

Consumption rate, food preferences and transit time of captive giant otters *Pteronura brasiliensis*: Implications for the study of wild populations

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Abstract

Food consumption, food preferences and transit time of digesta were determined in captive giant otters, *Pteronura brasiliensis*, at the National Institute of Amazon Research (INPA), Manaus, Brazil. Food consumption of an adult female was $0.0997 \text{ kg day}^{-1}$. Giant otters showed significant and varied preferences for the single Siluriformes (catfish) and various Characiformes species offered. The adult female preferred Anostomidae and *Hypophthalmus* (catfish), followed by *Triportheus*. Myleinae (pacu) were the least preferred, and other species of Characiformes offered were intermediate between *Triportheus* and Myleinae but not different from one another. The subadult male preferred *Psectrogaster*, *Potamorhina* and *Semaprochilodus*, followed by *Hypophthalmus* and finally Hemiodontidae. Within species, larger fish are chosen significantly more often than smaller fish (78.7% of trials, $P=0.002$). Species, size and individual otter significantly affected the percentage of times fish offered were consumed completely ($P<0.016$). Overall, most fish were consumed completely beginning with the anterior end. Characoids were consumed completely more often than siluroids (77.8% vs. 38.6% of trials, $P<0.0001$), but the percentage of times different characoids were consumed completely varied (range 0–100%). Small fish (5–15 cm) are more likely to be consumed completely than medium (15–25 cm) fish (84.9% vs. 80.2% of trials, $P<0.02$). Transit time of particulate markers averaged 3.13 h. Captive preferences are compared to diets of wild otters in the region (central Amazônia), and implications of study

results for determination of food habits in wild otters using scat analysis are discussed.

Introduction

The giant otter, *Pteronura brasiliensis*, is endemic to South America, inhabiting remote areas of the Amazon, Orinoco and La Plata river basins from Venezuela south to southern Brazil (Carter & Rosas, 1997). Giant otters are classified as vulnerable by the World Conservation Union (IUCN), and are subject to increasing threats to the quantity and quality of their habitat from development, deforestation and exploitation of natural resources such as gold and oil in the Amazon and other regions of South America (Carter & Rosas, 1997).

Giant otters are primarily piscivores, fishing in the margins of rivers and lakes (reviewed in Carter & Rosas, 1997). Food habits studies of giant otters are most often based on identification and quantification of hard parts of prey species found in the feces (e.g. Laidler, 1984; Rosas *et al.*, in press). Occasionally direct observation is possible (e.g. Duplaix, 1980; Brecht-Munn & Munn, 1988), but this method is logistically difficult, costly and time consuming. Studies which utilize scats for diet determination are less intrusive and less costly. Uncertainty is introduced into results from such studies because hard parts found in scats depend on the consumption method of the prey, the rate at which parts pass through the animal's digestive system, the rate at which prey remains decay and other factors (Pierce & Boyle, 1991).

Few giant otters are maintained in captivity worldwide, and even fewer in regions within their

current natural range (Carter & Rosas, 1997). Thus opportunities to study dietary selectivity in this species are limited. Two giant otters are maintained in captivity at the National Institute of Amazon Research (INPA) in Manaus, Amazonas, Brazil. Studies conducted in such controlled situations may help identify potential sources of bias in determining diet from feces samples (Cottrell *et al.*, 1996) and determine factors influencing prey choice of wild giant otters (Hughes, 1980). We examined feeding rates, food preferences, method of prey consumption and transit time of captive giant otters. Results based on two individuals will necessarily be limited in scope and should be interpreted with caution, but our findings provide insight into potential factors influencing observed diets of giant otters in the wild.

Materials and methods

Consumption rate and food preferences

Food consumption, food preferences and consumption method of fish were determined for an adult female of seven years and a juvenile male of approximately one year at INPA. Locally caught fish were defrosted in running water, identified, weighed and measured before each feeding (morning and afternoon). Diet consisted primarily of the following fish of the order Characiformes (common Portuguese names are given in parentheses): *Semaprochilodus* spp. (jaraqui), *Anodus elongatus* and *Eigenmannina melanopogon* (cubiu and orana), *Triporthesus* spp. (sardinha), *Potamorhina* spp. (branquinha), *Prochilodus nigricans* (curimatã), *Schizodon fasciatus* and *Leporinus trifasciatus* (aracu), *Psectrogaster* spp. (cascuda), *Mylossoma* spp. (pacu), *Brycon melanopterus* (matrinchã) and *Serrasalmus* spp. (piranha). One Siluriformes (catfish), *Hypophthalmus* spp. (mapará), was also eaten. In cases where one common name describes more than one genus of fish, we use the family or subfamily designations of Santos *et al.* (1984, pacus and piranhas) and Ortega & Vari (1986, other species). One milliliter of a vitamin and mineral supplement (Poliplex[®], Bristol-Myers) was given once daily, injected into the mouth of the first fish. At the end of each day any fish parts remaining in the pool were collected and weighed. Food consumption was measured for 46 days between March and October 1993 for the adult, and 22 days between February and March 1994 for the subadult. Food consumption data were analyzed using a two tailed t-test assuming unequal variances. An F-test was used to compare variability in consumption between otters. Effect of date on food consumption was determined using nonlinear regression. The level of significance was $\alpha=0.05$ for all analyses.

