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Correspondence of Food Habits and Morphology in Insectivorous Bats

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force to function properly, but more importantly, dull blades would allow food material to jam between the blades and pry them apart. Thegosis (Every, 1970), or tooth on tooth abrasion, maintains the continuous sharpness required for the teeth to function properly.

The third condition, that of maintaining close apposition of the shearing edges, is probably the most critical element in occlusion, and its significance has gone unappreciated by most workers. Scapino (1965) did consider it in candids, and argued that muscular coordination was responsible for the occlusal appression observed. I have found that muscular movement initiates the appression, but the tight contact is maintained by a mechanical interlocking of fibrous food material between the upper and lower teeth.

If the space between the opposing cutting edges is too wide, shear is replaced by a simple turning moment that would force the teeth apart. Such rotation will always occur if the piece between the blades is not fixed transversely by another agent; one can appreciate this problem by attempting to cut a small piece of stiff cardboard with a pair of scissors having loosely bolted blades. In mammalian carnassials, the upper tooth lies labial to the lower, and a turning moment that would tend to force the teeth apart is expected, but does not occur. The facing portions of the teeth are convex toward one another (Fig. 1B, C, D) and when occlusion commences, the lingualmost edge of the upper tooth comes to lie medial to the labialmost edge of the lower tooth, the topological reverse of their actual positions. Fibrous food material is contacted by these extreme edges first and is forced into the lingual valley of M_1 and the labial valley of P^4 (Fig. 1D). The result is that a turning moment occurs in the opposite direction to that expected, holding the teeth firmly appressed to one another until the food material is sliced.

This mechanical interlocking of upper and lower teeth by food material is here named the "Every Effect", in honor of Dr. Ronald G. Every of Christchurch, New Zealand. Every alluded to this mechanism earlier (1972), but did not illustrate or develop it.

The Every effect is not limited to carnassials alone, but can operate on any portion of a mammalian dentition wherever opposing edges of a shearing system are convex toward one another. It operates in all tribosphenic dentitions, and may have been independently derived in a number of mammalian lineages.

Thanks go to my dentist, Dr. M. Rifkin, for providing the cotton rolls and for giving me some insight to human occlusal mechanics, and to Dr. S. Anderson of the American Museum of Natural History for loan of the hyaena skull.

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CORRESPONDENCE OF FOOD HABITS AND MORPHOLOGY IN INSECTIVOROUS BATS

In a morphometric study of molossid bats (Freeman, in press), I found that the first principal component (PC) reflected overall size. The second PC was concerned with a suite of jaw and skull measurements that separated molossids with thicker jaws, fewer but larger teeth, and well-developed cranial crests (i.e., bats with robust skulls) from those with thinner jaws, more but

smaller teeth, and less developed cranial crests. Subsequently, I found (Freeman, 1979) that molossids with robust skulls ate hard-shelled insects such as beetles, and that molossids with gracile skulls ate soft-bodied insects such as moths. Given these conclusions I was curious as to the generality of this observation in other species of microchiropterans. This paper reports my findings on the correspondence of morphology and food habits of 41 species of insectivorous bats.

I examined one adult specimen for each of 41 species and took 14 measurements for each specimen with Helios dial calipers under a Wild M8 dissecting microscope. All measurements were converted to ratios to eliminate the effects of size (Simpson et al., 1960:13–19; but see Atchley et al., 1976; and rebuttals by Hills, 1978; Dodson, 1978; and Albrecht, 1978). The upper occlusal surface was drawn under a camera lucida to facilitate measurement. Tooth areas were determined from an enlarged drawing with a Keuffer and Esser polar planimeter. The measurements used were: maxillary toothrow (MTR) over condylo-canine length, height of upper canine over MTR, anterior-posterior thickness of upper canines over MTR, maxillary width at the upper canines over greatest width at the upper third molars, length of M^3 over MTR (taken from drawing), length of the premetacrista of M^3 over MTR (taken from drawing), length of the postparacrista of M^3 over MTR (taken from drawing), length of the cusp row of P^4–M^3 over MTR (taken from drawing), area of P^4–M^3 over MTR^2 (taken from drawing), length of dentary condyle to protoconid of M_1 over dentary length (DL), width of M_3 talonid over width of M_3 trigonid, lateral dentary thickness at the protoconid of M_2 over DL, height of coronoid process over DL, height of dentary condyle above the lower toothrow over DL (horizontal crosshair in scope aligned with valleys at the bases of the hypoconid and protoconid of M_1 and M_3; height is taken from this line to top of condyle).

