SALIVARY pH AND BUFFERING CAPACITY IN FRUGIVOROUS AND INSECTIVOROUS BATS

ELIZABETH R. DUMONT

Department of Anatomy, Northeastern Ohio Universities, College of Medicine, 4209 State Route 44, P.O. Box 95, Rootstown, OH 44272

Histochemical and ultrastructural studies suggest that bats possess a diverse array of salivary chemistries that are associated with variation in dietary habits. Two fundamental chemical properties of saliva are pH and buffering capacity. This study documents variation in the pH and buffering capacity of whole saliva in 21 chiropteran species; frugivorous species from the families Phyllostomidae and Pteropodidae and insectivorous species from the families Vespertilionidae, Molossidae, and Rhinolophidae. Buffering capacity and pH were measured primarily in free-ranging individuals close to feeding and after a fasting period. Phyllostomids, pteropodids, and insectivores differ in salivary pH and buffering capacity at both sampling times. Insectivores produce saliva of significantly higher pH and buffering capacity than frugivores, suggesting the presence of fundamentally different oral physiologies between these two broadly defined dietary categories. Among frugivores, saliva of phyllostomids has significantly higher pH and buffering capacity after fasting than pteropodids, which exhibit the lowest values of salivary buffering capacity and pH known for any mammal. Patterns of diversity in salivary pH and buffering capacity appear to reflect dietary habits more closely than taxonomic relationships.

Key words: Chiroptera, saliva, pH, buffering, dietary habits

Bats exhibit perhaps the broadest range of feeding and foraging strategies of any mammalian order, with specializations ranging from nectivory to sanguivory, piscivory, insectivory, and frugivory. Gross morphological adaptations are found in the craniodental apparatus (Dumont, 1997; Freeman, 1988), as well as within the postcranial skeleton (Schlosser-Sturm and Schliemann, 1995; Schutt, 1995). At the microscopic level, dietary adaptations of bats often are reflected in the histochemistry and ultrastructure of the digestive tract and salivary glands (Makanya et al., 1995; Phillips et al., 1984, 1993; Tandler et al., 1990). Much of the variation in salivary glands of bats is within secretory granules of acinar cells, suggesting diversity in salivary composition among different species of bats. Despite this evidence, only one study has documented differences among species in chemical composition of salivary glands and assessed their variation with respect to dietary adaptation (Junquierra et al., 1973).

Saliva functions in digestion, lubrication of food, and in clearing the oral cavity of debris (Etzel, 1993). Saliva also plays a role in binding secondary compounds, combatting oral bacteria, and providing a vehicle for interspecific communication (Balasingh et al., 1995; Gray et al., 1984; Lagerlof and Oliveby, 1994; McArthur et al., 1995). Another role of saliva is defending against erosion of dental enamel that results when pH in the oral cavity is <5.5 (Newbrun, 1989). Over time, erosion leads to the development of small fissures in the enamel that are prime sites for colonization by caries-causing bacteria (Frank, 1990). Salivary buffers and elevated pH play a protective role by moderating the erosive effects of acids and, thereby, prolonging dental function (Newbrun, 1989).

Dietary acids are commonly cited as the primary cause of erosion of enamel in hu-

mans (Zero, 1996). Because many fruits are highly acidic (Grobler, 1991; Ungar, 1995), frugivorous mammals might be expected to have either high rates of erosion or high values of salivary pH and buffering capacity to protect the teeth against erosive dietary acids. Free-ranging frugivorous bats do exhibit eroded enamel (Phillips, 1971), but the range of salivary pH and buffering capacity in these species is unknown. The present study investigates salivary pH and buffering capacity in frugivorous bats and compares those values to data gathered from insectivorous species.

In the present study, data on salivary pH and buffering capacity are reported for New World fruit bats (Phyllostomidae), Old World fruit bats (Pteropodidae), and insectivorous species (Molossidae, Vespertilionidae, and Rhinolophidae) and used to test two null hypotheses. The first hypothesis is that there are no significant differences among the three groups in salivary pH and buffering capacity, either at rest or at time of feeding. A second hypothesis is that pteropodids and phyllostomids are homogeneous with respect to salivary pH and buffering capacity. This hypothesis is based on the prediction, partly derived from comparative microscopic and histochemical analyses of salivary glands (Phillips et al., 1987, 1993; Tandler et al., 1988, 1990), that salivary secretions reflect dietary adaptations. In addition, the data provide the opportunity to investigate salivary pH and buffering capacity for patterns of variation that may reflect either phylogeny or dietary similarities.

