

- infant. An immigrant male bit an 11-month-old infant behind the ear (K. S. Smith, personal communication). Finally, a male from an unknown troop wounded a weaned 14-month-old juvenile during an intertroop interaction.
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16. Carrying males chased or displaced opponents during four interactions and were chased or displaced by opponents during 11 interactions.
17. We are indebted to Mr. Ngwamotsoko and the Office of the President of Botswana for permission to study in Botswana. We thank K. S. Smith for invaluable help in the field and P. S. Rodman, R. L. Tilson, L. R. Becker, S. Blaffer Hrdy, R. Boyd, A. B. Clark, R. O. Davis, M. F. Miller, D. Owens, M. Owens, M. P. Rowe, J. B. Silk, and D. M. Stein for comments on the manuscript. Supported by NIH grant 5-RO1-RR01078.

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Vagotomy Abolishes Cues of Satiety Produced by Gastric Distension

Abstract. Subdiaphragmatic vagotomy in the rat abolishes responsiveness to gastric distension, one of the cues of satiety. However, vagotomized rats remain responsive to gastric nutrient content, another cue of satiety.

Meal size in the rat is regulated by sensory information originating from the preintestinal segment of the gastrointestinal tract. When passage of food from the stomach to the intestine is prevented by blocking the pyloric sphincter with a noose (1, 2) or an inflatable cuff (3, 4), subjects consume meals of normal size. Since rats overeat when food is removed from their stomachs (2-5), gastric rather than oropharyngeal receptors are the likely source of satiety messages.

The stomach produces two types of satiety signals. One conveys information concerning the nutrient content of the

stomach and is independent of gastric volume. The other signals gastric distension and is given only after the animal has consumed a large meal (4). We examined the effects of interrupting the parasympathetic innervation of the stomach on these satiety signals and demonstrated the pathway of one of them to the central nervous system.

Nine male Sprague-Dawley rats (325 to 495 g) were used as subjects. The animals were habituated to a restricted feeding schedule consisting of two meals of undiluted canned milk (Carnation) a day. The first meal (30 minutes) began at 1000 hours while the subjects were in restraining cages. The second meal (3 hours) began at 1600 hours in the home cages. The animals had free access to water at all times, except when undergoing testing in the restraining cages.

After the food intakes and weights of the subjects had stabilized, they were randomly assigned to a vagotomized or a control group. Six subjects were vagotomized at the subdiaphragmatic level by stripping all neural and connective tissue surrounding the 3- to 5-mm portion of the esophagus immediately rostral to the stomach (6). The hepatic branch of the nerve was spared. In three control subjects the subdiaphragmatic vagus was identified but not injured.

All subjects were allowed to recover for 21 days under the feeding conditions described. They were then implanted with inflatable pyloric cuffs and stomach tubes (7). After a second convalescence period of at least 10 days, the ingestive behavior of the subjects during their 30-minute meals was examined. The mea-

surements consisted of (i) baseline consumption, (ii) consumption when a proportionate amount (50 percent by volume) of 0.9 percent saline was infused into the rat's stomach as it drank (8), and (iii) consumption when a fixed volume (5 ml) was siphoned from the rat's stomach as it drank at the beginning of the test. These measurements were made in the order described, first with the pylorus unoccluded, then with pyloric cuff inflated with 1.5 ml of water to prevent emptying of the stomach. The results were analyzed with one-tailed *t*-tests for paired data.

Figure 1 presents a summary of the results. After being infused with saline, the control rats decreased their intake of milk by 23 and 22 percent after 15 and 30 minutes, respectively ($t = 4.529$, $P < .05$ and $t = 4.695$, $P < .05$, respectively). The vagotomized subjects showed a small but nonsignificant increase in consumption (7 and 5 percent). When 5 ml was siphoned from the stomachs of the control rats, they increased their intake by 6.2 and 3.5 ml after 15 and 30 minutes, respectively. The increase measured after 15 minutes is significant ($t = 15.105$, $P < .01$); the increase measured after 30 minutes is not. Vagotomized rats drank 6.5 and 7.1 ml more when 5 ml was siphoned from their stomachs; both increases are significant at $P < .01$ ($t = 3.758$ and 4.369 , respectively). The same pattern of results was observed when the subjects were tested after their pyloric cuffs were inflated to confine the milk to their stomachs.

Since the vagotomized subjects drank considerably less than the controls, their milk intake was measured when a larger (100 percent) volume of saline was infused into their stomachs as they drank, thus doubling intragastric volume. Once again, these subjects were insensitive to the increase in volume. Their intakes after 15 and 30 minutes were 9.7 and 10.7 ml in the control condition and 10.7 and 11.1 ml in the saline infusion condition

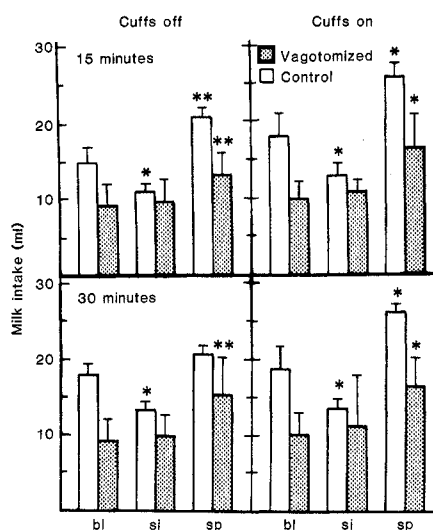


Fig. 1. Mean intakes of undiluted condensed milk for the experimental and control groups under baseline (bl), saline infusion (si), and siphoning (sp) conditions. Asterisks indicate that the value is significantly different from baseline (*, $P < .05$; **, $P < .01$).