The species examined were: *Nycteris macrotis* (Nm), *N. thebiaca* (Nt), *N. woodi* (Nw) (Nycteridae); *Rhinolophus blasii* (Rb), *R. simulator* (Rsr), *R. swinnyi* (Rsi), *Cloeotis percivali* (Cp), *Hipposideros caffer* (Hcf), *H. commersoni* (Hcm) (Rhinolophidae); *Macrotus californicus* (Mac) (Phyllostomidae); *Mormoops megalophylla* (Mor) (Mormoopidae); *Antrozous pallidus* (Ap), *Eptesicus fuscus* (Ef), *Euderma maculatum* (Eud), *Idionycteris phyllotis* (Ip), *Lasionycteris noctivagans* (Las), *Lasiurus borealis* (Lb), *L. cinereus* (Lc), *L. ega* (Le), *Miniopterus schreibersi* (Min), *Myotis auriculus* (Ma), *M. californicus* (Mc), *M. evotis* (Me), *M. keenii* (Mk), *M. lucifugus* (Ml), *M. sodalis* (Ms), *M. thysanodes* (Mt), *M. velifer* (Mvr), *M. volans* (Mvs), *M. yumanensis* (My), *Nycticeius humeralis* (Nyc), *Pipistrellus hesperus* (Ph), *P. subflavus* (Ps), *Plecotus townsendi* (Plt) (Vespertilionidae); *Eumops perotis* (Emp), *E. underwoodi* (Emu), *Molossus ater* (Moa), *M. molossus* (Mom), *Nyctinomops femorosacca* (Npf; Freeman, in press), *N. macrotis* (Npm), *Tadarida brasiliensis* (Tb) (Molossidae). All specimens were males except *Antrozous pallidus* and *Nyctinomops femorosacca*.

I ranked the invertebrate prey of these bats (see Appendix) on a qualitative scale of hardness from 1 (softest) to 5 (hardest). The Ephemeroptera, Isoptera, Trichoptera, Plecoptera, Neuroptera, Mecoptera, and Diptera were assigned a one. The Araneida, Odonata, Homoptera, and Lepidoptera were given a two. The Orthoptera and Scorpionida were given a three, and the Hemiptera, Hymenoptera, Chilopoda, Diplopoda, and large Aeschnoidea were given a four. The Coleoptera were assigned a five. Although this qualitative scale was based primarily on Nearctic invertebrates, it should be representative of Old World arthropod prey as well.

I used the principal components analysis (PCA) from the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS), developed by F. J. Rohlf and associates, and a Model II regression (Sokal and Rohlf, 1969) for the data analysis.

The first axis of the PCA accounted for 33% of the total variation and separated the bats into two broad groups (Fig. 1). The following characters loaded highly on the first PC: relative height of upper canine (−0.858), relative length of premetacrista of M^3 (0.833), relative thickness of dentary (−0.704), relative area of P^4–M^3 (−0.695), and talonid/trigonid ratio of M_3 (0.695). Bats on the positive end of PC I (Fig. 1) have a longer premetacrista of M^3 (the posteriormost cusp) giving the tooth an N-shaped appearance. As this cusp shortens the M^3 becomes V-shaped, an appearance that is characteristic of the bats on the negative end of PC I. Bats on the negative end of PC I (Fig. 1) also have thicker dentaries and larger teeth (P^4–M^3). These three characters correspond with the trend found in the molossid data (Freeman, in press), suggesting that a similar trend in skull robustness exists for the 41 species of bats. In addition, bats on the positive end of PC I have relatively shorter canines and a M_3 talonid/trigonid ratio approaching 1.0, indicating that the talonid and trigonid are nearly equal in size. This equality is functionally