Materials and Methods

Data on salivary pH and buffering capacity were collected from 174 individual bats, representing 21 species and 5 families (Appendix I). Most data were gathered from recently captured animals, although captive individuals of the larger pteropodids (*Pteropus* and *Dobsonia moluccensis*) also were sampled. Bats were captured in mist nets beginning 1 h after sunset and promptly removed. The pH and buffering capacity of whole saliva were measured within 30 min of capture, using papers that reflect differences in pH (ColorPhast, EM Science, Darmstadt, Germany) and buffering capacity (Dentobuff, Orion Diagnostica, Espoo, Finland; Ericson and Bratthall, 1989). Papers were trimmed to fit comfortably in an animal's closed mouth. Because salivary pH increases on exposure to air (Charlton et al., 1971), each paper was held in the animal's mouth, with the color-changing surface in contact with the superior surface of the tongue, for 1 min, before recording pH. This procedure was immediately repeated using papers that measured buffering capacity; however, these were left in the mouth for 2 min prior to reading the change in color. Salivary pH was measured to the nearest 0.3 pH units, and buffering capacity was scored on a scale of 1–5 (low–high). Buffering capacity is measured as the final pH of saliva after it is combined with the small amount of acid embedded in the buffering-capacity strip. A score of 1 indicates a final pH ≤ 4, whereas a score of 5 indicates a final pH ≥ 6 (Ericson and Bratthall, 1989).

After the first samples were collected, insectivorous bats were offered plain water and frugivorous species were given sweetened water before being placed in individual cloth bags and held overnight. The same sampling procedure was repeated after the animals were fasted for an average of 9.7 h (elapsed time measured to the nearest 5 min, $SE = 0.1$ h, $n = 140$; some individuals were released immediately after the first sample was collected). Most animals were released on the following evening, although voucher specimens were collected for some species (Appendix I). To the extent possible, procedures for collection of data from captives mimicked those used on wild individuals. In several cases, however, large pteropodids were sampled after extended fasting periods (≥ 12 h) and again immediately after hand-feeding.

Bats were captured well after darkness, but early in the evening, so data collected at the time of capture should represent salivary pH and buffering capacity at feeding. Data collected from animals that did not produce feces, either at capture or during the overnight fasting period, were omitted from the analysis because it was uncertain whether they had been feeding prior to capture. Data collected after fasting represented resting salivary pH and buffering capacity.

Sources of natural variation in salivary pH

and buffering capacity have been studied extensively only in humans. Except during the 3rd trimester of pregnancy, adult humans are not sexually dimorphic in salivary pH and buffering capacity (Muerman and Rantonen, 1994; Orosz et al., 1980), although salivary buffering capacity, and probably pH, are more variable among juvenile humans than adults (Soderling et al., 1993). Consequently, only adults and subadults were included in this study. Although a few palpably pregnant females also were included, salivary pH and buffering capacities of these individuals fell well within the range of variation of conspecifics.

Homogeneity of salivary pH and buffering capacity among phyllostomids, pteropodids, and insectivorous bats was investigated using single-classification analysis of variance (ANOVA) applied to each variable and sampling time (SAS Institute, Inc., 1989). Differences between frugivores and insectivores and similarity between phyllostomids and pteropodids were tested through orthogonal decompositions of the ANOVAs (Sokal and Rohlf, 1981). Because sample sizes among species differ, means of species were used in these comparisons. One set of data (buffering capacity at feeding) failed tests for normality and was rank-transformed prior to analysis (Conover and Iman, 1981). Clustering was done by applying the unweighted pair-group method using arithmetic averages (UPGMA) to a matrix of average taxonomic distances (summarizing both variables and sampling times) to assess the patterns of similarities over all species (Rohlf, 1990).