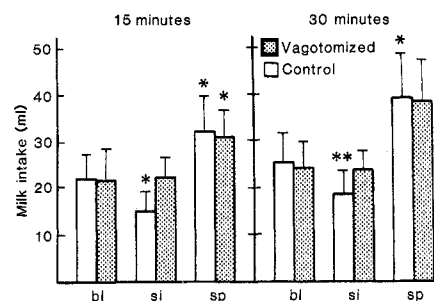


Fig. 2. Mean intakes of diluted milk for the experimental and control groups under baseline, saline infusion, and siphoning conditions. Abbreviations are as in Fig. 1.

($t = 0.886$, $P > .5$ and $t = 0.243$, $P > .05$, respectively). In the latter condition the subjects were receiving 21.4 and 22.2 ml, which is more than the 16.5 and 19.9 ml that the control subjects received when their intake was inhibited by the saline counterinjections; however, since these differences in volume are not very large, one more experimental manipulation was undertaken.

For this final test, the vagotomized and control groups were tested under the three experimental conditions as before; however, this time their milk was diluted 1:1 with tap water during the 30-minute meal. Under these conditions the intake of the normal subjects increased only slightly, but the intake of the vagotomized subjects showed a steady increase until, after 4 days, it reached the control level. On the fifth day the animals were tested under baseline conditions to make sure that stabilization had occurred. Then they were tested under two experimental conditions. In one, 0.9 percent saline was infused into their stomachs at a rate equal to half the voluntary consumption. In the second condition, 10 ml of their gastric contents was siphoned off as they drank. The results are presented in Fig. 2. Milk intake by control subjects was affected by both saline infusions and nutrient withdrawal. Vagotomized subjects adjusted their intake only in relation to nutrient withdrawal.

After the behavioral tests were completed the subjects were anesthetized with sodium pentobarbital, the condition of their implants was checked, and the success of the denervation operation was verified by an electrophysiological test involving electrical stimulation of the cervical vagus nerve (6). Finally, the possibility that the vagotomized subjects were not responsive to gastric distension due to an enlargement of their stomachs was investigated. [Such enlargement has been observed in vagotomized subjects kept on solid food (9).] Autopsies showed the stomachs to be of normal size (10).

It appears that gastric distension, one of the signals that control meal size, has no effect on consumption after the vagus nerve is cut. However, gastric nutrient content is still monitored in the normal manner. Clearly, signals conveying information about nutrient content must take another route to the central nervous system.

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the milk in the U tube and a 20-cm² syringe that delivered the infusion. The diameters of these syringes were such that the larger one pumped twice as much fluid per unit time as the smaller one. While the pump was activated the rate of intragastric infusion was 2.2 ml/min.

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10. Three indices of stomach size were collected: surface area, weight, and volume of water required to elevate intragastric pressure to a standard of 30 cm in a water manometer. None of the differences in these values between the control and experimental groups was significant. It is also unlikely that the difference in milk consumption between vagotomized and control rats could be due to differential rates of gastric emptying. While it has been suggested [P. R. McHugh and T. H. Moran, *Am. J. Physiol.* **236**, R-254 (1979)] that rate of gastric emptying could function as a satiety signal, we have shown (3, 4) that satiety is unaffected by occlusion of the pylorus.
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Predatory Salamanders Reverse the Outcome of Competition Among Three Species of Anuran Tadpoles

Abstract. *The outcome of competition among three species of anuran tadpoles in replicated artificial pond communities depends on the density of predatory salamanders present in the community. Predators differentially affect the survival of anuran species to metamorphosis and reverse the pattern of anuran relative abundance resulting from interspecific competition among tadpoles in the absence of predators.*

Theoretical community ecology has been dominated by the assumption that interspecific competition is of paramount importance in the determination of the species composition of most communities (1). In contrast, experimental studies of assemblages of plants and sessile invertebrates have demonstrated that predators may alter the outcome of interspecific competition among their prey (2). Despite the demonstration of an interaction between predation and competition in communities of potentially

space-limited sessile species, the study of the interaction between competition and predation in free-ranging vertebrate prey has been neglected (3) even though descriptive and experimental studies of vertebrates have provided the foundation of arguments for the preeminence of interspecific competition as a mechanism producing patterns of community structure (4). While interspecific competition undoubtedly occurs in some vertebrate communities (5), the effects of variation in intensity of predation on the outcome of competition are usually unknown. Recent reevaluations of earlier descriptive studies of vertebrate communities have also questioned the statistical validity of much of the indirect evidence (for example, character displacement) that has been cited to support the role played by competition in the structuring of communities (6). These studies have suggested that much of the purported pattern in vertebrate communities simply reflects stochastic interspecific variation in morphological attributes usually associated with resource utilization, rather than a systematic partitioning of resources consistent with competition and niche theory.

I have investigated the potential interaction between predation and competition by conducting a community-level experiment on the effects of different

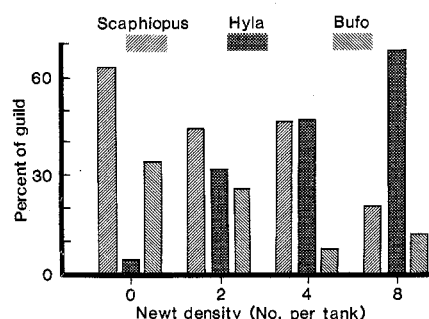


Fig. 1. Summary of the effects of newt density on the mean relative abundance of three species of anurans at metamorphosis. Percentages refer to the mean composition of the tadpole guild over four replicate communities at each level of newt density. Increasing intensity of predation corresponding to increasing newt density leads to a significant reversal in the composition of the tadpole guild (9); $\Lambda = .170$; $P = .02$.