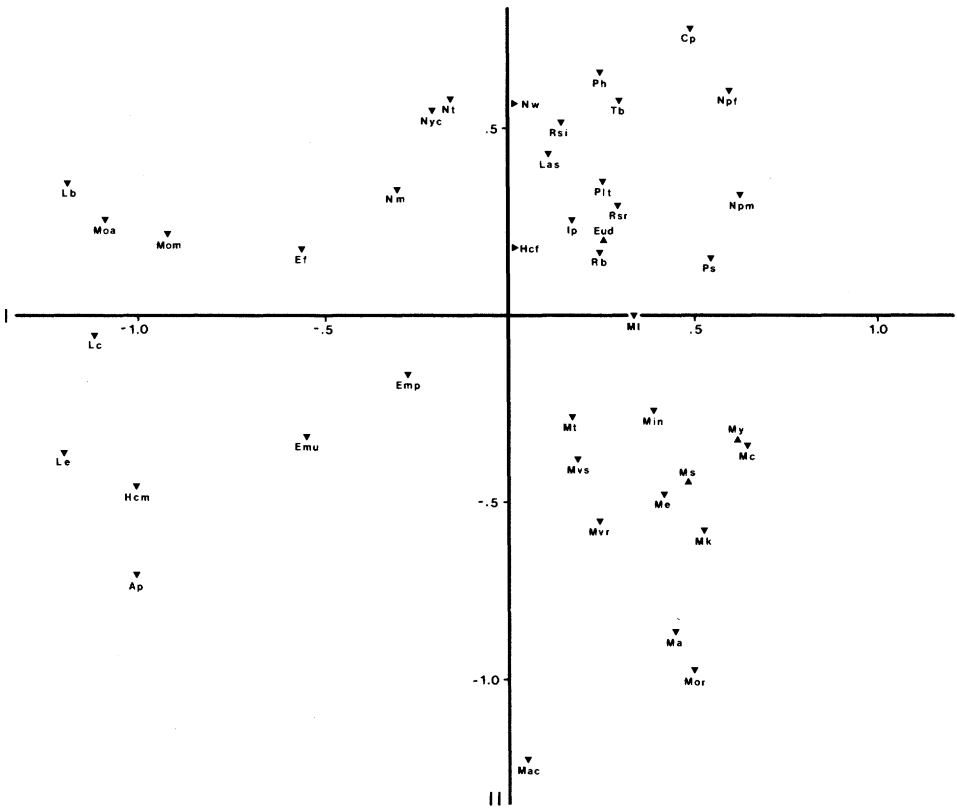

FIG. 1. A principal components analysis of 41 species of bats based on 14 ratio characters. The first axis arrays the bats such that species on the negative end have relatively thicker jaws, longer canines, larger molars, and abbreviated M^3s. Abbreviations of the species names and loadings of the important characters are in the text.

related to the lengthening premetacrista of M^3 with which the M_3 talonid occludes. These characters indicate that bats on the negative end of PC I have robust skulls and probably consume hard-shelled prey. Bats on the positive end of PC I have gracile skulls and likely eat softer-bodied prey.

To ascertain the relationship between skull morphology and food habits, I regressed the weighted average of the food habits of each bat (see Appendix) against the score of that bat on PC I (Fig. 2). The dashed regression line, which includes all species, is significant ($P < 0.01$, $r^2 = 0.375$) and shows that harder food items are taken by bats on the negative end of the first principal component. These bats have stout jaws, large molars, long canines, and abbreviated upper third molars.

Six of the nine species with the most robust skulls feed primarily on hard items. They are *H. commersoni*, *A. pallidus*, *E. fuscus*, *E. underwoodi*, *M. molossus*, and *M. ater*. The remaining three are species of *Lasiurus* that prey on moths or insects of intermediate hardness. Clearly, *Lasiurus* does not fit the trend shown by the other species. When the three species of *Lasiurus* were omitted from the regression analysis, the fit of the regression line to the points improved, but not significantly so (Fig. 2; $r^2 = 0.578$). There are accounts of *L. cinereus* eating or chasing pipistrelles in September (Bishop, 1947; Orr, 1950), and Ross (1967) reported lizards in the stomach of *L. ega*. Zinn (1977) captured a specimen of *L. cinereus* in the fall in Florida that had eaten large dragonflies, wasps, and beetles. *Lasiurus* are probably more catholic in their food habits than current evidence suggests, and their diet may vary seasonably.