Results

Salivary pH and buffering at feeding and after fasting differed among phyllostomids, pteropodids, and insectivorous species ($P \leq 0.001$, $d.f. = 2,18$, and $P \leq 0.01$, $d.f. = 2,18$, respectively). Differences between frugivores and insectivores were significant for each variable and each sampling time ($P \leq 0.001$ at feeding and $P \leq 0.01$ after fasting; $d.f. = 1,18$). Buffering capacity for pteropodids and phyllostomids was significantly different at both sampling times (both $P \leq 0.001$, $d.f. = 1,18$), although the salivary pH of phyllostomids and pteropodids was statistically distinct only after feeding ($P \leq 0.05$, $d.f. = 1,18$).

Insectivores exhibited significantly higher salivary pH than frugivores at each sampling time (Fig. 1). Salivary pH among phyllostomids was about intermediate between insectivores and pteropodids, although individual phyllostomids overlap with each of the other groups. Although the pattern of differences in pH among groups was similar at feeding and after fasting, the overall distribution of pH was more compressed after the fasting period. Differences among insectivores, phyllostomids, and pteropodids in buffering capacity were much more distinct at feeding (Fig. 2). Although buffering capacity was more variable after fasting than at feeding, insectivores were consistently well buffered, and pteropodids were the most poorly buffered.

Cluster analysis of data on salivary pH and buffering capacity, at feeding and after fasting, yielded two principal clusters (Fig. 3). One contained insectivores plus species of *Carollia* and *Platyrrhinus,* and the other cluster was composed of the remaining frugivores. The insectivorous cluster was subdivided into three groups that included molossids, vespertilionids plus *Carollia castanea,* and a third group consisting of *Hipposideros, Platyrrhinus,* and the remaining species of *Carollia.* Within the frugivorous cluster, species of *Dobsonia* and *Paranyctimene raptor* formed a group that excluded other taxa. Among the remaining frugivores, there was broad overlap among phyllostomids and pteropodids.

Discussion

All analyses comparing phyllostomids, pteropodids, and insectivores yielded statistically significant differences and support the alternative hypothesis that frugivores have lower salivary pH than insectivores (Fig. 1). Despite the low pH of their saliva, frugivores do not exhibit high buffering capacities to provide protection against erosion of enamel (Fig. 2). Insectivores have high buffering capacities at feeding, whereas frugivorous bats, especially pteropodids, are poorly buffered. The presence of differ-