Preferences of the adult female and subadult male for specific species and sizes of fish were also examined. 318 trials were conducted with the adult female between March and October 1993, and 65 trials were conducted with the subadult male in February and March 1994. Species and sizes of fish offered to the otters each day were dependent on availability at the Manaus fish market, but we attempted to offer a variety of species and sizes of fish at each feeding. Trials began at each meal after at least three fish had been consumed. Two (rarely three) fish of various species and sizes were offered to the otters by placing them on the edge of the otter's pool. The order of presentation and spatial position of fish were varied haphazardly. The species and size of each fish offered was recorded, as well as the fish chosen by the otter and the method of consumption of the fish. Fish of similar sizes were offered when comparing species preferences. Size preferences are only examined within species. Fish were classified as small (5–15 cm), medium (15–25 cm) or large (>25 cm). Method of consumption was determined for an additional 1084 and 263 fish for the female and male otter, respectively. Only observations on fish fed in the first two thirds of each meal are included. In 211 cases when fish were only partially consumed by the otters, the specific parts of the fish not consumed were recorded.

Data from food preference trials were analyzed using multinomial logit discrete choice models (Ben-Akiva & Lerman, 1985; Cooper & Millspaugh, in press). These models are similar to logistic regression except they allow for an individual to choose between more than two items and allow the set of options from which the individual chooses to vary. The output of the discrete choice model is a set of coefficients referred to as preference scores, one for each fish genus or group. Genera with higher preference scores are preferred to genera with lower preference scores, and an otter is predicted to be indifferent when choosing between genera with equal preference scores. The statistical significance of differences between preference scores is determined using a Chi-square distributed likelihood ratio test. Size preference and method of consumption data were analyzed using logistic regression.

Passage time

Trials were conducted with one female (age 7 years) and 2 male (ages approx. 1 year) giant otters at INPA in July and August 1995. Animals were housed in large pens with free access to fresh water in pools 3 × 3 × 0.8 m, except during trials when they were contained in smaller cement enclosures to facilitate collection of feces. Particulate markers consisting of known numbers of coloured plastic beads (4 mm in diameter × 3 mm in depth) were

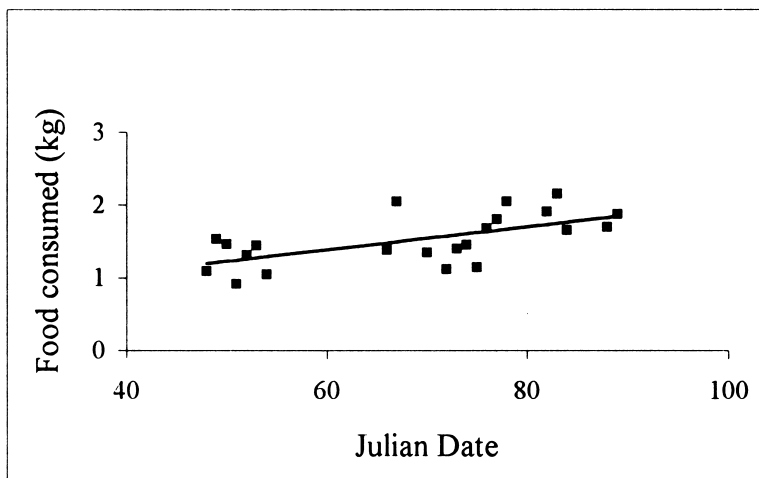


Figure 1. Daily food consumption of a subadult male giant otter at INPA. The linear equation is $y=0.4290+0.01587*\text{date}$. The slope of this line is significant ($P=0.002$).

inserted into the mouth or body cavity of the first fish fed at the morning or afternoon feeding of each animal. Feces passed after feeding with markers were collected until all possible markers were recovered and examined by washing over a fine sieve. The time of each defecation and the number of markers in each scat were recorded until the end of each trial. Transit time, the time elapsing before the defecation containing the first marker (Kotb & Luckey, 1972), was measured. Transit time data were analyzed using single factor ANOVA.