Most of the other relationships found in this study seem logical. Those bats concentrated on

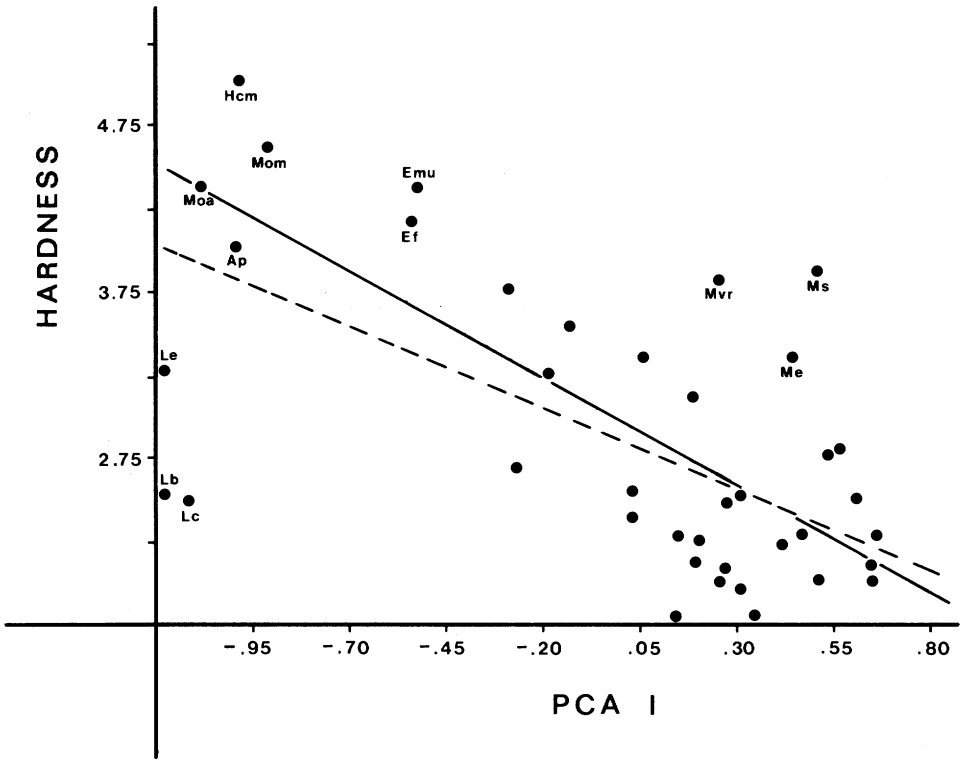

FIG. 2. Food hardness score of each bat regressed against the score of each bat on the first principal component. All 41 species are represented by the dashed regression line. Three species of *Lasiurus* are excluded in the solid regression line. The hardness score is listed by each species in the Appendix.

the positive side of PC I (Fig. 1) feed on moths or on insects of intermediate hardness. Several species (*N. thebiaca, N. woodi, N. macrotis, H. caffer, M. californicus, N. humeralis,* and *E. perotis*) that are intermedate in skull robustness are known to eat both moths and beetles.

Three species of *Myotis (M. evotis, M. velifer,* and *M. sodalis*) take harder prey than their congeners (Fig. 2). Black (1974) and Husar (1976) believed that *M. evotis* took beetles rather than moths when in sympatry with *M. auriculus*. Indeed, in a comparision of the jaw structure and musculature of *M. evotis* and *M. volans,* Reduker (1979) found that the former was better adapted to consume hard prey.

I believe that, in the absence of food habits data, reasonable estimates concerning prey selection can be made from the morphology of the teeth, jaws, and skulls of bats. Characteristics that are particularly important in distinguishing beetle eaters from moth eaters in this study are the relative height of the upper canine, relative length of the premetacrista of M^3, relative dentary thickness, relative area of P^4–M^3, and the ratio of the width of the talonid over the width of the trigonid of M_3.

Morphology reveals only part of the answer, however, as shown in the discrepancy between what *Lasiurus* are capable of eating and what they are known to eat. Estimates of food habits based on morphology represent prey selection capabilities in these bats; beetle eaters may have broader capabilities than do moth eaters. In addition, a bat exhibiting the characteristics of a beetle eater probably does not eat just beetles. Black (1974) used the term "strategist," in describing bat food habits because this word connotes a preference for a given prey item. What a species of bat eats probably varies depending upon the relative abundance of insects and the other species of bats with which it shares the habitat. Nonetheless, predicting food habits from morphology may be the only way to discern the potential prey of many bats, especially rare or fossil bats.