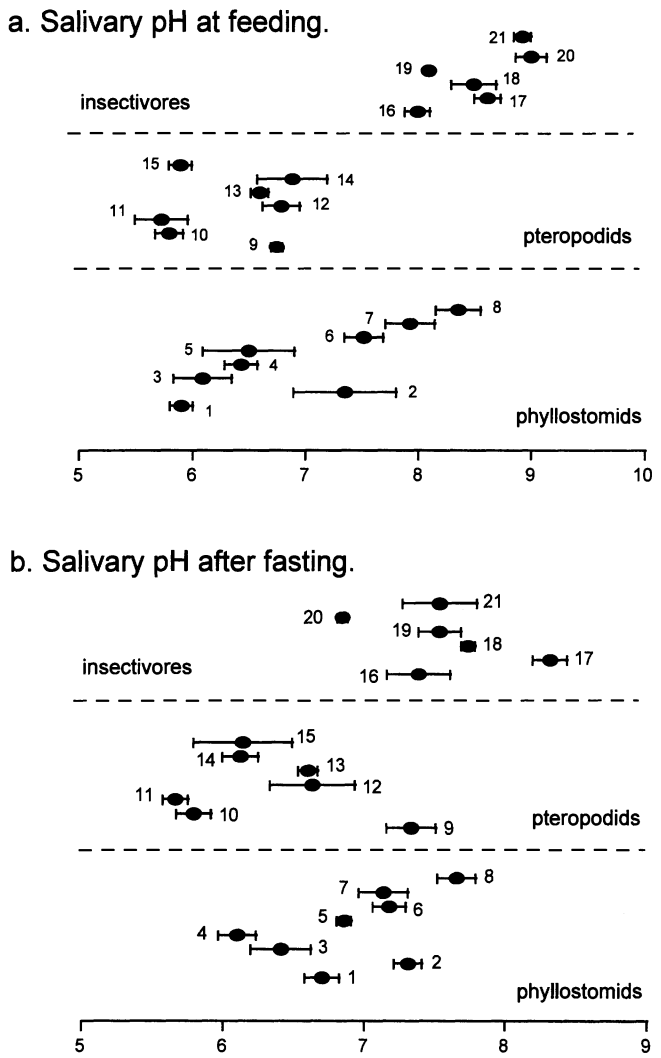

FIG. 1.—Means and standard errors of salivary pH a) at feeding and b) after fasting. Species are: 1, *Artibeus jamaicensis*; 2, *Platyrrhinus helleri*; 3, *Sturnira lilium*; 4, *Phyllostomus discolor*; 5, *Uroderma bilobatum*; 6, *Carollia perspicillata*; 7, *Carollia brevicauda*; 8, *Carollia castanea*; 9, *Epomophorus labiatus*; 10, *Dobsonia minor*; 11, *Dobsonia moluccensis*; 12, *Pteropus conspicillatus*; 13, *Pteropus hypomelanus*; 14, *Nyctimene albiventer*; 15, *Paranyctimene raptor*; 16, *Hipposideros maggietaylorae*; 17, *Lasiurus borealis*; 18, *Myotis lucifugus*; 19, *Myotis septentrionalis*; 20, *Mops condylurus*; 21, *Chaerephon pumila.*

ences in salivary pH and buffering capacity between these broadly defined dietary categories suggests that further biochemical assays may demonstrate functional divergence in salivary secretions.

In addition to the robust differences between insectivorous and frugivorous bats, there also are significant differences between phyllostomids and pteropodids. Although the two groups exhibit similar pH at feeding, phyllostomids have significantly higher pH after fasting and significantly higher buffering capacity at both sampling times. The hypothesis that phyllostomids and pteropodids are homogeneous because of broad similarity in dietary habits is re-

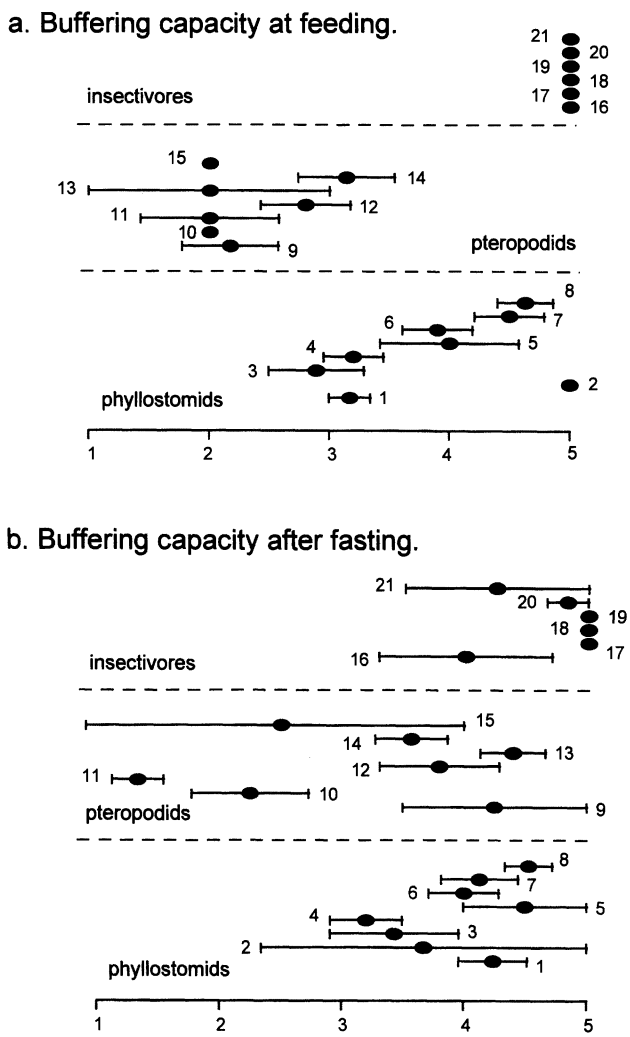

FIG. 2.—Means and standard errors of salivary buffering capacity a) at feeding and b) after fasting. Key to identification of species is as in Fig. 1.

jected. While similarity in salivary pH at feeding may indicate similarity in the pH of the fruits that the bats eat, factors that reflect basic differences in digestive physiology (Thomas, 1984) or salivary composition could explain the remaining differences. Heterogeneity in salivary pH and buffering capacity among frugivores mirrors the variation in anatomical systems among frugivores (Dumont, 1997; Freeman, 1988). In this respect, salivary pH and buffering capacity offer additional evidence that the dietary category of frugivore contains species with a range of morphological and physiological adaptations.