Results

Food consumption

Daily food consumption of the adult female averaged 2.29 kg (range 1.38–3.69 kg, $SD=0.55$, $n=46$). The otter weighed 23 kg at the beginning and end of the experiment, indicating a mean consumption rate of $0.0997 \text{ kg kg}^{-1} \text{ day}^{-1}$. Daily food consumption of the young male averaged 1.52 kg (range 0.91–2.15 kg, $SD=0.35$, $n=22$). The male weighed 11.5 kg at the beginning of the experiment. The male was not weighed at the end of the experiment, so consumption rate could not be calculated. The adult female consumed significantly more food per day than the subadult male ($P<0.001$). Daily consumption of the subadult increased with date (Figure 1, $P=0.002$, $r^2=0.38$) over the period studied. Daily consumption of the adult varied significantly more than that of the subadult ($P=0.016$), and is best described by a fourth order polynomial (Figure 2, $P<0.005$, $r^2=0.30$).

Food preferences

The two otters differed significantly in their preferences for different genera of fish offered (Table 1). The adult female preferred *Hypophthalmus* (catfish) and Anostomidae ($P<0.0001$), but was indifferent between these ($P>0.85$). *Triportheus* was the next most preferred genus ($P<0.0001$). Myleinae (pacus) were the least preferred ($P<0.0001$). Preferences for *Psectrogaster*, *Potamorhina*, *Prochilodus*, Hemiodontidae, *Semaprochilodus*, *Brycon* and Serrasalminae (piranhas) were intermediate between *Triportheus* and Myleinae ($P<0.001$) and not different from one another (all $P>0.15$). The subadult male, which was not exposed to all genera listed above, preferred *Psectrogaster*, *Potamorhina* and *Semaprochilodus* ($P<0.001$), but was indifferent between these (all $P>0.20$). *Hypophthalmus* was the next most preferred genus ($P<0.0001$), and Hemiodontidae were least preferred ($P<0.0001$). The adult female and subadult male valued *Psectrogaster*, *Potamorhina* and *Semaprochilodus* at the same level (the magnitude of the preference score), but the relative ranking differed. Genus did not affect size preference for the three genera tested (*Triportheus*, *Semaprochilodus* and *Prochilodus*, $P=0.74$). Within species, larger fish were chosen more often than smaller fish (78.8% of 33 trials, $P=0.002$).

The consumption method of fish varied with taxonomic group ($P<0.001$, Table 2), individual otter ($P<0.001$) and size ($P=0.015$). Overall, more fish were consumed completely than partially (75.7%, $P<0.001$, $n=1335$), and most fish were consumed beginning with the anterior end (73.7%,

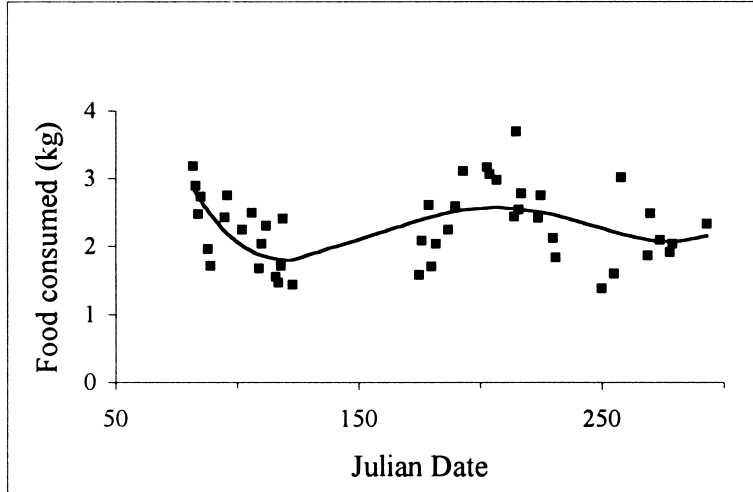


Figure 2. Daily food consumption of an adult female giant otter at the National Institute of Amazon Research (INPA), Manaus Brazil. The equation describing the curve is $y = 21.37754 - 0.4596 \cdot \text{date} + 0.003829 \cdot \text{date}^2 - 1.3302 \times 10^{-5} \cdot \text{date}^3 + 1.6451 \times 10^{-8} \cdot \text{date}^4$. All coefficients are significant ($P < 0.02$).

