of 1987, when the salamanders began emerging from their summer retreats underground and

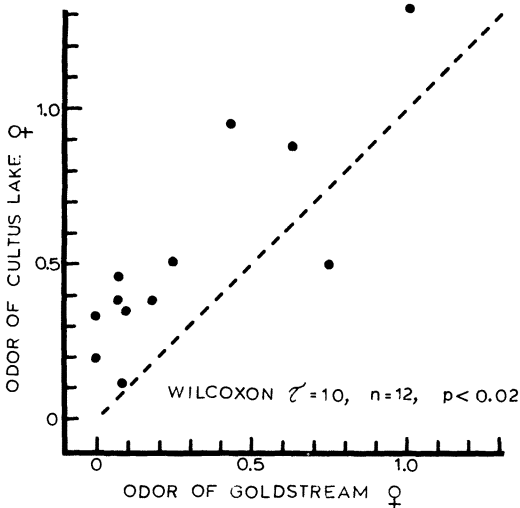


Fig. 2. Rate of nose-tapping per min for males from Goldstream when simultaneously presented with odors of reproductive females from Goldstream, Vancouver Island, and from Cultus Lake, mainland British Columbia. Broken line represents hypothetical break-even points. Circles represent responses by individual males.

resumed activity on the forest floor. Therefore, they probably had had few opportunities to mate in the natural habitat before the experiments and should have been particularly sensitive to odors of potential mates. The effects of captivity on behavior and receptivity of *P. vehiculum*, however, are unknown.

The results of this study suggest that *P. vehiculum* responded to general epidermal odors rather than to specialized courtship pheromones. Female *Plethodon* lack specialized glandular structures present in males, including pheromone-producing cloacal glands (Sever, 1978a, 1978b), and individuals of both sexes showed an ability to discriminate between odors of conspecific individuals of the opposite sex from different populations. The possibility that males and females responded to odors originating from different sources, however, can not be ruled out. Females could have discriminated between odors of males on the basis of specialized courtship pheromones, whereas males could have used general epidermal odors of females. *Plethodon vehiculum* is the only species of the genus on both Vancouver Island and mainland British Columbia. Therefore, modification of pheromones at either locality as a premating isolating mechanism evolved through reinforcement can not explain the observed divergence. I suggest that pheromonal divergence between the Vancouver Island and the mainland populations involves differences in generalized epidermal odors brought about by pleiotropic effects associated with other changes evolved in isolation.

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**ALLOTOPIC DISTRIBUTION OF NATIVE FROGS AND INTRODUCED FISHES IN HIGH SIERRA NEVADA LAKES OF CALIFORNIA: IMPLICATION OF THE NEGATIVE EFFECT OF FISH INTRODUCTIONS.**—In high elevation (>2500 m) lakes in the Sierra Nevada of California, the distributions of a native ranid frog (*Rana muscosa*) and introduced trout (*Salmo* spp.) and charr (*Salvelinus* spp.) appear to be allotopic, i.e., populations of frogs and fish appear not to co-occur in the same lake (e.g., Grinnell and Storer, 1924; Cory, 1963; Zardus et al., 1977). Although quantification of this relationship is poor, the pattern is substantiated by the occurrence of conspicuously large numbers of *R. muscosa* in some lakes that lack fish. Prior to the stocking of high Sierra Nevada lakes with salmonid fishes, which began over a century ago, fish were entirely absent from most of this region (Hubbs and Wallis, 1948; Christenson, 1977). Today, hundreds of high Sierra Nevada lakes are populated with trout and charr (Christenson, 1977).

The apparent allotopic distribution of frogs and fish has been interpreted as a case of elimination of native frog populations due to predation by introduced fishes (Grinnell and Storer, 1924; Walker, 1946; Hayes and Jennings, 1986). The hundreds of high Sierra Nevada lakes that now contain trout and charr may have previously supported substantial populations of frogs. Hayes and Jennings (1986) argued that predation by introduced fishes is the most compelling hypothesis explaining the apparent declines that have occurred among most of the native ranid frogs in western North America.

The present study tests the hypothesis that populations of two native frogs, *R. muscosa* and *Pseudacris* (= *Hyla*) *regilla*, and introduced fishes do not co-occur in high Sierra Nevada lakes. The study also assesses the importance of lake depth in determining the occurrence of these animals.

**Methods.**—Data were obtained for 67 lakes in the Tablelands and Ansel/Blossom lakes areas of Sequoia National Park and Kings Canyon National Park, both in California. These two areas were selected because both frogs and fishes occur in each area, numerous lakes occur in each area, and both areas lie within a 1 d hike from a road. The two areas, which together are approx. 18 km<sup>2</sup> in total area, lie 23 km apart in the watersheds of the Kings and Kaweah rivers. Forty-nine of the lakes surveyed appear on U.S. Geological Survey 15 min quadrangles (Mineral King, Triple-Divide Peak); the remainder are small and, in some cases, ephemeral. The precise locations and other data for all lakes are on file at Headquarters, Sequoia and Kings Canyon National Parks, Three Rivers, California.

Surveyed lakes ranged from approx. 2910–3430 m in elevation, from approx. 0.004–7 ha in area, and from 0.3–37 m in maximum depth. Rooted vegetation was generally sparse and restricted to water shallower than 0.5 m deep. Shorelines were typically rocky, surrounded by subalpine forest or alpine fell-fields plant communities of Munz and Keck (1965). Fingerling rainbow trout (*Salmo gairdneri*), brook charr (*Salvelinus fontinalis*), and possibly golden trout (*Salmo aguabonita*) have been introduced to several lakes in each area at various times since about 1930, and possibly earlier (Meyer, 1965; Christenson, 1977; Zardus et al., 1977). Anuran amphibians observed in each area were the mountain yellow-legged frog (*R. muscosa*) and the Pacific treefrog (*P. [=Hyla] regilla*). *Bufo bo-*