To complement the variation among insectivores, phyllostomids, and pteropodids that is identified using univariate statistics, cluster analysis (Fig. 3) illustrates the pattern of overall similarities among all species in the analysis. Molossids and vespertilionids cluster according to family membership, although *C. castanea* is interposed between *Myotis* and *Lasiurus*. Consequently, one might suggest that variation in salivary chemistry reflects phylogenetic distance.

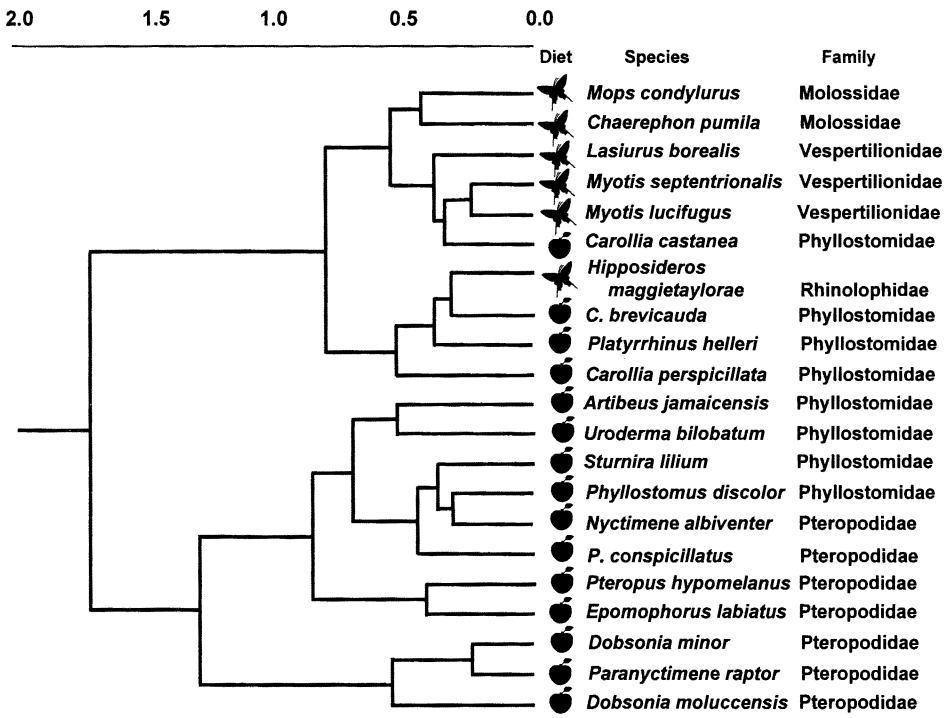

FIG. 3.—Phenogram resulting from clustering analysis (UPGMA) of salivary pH and buffering capacity at feeding and after fasting for all species. Dietary habits are symbolically indicated such that an apple represents a frugivore and a butterfly represents an insectivore. The scale at top left indicates relative distance between clusters.

However, salivary pH and buffering capacity are not closely linked with taxonomy among frugivores; pteropodids and phyllostomids are not clearly segregated. On a finer scale, closely related genera do not cluster together. In sum, there is no strong evidence that the pH and buffering capacity of saliva reflects evolutionary relationships. Rather, they appear to be associated with broadly defined dietary habits.

Saliva, however, is a complex fluid composed of secretions from many sources, and pH and buffering capacity are only general assessments of salivary chemistry. Given the ultrastructural variation seen within the salivary glands of bats, more detailed analyses of the composition of saliva may reveal taxonomically relevant differences among species. The data presented here strengthen the conclusions of previous studies (Phillips et al., 1987, 1993; Tandler et al., 1988, 1990) that salivary glands are rapidly evolving in response to a range of functional and physiological demands.

In terms of oral function, the consequence of low pH and buffering capacity among fruit bats is decreased protection from erosive dietary acids. This may have important consequences, because many fruits dispersed by bats have a pH that is low enough to produce erosion of dental enamel (Ungar, 1995). Unfortunately, it will remain uncertain whether variation in acidity of food drives the discrepancies in salivary pH between frugivores and insectivores until the pH of insects is documented. It also is unclear how frugivores, especially pteropodids, maintain oral health in the face of an acidic diet. Perhaps other aspects of salivary chemistry, such as the presence of antibacterial agents or variations in the microstructural

morphology of enamel, afford frugivores some degree of protection.