Table 1. Species preferences exhibited by captive giant otters at INPA. Otters 1 and 2 are an adult female and subadult male, respectively. Asterisks indicate value is significantly different from a 1:1 ratio

| Genus, subfamily or family | Common name | Order | Family | Percentage of trials preferred (n) | | Preference coefficient | |
|----------------------------|-------------|---------------|------------------|------------------------------------|---------------|------------------------|---------|
| | | | | Otter 1 | Otter 2 | Otter 1 | Otter 2 |
| Anostomidae | aracu | Characiformes | Anostomidae | 100% (17) | — | 14.79** | — |
| <i>Hypophthalmus</i> | mapará | Siluriformes | Hypophthalmidae | 100% (15) | 30.0% (10) | 14.79** | -0.44** |
| <i>Triportheus</i> | sardinha | Characiformes | Characidae | 86.8% (68) | — | 4.21** | — |
| <i>Psectrogaster</i> | cascuda | Characiformes | Curimatidae | 55.0% (20) | 83.3% (48) | 2.65* | 2.65* |
| Hemiodontidae | cubiu/orana | Characiformes | Hemiodontidae | 58.3% (36) | 5.0% (40) | 2.65* | -1.21** |
| <i>Potamorhina</i> | branquinha | Characiformes | Curimatidae | 50.0% (60) | 90.0% (10) | 2.65* | 2.65* |
| <i>Semaprochilodus</i> | jaraqui | Characiformes | Prochilodontidae | 26.8% (112) | 50.0% (20) | 2.65* | 2.65* |
| <i>Prochilodus</i> | curimatã | Characiformes | Prochilodontidae | 38.9% (18) | — | 2.65* | — |
| <i>Brycon</i> | matrinchã | Characiformes | Characidae | 25.0% (8) | — | 2.65* | — |
| Serrasalminae | piranha | Characiformes | Serrasalminidae | 25.0% (8) | — | 2.65* | — |
| Myleinae | pacu | Characiformes | Serrasalminidae | 3.3% (30) | — | 0.00** | — |

** $P < 0.0001$, * $P < 0.001$.

Table 2. Consumption method of various species of fish by captive giant otters at INPA. Otters 1 and 2 are an adult female and subadult male, respectively. Only results with $n \geq 3$ are included

| Genus, subfamily or family | Order | Percentage of trials in which fish was completely consumed (n) | | Percentage of partially consumed fish in which entire head was consumed (n) | |
|----------------------------|---------------|--|------------|---|---------|
| | | Otter 1 | Otter 2 | Otter 1 | Otter 2 |
| Anostomidae | Characiformes | 70.4% (27) | — | 16.7% (6) | — |
| <i>Hypophthalmus</i> | Siluriformes | 39.4% (66) | 25.0% (4) | 2.9% (34) | — |
| <i>Triporthus</i> | Characiformes | 77.1% (96) | — | 37.5% (8) | — |
| <i>Psectrogaster</i> | Characiformes | 75.0% (16) | 100% (70) | — | — |
| Hemiodontidae | Characiformes | 64.3% (196) | 79.3% (58) | 30.2% (39) | 0% (11) |
| <i>Potamorhina</i> | Characiformes | 43.6% (78) | 95.6% (45) | 40.0% (25) | — |
| <i>Semaprochilodus</i> | Characiformes | 83.4% (512) | 98.1% (53) | 76.6% (64) | — |
| <i>Prochilodus</i> | Characiformes | 76.3% (59) | 96.8% (31) | 70.0% (10) | — |
| <i>Brycon</i> | Characiformes | 25.0% (4) | — | — | — |
| Serrasalminae | Characiformes | 0% (4) | — | 0% (4) | — |
| Myleinae | Characiformes | 26.7% (15) | — | 0% (3) | — |

Table 3. Transit times for three captive giant otters at INPA. The adult female was housed alone on 25-07-95. Otters were housed in pairs in all other trials. NA indicates information not available

| Date | Animal | Ingestion time | Expulsion time | Markers ingested | Markers recovered | Transit time (hour) |
|----------|--------------|----------------|----------------|------------------|-------------------|---------------------|
| 01-08-95 | subadult M 1 | 13:56 | 16:47 | 8 | NA | 2.85 |
| 03-08-95 | subadult M 1 | 14:00 | 17:10 | 7 | 2 | 3.17 |
| 25-07-95 | adult F | 9:02 | 12:57 | 5 | 2 | 3.92 |
| 25-07-95 | adult F | 14:43 | ? | 7 | 0 | — |
| 25-07-95 | adult F | 14:48 | ? | 8 | 0 | — |
| 03-08-95 | adult F | 13:50 | 17:05 | 5 | 1 | 3.25 |
| 01-08-95 | subadult M 2 | 13:50 | 16:11 | 1 | 1 | 2.33 |
| 01-08-95 | subadult M 2 | 14:02 | 17:16 | 7 | 7 | 3.23 |

$P < 0.001$, $n = 1335$). Characoids were completely consumed more often than siluroids (77.8% of 1265 vs. 38.6% of 70 trials, $P < 0.0001$), but the percentage of times different characoid species were completely consumed varied widely (range 0–100%). Small (5–15 cm) fish were completely consumed more often than medium (15–25 cm) fish (84.9% of 425 vs. 80.2% of 329 trials, $P < 0.02$). Large fish (>25 cm) appear to be completely consumed less often than small and medium fish (60.5% of 5 trials), but this was not tested statistically due to the small sample size. The adult female completely consumed fish less often than the subadult male (77.8% of 504 vs. 92.5% of 255 fish, $P < 0.001$). The head (or parts of it) was the body part discarded by the otters in 97.1% of siluroids ($n = 34$) and 47.5% of characoids ($n = 177$) that were only partially consumed.

