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TADPOLES AND POLLEN: OBSERVATIONS ON THE FEEDING BEHAVIOR OF *HYLA REGILLA* LARVAE.—Anuran larvae are generally non-discriminatory suspension feeders (Wassersug, 1975) that ingest bacteria, diatoms, blue-green algae, green algae, protozoa, microscopic arthropods, their own fecal pellets and a wide variety of organic and inorganic debris (Gromko et al., 1973; Hendricks, 1973; Heyer, 1973; Hillis, 1982). These materials are commonly ingested in the same relative proportions as encountered (Jenssen, 1967). Here I provide evidence for the behavioral selection of conifer pollen by *Hyla regilla* tadpoles and describe the feeding behavior associated with the exploitation of this resource.

*H. regilla* is one of the most abundant frogs in western North America (Brattstrom and Warren, 1955). It is common in a wide variety of habitats from deserts to rainforests (Stebbins, 1951). Wassersug (1976) considers its larvae to be typical pond tadpoles, possessing a generalized oral morphology. There have been a number of studies of the adult stage, including their feeding habits (Johnson and Bury, 1965), but the larval stage has been largely neglected.

*Study site.*—Observations were made from June–Aug. 1984 at four breeding sites on the eastern slope of the Sierra Nevadas in the Sagehen Creek Drainage Basin, Nevada County, California. These locations included the Borrow Pit, an artificial pit at 2010 m; Hidden Fen, a bog with slowly moving shallow water at 2150 m; Leopold Wash, a temporary stream and associated pools at 2040 m; and Cirque Lake, a semi-permanent pond at 2520 m. Tadpole behavior was observed at these sites at irregular intervals and larvae were occasionally collected for more detailed examination. Voucher specimens were deposited in the Museum of Vertebrate Zoology (MVZ #193546–49), University of California, Berkeley.

*Field observations.*—Conifers produce prodigious quantities of pollen (Ho and Owens, 1974). During the summer of 1984, pollen was seen blowing in sheets across the forest, beginning in mid-June when the lodgepole pine (*Pinus contorta*) was shedding pollen. Exposed areas, including the surface of still water, were occasionally coated with a layer of pollen that persisted for many weeks. Pollen is known to be a valuable source of nutrients for a number of animals (Todd and Bretherick, 1942; Smith and Mommsen, 1984) and *Hyla* tadpoles were first seen ingesting lodgepole pine pollen on June 20 at the Borrow Pit.

In the absence of pollen, tadpoles variously swam through the water column, moved along the bottom, or rested motionless on the bottom of the pond, very rarely rising to the surface. In the presence of pollen this behavior changed. The larvae often swam just below the water's surface with the trunk oriented vertically and the tail projecting posteriorly at approximately a 45° angle to the body. A short funnel could be seen extending from the water's surface into the mouth. Water drawn into the oral cavity brought in both the surface layer and any trapped particles. Such surface feeding has been observed for other species (Belkin and Gans, 1968; Nathan and James, 1972), but its significance has not been fully documented.

When pollen grains were dispersed over the surface, the tadpoles swam in a seemingly random pattern. However, when dense packets were present and encountered by a tadpole, the tadpole often quickly doubled back and fed on the packet until it was depleted or dispersed. Tadpoles either remained stationary while feeding or pushed the packets forward while continuing to swim about. There was no indication that the larvae could detect these pollen aggregations from a distance, but rather that they moved about until they encountered one.

Because of wind patterns, pollen was differentially distributed on the surface of the Borrow Pit. Ten tadpoles were observed for a total of 300 s each both in areas with and without dense pollen. Tadpoles in areas of the pond with high surface pollen densities spent significantly more time feeding at the surface ($\bar{x} = 47$ s) than did tadpoles in areas of the pond with little surface pollen ($\bar{x} = 4.8$ s; $t = 2.420$, $P < 0.05$). Thus, tadpoles apparently alter their feeding behavior in the presence of pollen.

The other sites differed somewhat from the Borrow Pit. Both the Hidden Fen and Leopold Wash sites contained running water where pollen was not concentrated. Tadpoles in these areas were almost never seen feeding at the surface. At the Cirque Lake site, pollen was present on the surface from around June 20, whereas tadpoles were not observed until July 1, after much of the pollen had been shed from the surrounding lodgepole and Jeffrey pines (*Pinus jeffreyi*). On July 14 a sample of pollen collected directly from a number of lodgepole pines was fixed and stained with polyvinyl-lactophenol plus iodine. Pollen grains thus stained (97%) are considered nutritionally valuable (i.e., presumably contain exploitable nutrients). Only 46% of the pollen collected from the surface of Cirque Lake on July 19 stained. By July 31 only 17 of the grains stained in another sample from the surface of Cirque Lake. The nutritional value of pollen suspended in water thus seems to decrease with time due to the cytoplasmic contents being leached out. Presumably because of this, a very low percentage of the tadpoles at Cirque Lake were seen feeding at the surface, though all tadpoles examined had at least traces of pollen in their intestinal tracts. This suggests that in addition to being able to detect pollen, larvae can also sense differences in pollen value and may adjust their feeding behavior accordingly.

*Microscopic examinations.*—To determine that larvae extracted nutrients from ingested pollen, intestinal tracts of collected tadpoles were examined. Small sections of both the anterior and posterior tracts were smeared onto slides and stained with polyvinyl-lactophenol plus iodine. All tadpoles collected after pollen shedding began had some pollen in their intestinal tracts. Most of this was pine pollen (*Pinus* sp.), but fir pollen (*Abies* sp.) was also occasionally noted. Tadpoles from the Borrow Pit contained the most pollen, of which some had intestinal tracts that were visibly yellow through the body wall. For 10 of the Borrow Pit slides, 100 randomly chosen pollen grains were examined and the ratio of stained vs unstained grains determined for both the anterior and posterior gut sections. Using the percentage of stained pollen grains in the anterior tract as a baseline figure, 12.5% of the pollen was digested by the time it reached the hind gut. Very few of the cell walls were ruptured and those that were probably resulted from the mashing of the gut sections when fixed onto slides. As with honeybees (Stanley and Linskens, 1974), tadpoles probably digest nutrients through the pollen germination pores, thus mechanical or enzymatic breakdown of the cell wall may be unnecessary. Whether the nutrients extracted from the pollen are actually assimilated is unknown.

*Conclusions.*—Observations in the field suggest that *H. regilla* larvae alter their feeding behavior in response to surface pollen. Pollen is a nutritious food source and its exploitation by these tadpoles is best considered as an opportunistic tactic made possible by their generalized oral morphology. While the mechanics of suspension feeding allow some degree of particle discrimination to occur (Rubenstein and Koehl, 1977), behavioral selection provides a means of selectively feeding on desirable food items within the range of particle sizes that the filter can capture. The importance of behavioral selection in other species is unclear, but it seems premature to consider all anuran larvae as non-discriminating feeders merely because of oral morphology. The extent to which pollen can be utilized varies according to the microhabitat in which the tadpoles are located, as well as with the timing of pollen shedding in relation to egg deposition.

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