Digestion is initiated in the oral cavity and continued in the stomach, and therefore, it is particularly appropriate to consider the physiology of the oral cavity within the context of the physiology of the stomach. Ultrastructural and immunohistological studies of stomachs of bats suggest that frugivores and insectivores differ significantly in the rate of production of acid, pepsinogen, and mucus (Forman, 1972; Okon, 1977; Phillips et al., 1984; Studholme et al., 1986). Insectivores exhibit moderate numbers of pepsinogen-producing chief cells and mucous cells in conjunction with acid-producing parietal cells that are small and relatively inactive. In the presence of acid, pepsinogen is converted into pepsin (a protease), and mucus protects the stomach from damage caused by passing food particles and endogenous acids. In contrast to insectivores, frugivores exhibit relatively high numbers of active parietal and chief cells but few mucous cells.

One consequence of these differences is that the gastric environment of frugivores appears to be more acidic than that of insectivores. The presence of acidic saliva in frugivores may be a means of adding or maintaining acidity up front. One possible explanation for the increased acidity in the saliva of frugivores is that digestion of protein is maximized to offset the low content of protein in many fruits (Dinnerstein, 1986) and the swift passage times through the alimentary canal of many frugivorous bats (Thomas, 1984). The presence of high levels of pepsin in the esophagus and stomach of the pteropodid *Eidolon helvum,* in conjunction with high activity of maltase and invertase in the intestine (Ogunbiyi and Okon, 1976), lends support to this suggestion. Another hypothesis for the low pH of saliva and stomachs of frugivores is that it serves a protective function by neutralizing potentially harmful micro-organisms (Clarke, 1977). It is possible that ripe fruits carry a higher load of bacteria and fungi than do live insects. Destroying these organisms as they enter the digestive system may be advantageous.

Data presented here do not support the hypothesis that the saliva of stenodermatine bats is well buffered to protect the stomach from endogenous acids (Phillips et al., 1984; Studier et al., 1983). Nevertheless, there is correspondence between the pH and buffering capacity of salivary and gastric ultrastructure. This suggests that the origin of the coevolutionary relationship between enlarged salivary glands and derived anatomy of the stomach (Phillips et al., 1984) may lie in increasing salivary acidity, either to aid proteolysis or provide increased protection from biological contaminants associated with fruit.

Just as the low buffering capacity of the saliva of frugivores may promote acidity, the exceptionally high buffering capacity of the saliva of insectivores may function to preserve its alkalinity. It is not obvious why an insectivore would require relatively basic saliva, although some digestive enzymes (such as lipase) are active only at higher pH values (Vonk and Western, 1984). There do, however, appear to be ultrastructural correlates of the high buffering capacity of the saliva of insectivores. Models of salivary secretion agree that the ions necessary to produce bicarbonate (the primary salivary buffer) are actively transported through basal cell membranes, assembled within cells, and released through apical cell membranes into the lumen of the salivary ducts (Turner et al., 1993). The basal membranes of insectivorous bats exhibit much larger surface areas than those of frugivores, by virtue of extensive infoldings (Phillips et al., 1993; Tandler et al., 1990). Data presented here suggest that taxa with the greatest degree of infolding of the basal membrane have the highest buffering capacity.

The presence of intermediate pH and buffering capacity in *Carollia* accords well with descriptions of the ultrastructure of its stomach and salivary glands. Phillips et al. (1984) reported that the stomachs of *Car-*

ollia perspicillata are intermediate between animalivores-insectivores and frugivores in the number of mucous and parietal cells and the ultrastructural appearance of products of the chief cells, and Tandler et al. (1988:424) observed that *Carollia* exhibits secretory granules within the parotid salivary glands that are morphologically intermediate. Differences in salivary pH and buffering capacity among species of *Carollia* may also be associated with more subtle variation in diet, because species that consume fruits that are poor in protein have lower salivary pH and buffering capacity than species that consume fruits that are high in protein (Fleming, 1991; Figs. 1–2).