Transit time

Transit time did not differ between the three otters (Table 3, $P = 0.35$). The pooled mean transit time is 3.13 h (SD = 0.52 h).

Discussion

Food consumption

Estimates of food intake may help determine impacts of otter predation on prey species. Otters may consume significant portions of prey populations in local areas (e.g. Estes & VanBlaricom, 1985; Kruuk & Moorhouse, 1990), and this is of particular interest if the prey species are commercially valuable. Estimates of food consumption are also important to assess the significance of individual variation in foraging strategy, to determine the potential for ingestion of contaminants,

Table 4. Daily consumption rates of various aquatic and semi-aquatic mammals. Estimates are from captive animals except where noted. NS indicates age not specified in source

| Species | Average daily consumption (kg kg ⁻¹ day ⁻¹) | Age class | Source |
|--|--|---|--|
| Least weasel <i>Mustela nivalis</i> | 0.3–0.4 | 0.5–2 years | Moors, 1977 |
| Sea otter <i>Enhydra lutris</i> | 0.25–0.35 0.38 | NS captive wild adults and juveniles | Kirkpatrick <i>et al.</i> , 1955 VanBlaricom pers. comm. 1999 |
| Eurasian otter <i>Lutra lutra</i> | 0.15 0.12, 0.13 | 0.2–1.4 years adult | Stephens, 1957 Nolet & Kruuk, 1994 |
| Giant otter <i>Pteronura brasiliensis</i> | 0.28 0.10 0.07–0.10 | lactating, wild adult adult | This study Best, 1985 Zeller, 1960 |
| Grey seal <i>Halichoerus grypus</i> | 0.08 0.25 0.02–0.03 | NS subadult adult | Schweizer, 1992 Kastelein <i>et al.</i> , 1990b |
| Harbour seal <i>Phoca vitulina</i> | 0.05–0.08 | 3–12+ years | Cottrell <i>et al.</i> , 1996 |
| Northern fur seal <i>Callorhinus ursinus</i> | 0.07 0.07 | adult subadult | Spotte & Adams, 1981 Costa, 1987 |
| Steller sea lion <i>Eumetopias jubatus</i> | 0.04–0.05 | adult | Kastelein <i>et al.</i> , 1990a |
| California sea lion <i>Zalophus californianus</i> | 0.10 | subadult | Costa, 1987 |
| Walrus <i>Odobenus rosmarus</i> | 0.01 0.02 | adult immature | Fisher <i>et al.</i> , 1992 |
| Beluga <i>Delphinapterus leucas</i> | 0.01 | 9+ years | Kastelein <i>et al.</i> , 1994 |

for bioenergetics studies and for other facilities housing giant otters.

The average daily consumption of 0.10 kg kg⁻¹ day⁻¹ of the adult female is consistent with most observations of food consumption by captive giant otters, and less than Schweizer (1992) observed in a subadult (Table 4). Consumption rates of giant otters are similar to other otters, less than some other mustelids and much greater than other carnivorous aquatic mammals. Our results are consistent with the findings that metabolic rates of otters and other mustelids are higher than those of other terrestrial mammals (Iversen, 1972; Moors, 1977; Casey & Casey, 1979; Costa & Kooyman, 1982), and likely higher than those of pinnipeds and cetaceans (Lavigne *et al.*, 1986). Consumption rates of wild otters may be higher than captive otters, as wild otters must expend more energy obtaining their food (Nolet & Kruuk, 1994). Wild giant otters are estimated to consume 2.8–4.0 kg kg⁻¹ day⁻¹ (Duplaix, 1980; Schweizer, 1992), slightly higher than the amount consumed by our captive adult.

Food intake may vary with individual, age, size, sex, season, diet, activity, social group changes and changes in feeding techniques (Moors, 1977; Spotte

& Adams, 1981; Kastelein *et al.*, 1990a, 1990b, 1993b, 1994; Riedman & Estes, 1991). Seasonal variation is most often correlated with mating and reproductive activity and changing water temperatures (Spotte & Adams, 1981; Kastelein *et al.*, 1990a, 1990b, 1993b, 1994). Seasonal changes in temperature in the Amazon are minimal. Food consumption of the subadult male increased with time over the two month period of observation. This period was soon after the animal was acquired and likely a response to acclimation to the new surroundings (Kastelein *et al.*, 1993b). Food intake of the adult otter varied significantly more than that of the subadult. This may be an indirect result of the longer time she was observed, as the female showed significant species preferences (Table 1), and the species and quality of fish fed to the otters varied throughout the year. Large seasonal fluctuations in protein and fat content of some Amazonian fish also occur (Junk, 1985), which may affect food consumption (Greaves & Scott, 1960).