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APPENDIX

The food habits percentages are volumes unless marked "percent occurrence of prey," or "prey in X percent of the bats." Orders making up less than 10% are not listed unless they are unusual. Numbers in parentheses are weighted averages based on the hardness scale of invertebrate prey (see text); if no percentage is given, just the hardness scale was averaged; the percentage for class Insecta is not ranked.

Nycteris macrotis (3.25).—Orthoptera 51%, Coleoptera 29%, Isoptera 17%, n = 5, summer, Zambia (Whitaker and Black, 1976).

Nycteris thebiaca (3.52).—Coleoptera 45.2%, Orthoptera 31.6%, Lepidoptera 17.3%, n = 21, summer; Lepidoptera 38.2%, Coleoptera 25.7%, Orthoptera 14.1%, n = 12, winter, Zambia (Whitaker and Black, 1976).

Nycteris woodi (2.54).—Lepidoptera 63%, Coleoptera 20%, Isoptera 10%, n = 5, summer, Zambia (Whitaker and Black, 1976).

Rhinolophus blasii (2.00).—Lepidoptera 96.5%; n = 30, summer; Lepidoptera 100%, n = 4, winter, Zambia (Whitaker and Black, 1976).

Rhinolophus simulator (1.94).—Lepidoptera 72.9%, Coleoptera 13.3%, n = 34, summer; Lepidoptera 87.2%, Diptera 12.8%, n = 18, winter, Zambia (Whitaker and Black, 1976).

Rhinolophus swinnyi (2.27).—Lepidoptera 55.2%, Coleoptera 26.3%, n = 23, summer; Lepidoptera 55.6%, Diptera 44.1%, n = 9, winter, Zambia (Whitaker and Black, 1976).

Cloeotis percivali (2.00).—Lepidoptera 97.1%, n = 58, average for winter and summer, Zambia (Whitaker and Black, 1976).

Hipposideros caffer (2.37).—Lepidoptera 65.2%, Coleoptera 21.4%, n = 56, summer; Lepidoptera 92.7%, n = 34, winter, Zambia (Whitaker and Black, 1976).

Hipposideros commersoni (5.00).—Coleoptera (Scarabaeidae) 100%, n = 1, Zambia (Whitaker and Black, 1976). Large Coleoptera 100%, Kenya (Vaughan, 1977).

Macrotus californicus (3.33).—Large Orthoptera, Coleoptera, Lepidoptera, n = 41, Arizona and California (Ross, 1967).

Mormoops megalophylla (2.00).—Lepidoptera 100%, n = 2, Big Bend, Texas (Easterla and Whitaker, 1972).

Antrozous pallidus (4.01).—Large Orthoptera, Coleoptera; n = 22, Arizona (Ross, 1967). 17% occurrence of moth, 92% beetle, n = 12, New Mexico (Black, 1974). Coleoptera 68.2%, Orthoptera 26.4%, n = 11, Oregon (Whitaker et al., 1977). Insecta 38.9%, Lepidoptera 22.2%, Orthoptera 15.5%, Coleoptera 12.8%, n = 9, Big Bend, Texas (Easterla and Whitaker, 1972).

Eptesicus fuscus (4.14).—Coleoptera 49.6%, Hemiptera 16.8%, n = 184, Indiana (Whitaker, 1972). 61% occurrence of moth, 84% beetle, n = 165, New Mexico (Black, 1974). Coleoptera 34.7%, Lepidoptera 21.3%, Diptera 15.9%, n = 30, Oregon (Whitaker et al., 1977). Hymenoptera 42.5% (occurrence), Coleoptera 31.0%, n = 12, Arizona and Mexico (Ross, 1967). Coleoptera 36.1% (occurrence), Hymenoptera 26.3%, Diptera 13.2%, West Virginia (Hamilton, 1933).

Euderma maculatum (2.00).—Lepidoptera 97.1%, n = 15, Big Bend, Texas (Easterla and Whitaker, 1972). Lepidoptera 100%, n = 5, New Mexico (Ross, 1967). Lepidoptera 100%, 18 fecal pellets, New Mexico (Ross, 1961).