Although salivary pH and buffering capacity appear to covary with quality of diet in *Carollia,* this relationship may not hold for other species. For example, *Sturnira lilium* also primarily eats fruits that are high in protein (Willig et al., 1993), but its salivary pH and buffering capacity are similar to other stenodermatines. Similarly, although *Platyrrhinus helleri* is considered a frugivore (Fleming et al., 1972), its buffering capacity at feeding most closely resembles that of insectivores. Given the range of ultrastructural morphology in the salivary glands of frugivores (Phillips et al., 1987, 1993; Tandler et al., 1990), it is likely that several alternative approaches to dealing with the consequences of frugivory evolved. Understanding these strategies will require more detailed investigation into the integration of the chemical composition of saliva, digestive physiology, and dental microanatomy.

This study significantly extends the range of values of oral pH and buffering capacity for mammals. Mean oral pH for humans after fasting is typically near neutral, whereas average buffering capacity is ca. 4 on the scale used in this study (Meurman and Rantonen, 1994). Mean salivary pH for dogs and hamsters is 8–9 (Charlton et al., 1971; Grimberg et al., 1994). Salivary pH and buffering capacity in bats extends the range of known values at both ends (Figs. 1 and 2).

Finally, these data have implications for investigating rates of destruction of enamel. The combined presence of dietary acids and low salivary buffering capacity are associated with increased susceptibility to wear (Sorvari et al., 1995). On a finer scale, acidic diets may affect microscopic wear of enamel, and saliva may regulate this process (Lucas and Corlett, 1991). Data presented here demonstrate that salivary pH and buffering capacity may vary widely among closely related animals. Regardless of diet, saliva of some species appears less suited to protect against erosive chemicals than others, which suggests that comparative studies of microwear of enamel may benefit from considering the potential impact of salivary chemistry on rate of formation and morphology of this microscopic wear.

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APPENDIX I

The phyllostomids *Carollia brevicauda* (9♂♂, 7♀♀), *C. castanea* (10♂♂, 8♀♀), *C. perspicillata* (14♂♂, 6♀♀), *Artibeus jamaicensis* (8♂♂, 15♀♀), *Platyrrhinus helleri* (1♂, 3♀♀), *Sturnira lilium* (5♂♂, 3♀♀), *Uroderma bilobatum* (3♂♂, 1♀), and *Phyllostomus discolor* (8♂♂, 2♀♀) were surveyed at Bioforesta Ecological Center (Heredia Province), Curú National Wildlife Refuge (Puntarenas Province), and La Pacifica (Guanacaste Province) in Costa Rica. The pteropodids *Dobsonia minor* (2♂♂, 2♀♀), *Nyctimene abliventer* (4♂♂, 3♀♀), and *Paranyctimene raptor* (1♂, 2♀♀) were studied at the Kau Wildlife Area, Madang Province, Papua New Guinea. *Dobsonia moluccensis* (3♂♂, 3♀♀) was sampled from the Kau Wildlife Area, Yagaum Cave (Madang Province, Papua New Guinea), and the Christensen Research Institute Compound (Madang Province, Papua New Guinea), as well as in the captive colony at the Papua New Guinea National Museum (Port Moresby). The rhinolophid *Hipposideros maggietaylorae* (3♂♂, 1♀) was surveyed at Yagaum Cave. Voucher specimens of *D. minor, D. moluccensis, Nyctimene abliventer,* and *Hipposideros maggietaylorae* were deposited in collections of the Papua New Guinea National Museum. Captive pteropodids were surveyed at the Cape Tribulation Tropical Research Station, Queensland, Australia (*Pteropus conspicillatus* 3♂♂, 2♀♀), and the Lubee Foundation, Gainesville, Florida (*Pteropus hypomelanus* 9♂♂, 9♀♀). The pteropodid *Epomophorus labiatus* (4♂♂, 2♀♀) and two molossids (*Mops condylurus* 6♂♂, 1♀; *Chaerephon pumila* 4♂♂) were surveyed in Ethiopia (Lalibella, Wollo Province, and Coka Dairy Farm, Shoa Province, respectively). Voucher specimens collected in Ethiopia are in collections of the Carnegie Museum of Natural History (CMNH), Pittsburgh. The vespertilionids *Lasiurus borealis* (2♂♂, 1♀), *Myotis lucifugus* (2♂♂), and *M. septentrionalis* (2♂♂) were surveyed at the Powdermill Biological Station, CMNH, Westmoreland Co., Pennsylvania.