Food preferences

The two captive giant otters showed significant and varied preferences for genera of fish. The

adult female demonstrated strong preferences for Anostomidae and *Hypophthalmus*, whereas the subadult male ranked *Hypophthalmus* near the bottom of its preference scale. Several characoids did not differ significantly from one another in their preference level for either otter and seemed to be selected or not almost an equal proportion of the time. Serrasalminae were consistently rejected or only partially consumed and then discarded by the adult female. The discrete choice model was only able to statistically validate the otter's lack of preference for Myleinae, possibly due to small sample sizes for Serrasalminae. We are aware of only one other study reporting food preferences of giant otters in captivity, which indicates only a general preference for 'brightly shining fish' followed by 'less shining fish' and non-fish products (Zeller, 1960).

Nutritional content of prey may affect species preferences of captive otters. **Optimal foraging theory predicts that otters should choose prey items based solely on maximization of energy content per unit of energy expended.** Foraging behaviour of wild sea otters followed this pattern (Ostfeld, 1982). In captivity, otters are generally fed dead prey items, and therefore expend little or no energy in prey capture. It follows that captive otters might prefer high energy prey species over low energy species. Fat content can vary dramatically (and protein to a lesser extent) between species, and also between seasons within species for the fish offered in this study (Junk, 1985). Nutritional content of prey was not determined in our study. Published values (Junk, 1985) of fat and protein content of species offered in this study were not obviously related to species preferences. For example, two of the most fatty species, *Hypophthalmus* and Myleinae, had very different preference coefficients. This suggests that other factors are likely affecting species preference. Individual otters in the wild may differ in their preferences for particular prey species (Kirkpatrick *et al.*, 1955; Riedman & Estes, 1988, 1991), and Ridgway (1972) found that captive odontocetes exhibited strong individual preferences for prey species. In our study, the subadult male otter appeared to prefer smaller and possibly more familiar species. Prey consumed by juvenile sea otters and black-footed ferrets influence their preferences later in life (Riedman & Estes, 1991; Vargas & Anderson, 1996).

Captive preferences generally agree with diets of wild giant otters. Characiformes are widely consumed by wild otters, along with Perciformes and Siluriformes (Carter & Rosas, 1997). Captive otters readily consumed a variety of characoids and the only siluroid offered. At a species level, however, fish preferred by captive otters are not always consumed in the same proportions by wild otters in the same region (central Amazônia). For example,

Anostomidae were preferred in 100% of captive trials, and *Schizodon* sp. was the most common prey of giant otters in the Curuá-Una hydroelectric reservoir (Best, 1984). However, Anostomidae were only present in 16.2% of scats from a tributary of the upper Jauaperi river (Rosas *et al.*, in press). Similarly, siluroids were highly preferred in captivity, but present in only 5.4% of scats (Rosas *et al.*, in press). Serrasalminae were generally not preferred in captivity (25.0% of trials), but were relatively common in scats (18.9%, Rosas *et al.*, in press). Serrasalminae were also commonly consumed (25% of scats) by otters in the Balbina hydroelectric reservoir (Benetton *et al.*, 1990). Captive preferences and wild consumption of Myleinae were similar (3.3% of captive trials, 5.4% of scats, Rosas *et al.*, in press).

Prey abundance may explain some differences in captive preferences and observed diets of wild giant otters. River otters (*L. lutra* and *L. canadensis*) are opportunistic feeders, preying on species which are most available through abundance or behavioural characteristics which render easier detection or capture by otters (Toweill, 1974; Kruuk & Moorhouse, 1990; Reid *et al.*, 1994). Giant otters also appear to feed opportunistically (Duplaix, 1980; Laidler, 1984; Schweizer, 1992). In our study, Serrasalminae (especially Myleinae) was the least preferred of all families tested. When otters accepted serrasalminids, often only small chunks of flesh of the back were consumed before the fish was discarded. The relatively common occurrence of serrasalminids in diets of wild otters (Benetton *et al.*, 1990; Rosas *et al.*, in press) suggests that although serrasalminids are not particularly preferred, they may be abundant or easy to catch in some habitats. Serrasalminid abundance was not measured in either study area, but construction of hydroelectric dams on Amazonian rivers results in at least a short term increase in predatory fish in the reservoir, particularly *Serrasalmus* sp. (Leite & Bittencourt, 1991). Increased abundance of predatory fish in hydroelectric reservoirs may also explain differences in consumption of Anostomidae (Best, 1984; Rosas *et al.*, in press).