Idionycteris phyllotis (2.12).—Lepidoptera 84.1% (occurrence), Hymenoptera 11.4%, n = 25, New Mexico and Arizona (Ross, 1967). 100% occurrence of moth, 0% beetle, n = 3, New Mexico (Black, 1974).

Lasionycteris noctivigans (1.75).—100% occurrence of moth, 0% beetle, n = 19, New Mexico (Black, 1974). Lepidoptera 32.0%, Diptera 18.9%, Isoptera 14.0%, n = 15, Oregon (Whitaker et al., 1977).

Lasiurus borealis (2.52).—Coleoptera 28.1%, Lepidoptera 26.2%, Homoptera 18.5%, n = 128, Indiana (Whitaker, 1972). Homoptera 88.9% (occurrence), n = 27, Indiana and Illinois (Ross, 1967). Lepidoptera 60% (occurrence), Orthoptera 39%, California (Ross, 1961).

Lasiurus cinereus (2.47).—Lepidoptera in 97.8% of bats, Hymenoptera in 6.5%, Coleoptera in 6.5%, n = 139, New Mexico and Arizona (Ross, 1967). 100% occurrence of moth, 5% beetle, n = 39, New Mexico (Black, 1974). Lepidoptera 100%, n = 2, Lepidoptera 65%, Coleoptera 25%, n = 1, Indiana (Whitaker, 1972). Lepidoptera 50%, Diptera 50%, n = 2, Oregon (Whitaker et al., 1977). Large Aeschnoidea 60%, Hymenoptera 35%, Coleoptera 5%, n = 1, September, Florida (Zinn, 1977).

Lasiurus ega (3.27).—Eight bats all contained Hemiptera, Homoptera, Coleoptera, and Lepidoptera; Hymenoptera in one bat, New Mexico and Mexico (Ross, 1967).

Miniopterus schreibersi (2.22).—Isoptera 34.3%, Lepidoptera 33.8%, Coleoptera 25.0%, n = 21, summer; Lepidoptera 98.5%, n = 2, winter, Zambia (Whitaker and Black, 1967).

Myotis auriculus (2.28).—90% occurrence of moth, 20% beetle, n = 10, New Mexico (Black, 1974). Moth strategist both in sympatry, n = 10, and allopatry, n = 37, with *Myotis evotis* in New Mexico (Husar, 1976).

Myotis californicus (2.27).—Diptera 60.2%, Lepidoptera 14.4%, Arachnida-Araneida 7.3%, n = 31, Oregon (Whitaker et al., 1977). *M. californicus-leibii* 94% occurrence of moths, 69% beetle, n = 16, New Mexico (Black 1974).

Myotis evotis (3.33).—Lepidoptera 46.3%, Diptera 12.3%, Coleoptera 18.0%, n = 13, Oregon (Whitaker et al., 1977). 62% occurrence of moths, 92% beetle, n = 13, New Mexico (Black, 1974). Beetle strategist in sympatry with *M. auriculus*, n = 13, moth strategist in allopatry, n = 32, in New Mexico (Husar, 1976).

Myotis keenii (2.75).—One specimen in Indiana with 60% Hemiptera, 30% Hymenoptera, 10% Homoptera; a second with 70% Lepidoptera, 30% Diptera; and a third with 100% unidentified Insecta (Whitaker, 1972).

Myotis lucifugus (1.42).—Diptera 44.8%, Trichoptera 31.5%, Lepidoptera 11.0%, n = 108, Nova Scotia, Ontario, New York (Belwood and Fenton, 1976). Diptera 51.7%, Insecta 16.9%, Isoptera 8.9%, Trichoptera 8.4%, n = 67, Oregon (Whitaker et al., 1977). Diptera 50.1%, Lepidoptera 15.0%, Coleoptera 10.5%, Ephemeroptera 9.1%, n = 62, New Hampshire (Anthony and Kunz, 1977). Lepidoptera 21.6%, Homoptera 20.4%, Coleoptera 18.7%, Diptera 15.4%, Trichoptera 13.1%, n = 16, Indiana (Whitaker, 1972). Ephemeroptera 76.7%, Diptera 12.6%, n = 9, New York (Buchler, 1976).

Myotis sodalis (3.85).—Hymenoptera 50%, Coleoptera 23.8%, Homoptera 18.8%, n = 4, Indiana (Whitaker, 1972).