Physical characteristics of prey may be important in understanding differences between captive preferences and observed diets of wild otters. *Hypophthalmus* was highly preferred by the captive adult otter. Siluroids, however, were much less common in diets of wild otters than characoids (5.4% vs. 86.5% of scats, Rosas *et al.*, in press). Siluroids may be rare in the Jauaperi river, or they may be difficult to catch because of their pelagic diurnal habits. Biases in scat analysis may also explain the apparent discrepancy. Species consumed by giant otters are generally identified by hard parts such as mandibles, teeth, scales, fin

spines and (less often) vertebrae (e.g. Rosas *et al.*, in press). If consumption method varies with species, parts of some species may never be ingested, decreasing the likelihood that the species will be detected in scats. Captive giant otters consumed heads of siluroids less often than heads of characoids (40.4% vs. 88.3% of trials). The difference appeared to be a result of the large and bony heads of the siluroid. This behaviour has been observed in wild river otters (Melquist & Hornocker, 1983) and could lead to biases against siluroids and other morphologically similar species in diet studies of wild otters.

Captive otters preferred larger over smaller fish within species in the range of sizes tested (5–25 cm). This size range is well within the upper size limit of fish consumed by wild giant otters (40–60 cm, Duplaix, 1980). *L. lutra* in captivity preferred to hunt larger versus smaller fish, but Erlinge (1968) concluded that size had less influence than prey mobility. Size preference did not reflect availability in our study, as all prey were dead. Wild *L. lutra* in Shetland selected the larger individuals in populations of at least some species (Kruuk & Moorhouse, 1990), but other studies found no size selection of prey by *L. lutra* (Wise *et al.*, 1981; Heggberget & Moseid, 1994).

Captive otters generally consumed fish completely beginning with the head. In contrast, *L. lutra* showed no consistent pattern in consuming dead fish, although they almost always ate live fish head first (Erlinge, 1968). Consumption of fish head first may reduce injuries from fish spines (Harrison & King, 1980) and reduce the likelihood that live prey will escape. Captive giant otters also completely consumed larger fish less often than smaller fish, likely resulting in hard parts of larger fish being consumed less often than those of smaller fish. Erlinge (1968) found similar results with captive river otters, and Hewson (1973) and Larsen (1984) observed this behaviour in wild river otters. Wild giant otters generally consume fish completely beginning with the head (Duplaix, 1980; Laidler, 1984; Brecht-Munn & Munn, 1988), but the head and spines of large catfish were not consumed in at least one study (Laidler, 1984). Such behaviour may lead to under representation of larger species in diets of wild giant otters if otoliths or other bones of the head are used for prey identification. Size distributions of prey species based on otolith sizes will also be biased toward smaller individuals if otoliths of larger individuals are not consumed.

Transit time

Transit time, the time it takes for a marker or prey item to first appear in the feces (Kotb & Luckey, 1972), is easily determined and widely used in studies of aquatic mammals. Transit time by

definition does not incorporate the time for all parts of a meal to clear the digestive system, but it is considered a good indication of the overall rate of passage of digesta (Helm, 1984). Passage rate is an important indication of the health of an animal and a primary factor determining the efficiency of utilization of food (Kotb & Luckey, 1972; Helm, 1984). Passage times in conjunction with calculated swimming speeds can also provide estimates of the spatial applicability of feces samples (Pierce & Boyle, 1991).

The transit time for giant otters in this study was slightly longer than found in previous studies, similar to other mustelids, and in most cases significantly shorter than found for other piscivorous aquatic mammals (Table 5). Shorter transit times of giant otters (and other river otters) in comparison with pinnipeds may be due to high metabolic rates or shorter digestive tracts (Helm, 1984). The digestive tract of the giant otter remains unstudied, but is probably similar in proportion to the mink (4 times body length, Szymeczko & Skrede, 1990). Digestive tracts of pinnipeds are generally much longer (e.g. 16, 19 and 26 times body length in harbour seals, California sea lions and Northern elephant seals, respectively, Helm, 1983).

Sex, age, activity level, food intake, time of day, and prey species and nutritional content may also affect transit time (Fish, 1923; Seerley *et al.*, 1962; Marlett *et al.*, 1981; Helm, 1984; Dellinger & Trillmich, 1988; Harvey, 1989; Bowland & Bowland, 1991; Kastelein *et al.*, 1993a; Markussen, 1993; Krockenberger & Bryden, 1994; Lanyon & Marsh, 1995; Jurisch & Geidezis, 1997; Carss *et al.*, 1998). The longest transit time observed in this study was during a morning trial on an animal housed alone. Giant otters housed in pairs may be more active than those housed alone. Transit times of active river otters are much faster than inactive otters (Carss *et al.*, 1998), and defecation by one otter may instigate defecation by other members of a social group (Melquist & Hornocker, 1983). Different species of fish were also used in transit time trials (*Psectrogaster* and *Potamorhina*). Protein, fat and water content may have differed between species (Junk, 1985), and fats are known to delay digestion (Forbes & Swift, 1944).

Marker type may have affected observed transit times. Liquid, digestible solids and indigestible solids move through the digestive system at different rates (see discussion in Jobling & Breiby, 1986), reflected in the faster transit times generally found when using liquid phase (e.g. dyes) versus solid phase markers (e.g. bones or indigestible particulates, Fish, 1923; Helm, 1984; Mårtensson *et al.*, 1998). We cannot assess effects of marker type on transit time in giant otters because of the lack of data using other markers. Because of the potential

Table 5. Transit times of various aquatic and semi-aquatic mammals. Transit times are in hours unless otherwise indicated

| Species | Average transit time (range) | Marker | Source |
|---|--------------------------------|-----------------------------------|---|
| Least weasel <i>Mustela nivalis</i> | 3.4 | dye | Short, 1961 |
| Mink <i>Mustela vison</i> | 2.4 3.5 | dye prey item | Sibbald <i>et al.</i> , 1962 Szymeczko & Skrede, 1990 |
| Sea otter <i>Enhydra lutris</i> | 3 | molluscs | Kirkpatrick <i>et al.</i> , 1955 |
| Eurasian otter <i>Lutra lutra</i> | 3.2 1.1–2.8 | plastic granules prey item | Jurisch & Geidezis, 1997 Carss <i>et al.</i> , 1998 |
| Giant otter <i>Pteronura brasiliensis</i> | 3.1 2 | plastic beads plastic beads | This study Best, 1985 |
| Harbour seal <i>Phoca vitulina</i> | 3.8 5.0 12.5 2–3 days | dye dye otolith charcoal | Markussen, 1993 Helm, 1984 Harvey, 1989 Helm, 1984 |
| South American fur seal <i>Arctocephalus australis</i> | 4 20 | otolith glass beads | Dellinger & Trillmich, 1988 |
| Northern fur seal <i>Callorhinus ursinus</i> | (6–22) (7–22) | otolith cephalopod beak | Bigg & Fawcett, 1985 |
| California sea lion <i>Zalophus californianus</i> | 4.2 18 21 | dye otolith glass beads | Helm, 1984 Dellinger & Trillmich, 1988 |
| Northern elephant seal <i>Mirounga angustirostris</i> | 4.8 2–3 days | dye charcoal | Helm, 1984 |
| Southern elephant seal <i>Mirounga leonina</i> | 9.1 | dye | Krockenberger & Bryden, 1994 |
| Beluga <i>Delphinapterus leucas</i> | 4.5 | dye | Kastelein <i>et al.</i> , 1994 |
| Commerson's dolphin <i>Cephalorhynchus commersonii</i> | 2.4 | dye | Kastelein <i>et al.</i> , 1993a |

for bias due to marker type, we reported transit time rather than a measure quantifying movement of all markers through the digestive system. Our results are similar to those for other mustelids, suggesting that particulate markers provide a valid indicator of solid phase transit time in giant otters.

Markers from the same prey item were present in more than one scat deposited within a day on at least two occasions. Markers not recovered during the experiment may not have been ingested or may indicate longer retention times. Passage times of river otters vary with prey species, and parts of some species may be present in up to 60 scats (Carss & Parkinson, 1996). Passage rates of other carnivores also vary with prey species (Harvey, 1989; Bowland & Bowland, 1991). The potential for longer passage times indicates that the number of prey items consumed by wild otters may be overestimated if each occurrence of a species in a different scat is assumed to be a separate prey item. If passage rate differs with prey species, frequency of occurrence in scats may overestimate consumption of some species by wild giant otters.

In summary, captive giant otters exhibited significant preferences for different genera and sizes of fish, and preferences varied with individual otter. Differences between captive preferences and observed diets of wild giant otters suggest that prey availability may be more important than preference in determining diet composition of wild otters. Method of consumption of fish by captive otters varied with the species and size of fish. This should be considered when determining diet composition from scats, as hard parts, particularly otoliths, of some species and sizes of prey may not be consumed. Transit time is relatively short in giant otters, but some hard parts may be retained in the digestive system for longer periods of time, introducing potential bias to studies using frequency of occurrence to describe feeding habits of giant otters in the wild.

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