Myotis thysanodes (3.10).—36% occurrence of moth, 73% beetle, n = 11, New Mexico (Black, 1974). Lepidoptera 42.4%, Arachnida-Phalangida 26.2%, Orthoptera 16.3%, n = 4, Oregon (Whitaker et al., 1977).

Myotis velifer (3.63).—Coleoptera 37.4%, Homoptera 17.9%, Diptera 14.4%, Hemiptera 9.2%, n = 47, Kansas and Oklahoma (Kunz, 1974). Coleoptera 55.3% (occurrence), Microlepidoptera 37.2%, n = 22, Arizona and Sonora (Ross, 1967).

Myotis volans (2.23).—96% occurrence of moth, 17% beetle, n = 29, New Mexico (Black, 1974). Lepidoptera 78.2%, n = 25, Oregon (Whitaker et al., 1977).

Myotis yumanensis (2.07).—Diptera 42.9%, Isoptera 18.8%, Lepidoptera 14.8%, Insecta 10%, n = 25, Oregon (Whitaker et al., 1977). 53% occurrence of moth, 24% beetle, n = 16, New Mexico (Black, 1974). Lepidoptera 39.5%, Diptera 24.6%, Coleoptera 10.3%, n = 14, Big Bend, Texas (Easterla and Whitaker, 1972).

Nycticeius humeralis (3.24).—In one specimen from Indiana: Homoptera 35%, Coleoptera 35%, Hemiptera 20%, in another: Lepidoptera 50%, Coleoptera 30%, Hemiptera 20% (Whitaker, 1972). One specimen from Indiana contained Coleopteran remains, including June beetles, and some Dipterans (Ross, 1967).

Pipistrellus hesperus (2.46).—Homoptera 36.2% (occurrence), Microlepidoptera 21.8%, Coleoptera 16.7%, Hymenoptera 16.6%, n = 91, Arizona and Sonora (Ross, 1967: table 1). 100% occurrence of moth, 0% beetle, n = 7, New Mexico (Black, 1974).

Pipistrellus subflavus (2.77).—Homoptera 29.9%, Coleoptera 29.6%, Diptera 18.4%, n = 23, Indiana (Whitaker, 1972). One specimen from Indiana with 80% Homoptera, 20% Hymenoptera (Ross, 1967). One specimen from Florida contained Diptera and Hymenoptera (Sherman, 1939).

Plecotus townsendi (2.08).—Small Lepidoptera in 92.1% of bats, Coleoptera in 5%, n = 38, New Mexico and Arizona (Ross, 1967). Lepidoptera 99.7%, n = 16, Oregon (Whitaker et al., 1977).

Eumops perotis (2.67).—Lepidoptera 79.9%, Orthoptera 19.3%, n = 18, Big Bend, Texas (Easterla and Whitaker, 1972). Nine bats contained only abdomens of large sphingid moths, Arizona (Ross, 1967). Hymenoptera 58% (occurrence), Coleoptera 11%, Orthoptera 10%, Lepidoptera 10%, Hemiptera 10%, n = 4, Arizona (Ross, 1961).

Eumops underwoodi (4.36).—Coleoptera 47%, Orthoptera 31%, Homoptera 12%, Lepidoptera 10%, n = 6, Arizona; one bat from Mexico contained 4 large scarabs and 2 large cerambycids (Ross, 1967).

Molossus ater (4.37).—Mostly Coleoptera, few moth scales, n = 4, Mexico and Costa Rica (Freeman, in press). Hymenoptera 85.7%, small and large Coleoptera 11.5%, n = 1, Costa Rica (Pine, 1969). Coleoptera, Orthoptera, Hymenoptera, n = 1, Costa Rica (Howell and Burch, 1974).

Molossus molossus (4.60).—Coleoptera 90%, Diptera 10%, n = 10, Costa Rica (Howell and Burch, 1974).

Nyctinomops femorosacca (2.49).—Lepidoptera 36.9%, Hymenoptera 28.4%, Hemiptera 9.6%, n = 13, Big Bend, Texas (Easterla and Whitaker, 1972). One specimen in Arizona with 100% Macrolepidoptera and another with 85% Microlepidoptera, 15% Coleoptera (Ross, 1967).

Nyctinomops macrotis (2.00).—Lepidoptera 86.1%, n = 49. Big Bend, Texas (Easterla and

Whitaker, 1972). Lepidoptera 100%, n = 4, New Mexico (Freeman, in press). Macrolepidoptera 100%, n = 1, Arizona (Ross, 1967).

Tadarida brasiliensis (2.51).—Lepidoptera 34.0%, Hymenoptera 26.2%, Coleoptera 16.8%, Homoptera 15.0%, n = 88, New Mexico, Arizona, Mexico (Ross, 1967). Hymenoptera 32.5% (occurrence), Diptera 22.5%, Lepidoptera 20.0%, Coleoptera 12.5%, n = 8, Florida (Sherman, 1939). Lepidoptera 95%, n = 7, Arizona (Ross, 1961). Lepidoptera 100%, n = 5, New Mexico (Freeman, in press).

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EFFECT OF FASTING ON RATE OF FOOD PASSAGE AND ASSIMILATION EFFICIENCY IN BADGERS

Like other northern carnivores, badgers (*Taxidea taxus*) are subjected to periods of prey abundance and extended scarcity (Long, 1972; Jense, 1968; Lampe, 1976). In addition, badgers can spend many weeks beneath the ground without food during the winter (Harlow, in press). How badgers and other carnivores adjust to periods of changing food abundance is not fully understood.

Young (1944) and Whitney (1948) suggested that the stomach in wolves and dogs acted as a storage organ and allowed food to pass a little at a time into the intestine. For an opportunistic carnivore, this would convey the benefit of offering a continuous supply of nutrients during periods of food deprivation thereby causing less drastic shifts in blood glucose. Errington (1967) proposed a second strategy for carnivores—during periods of prey abundance, they must be able to consume rapidly, digest, and assimilate large quantities of food. However, mink (*Mustela vision*) seasonally ate considerably more food than was required for subsistence and their droppings contained much undigested food (Errington, 1967). In addition, Lampe (1976) found assimilation efficiency in badgers to be negatively correlated with biomass consumed. Gorging by a carnivore, therefore, may result in a lower assimilation efficiency and food wastage.

Assimilation of digested nutrients is affected by (1) passage rate of food through the gut, (2) blood circulation, (3) catabolic activity of gut enzymes, and (4) absorption of nutrients from the small intestine. Passage rates are influenced by temperature (Reed, 1966; Vakolyuk, 1966), hypoxia (Szurszenski and Steggersa, 1968), and altitude (Krabill and Hannon, 1972). However, effects of fasting on passage rate is poorly understood. Rates of food passage in some ectotherms slows after a fast (Windell and Sarokon, 1976). With reduced passage rates, ingesta is exposed longer to digestive and absorptive processes. Therefore, an addtional strategy to food storage in the stomach (Young, 1944) or gorging (Errington, 1967) may be for an animal to have a slower passage rate and higher digestive efficiency after a prolonged period without food, thereby maximizing the utilization of available nutrients.

I wished to (1) establish if badgers store food in the stomach, (2) determine if gorging occurs after food deprivation, and (3) test the hypothesis that badgers assimilate available food more efficiently after fasting.

Badgers were collected from Albany Co., Wyoming, in summer 1977 and were maintained on Purina dog chow consisting of 21% crude protein, 8% fat, and 4.5% fiber with an energy content of 5.16 kcal/g. Six adult female badgers that weighed an average of 8.0 kg were fed dog food 2 months before the study and habituated to 36- by 36- by 58-cm steel cages for 3 days. Each cage had a 2-cm^2 mesh-steel bottom that allowed passage of urine and feces. Water consumption was measured twice daily from samples collected by a funnel attached to a bottle containing mineral oil. A portion of each urine sample was frozen for caloric determination. Dry weight of food consumed in a 1-h feeding period was measured. Feces were collected twice daily, dried in an oven at 65°C, weighted to the nearest 0.001 g, and a portion pelletized for caloric determination. A 3-ml subsample of urine was added to a calorimeter crucible and dried on a preweighed amount of oxidized cellulose in a Vir Tis freeze dryer for 24 h. Because of the cellulose, freeze dried urine samples appeared as a light honey-comb pellet that permitted more efficient ignition. The caloric compositon of food, feces, and urinary pellets was determined in a Parr oxygen bomb-calorimeter. Urine caloric values were corrected for the amount of added cellulose. Assimilation efficiency