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HOW OFTEN DO FISHES ‘‘RUN ON EMPTY’’?

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Abstract. We used a large data set of African, Neotropical, and North American fishes to examine the frequency with which fishes have empty stomachs ($n_{\text{species}} = 254$; $n_{\text{individuals}} = 36\,875$). Mean percentage of empty stomachs was low across all fishes (16.2 ± 1.2%) but varied from 0% to 79.4% among individual species. Nocturnal fishes had empty stomachs more frequently than diurnal fishes. Trophic classification was strongly associated with the percentage of empty stomachs, a pattern also revealed from an intraspecific analysis. Fishes appear to adjust their feeding intervals relative to the energy density, conversion efficiency, and particle size of their food. Piscivorous fishes seem to be the only trophic group that regularly experience long periods of empty stomachs, with species that consume prey whole and those that provide extended parental care having the highest proportions of empty stomachs. Activity patterns and life histories of some piscivorous species probably have evolved in partial response to energetic benefits of large, energy-rich food resources.

Key words: diet; diurnal vs. nocturnal; energy balance; feeding success of fishes; life history evolution; parental care; trophic classification.

INTRODUCTION

Acquisition of energy is a challenge common to all organisms. Energy acquisition directly affects fitness, is optimized by natural selection (Schoener 1971, Perry and Pianka 1997, Robinson and Wilson 1998), and affects the evolution of life histories (Reznick and Braun 1987, Winemiller 1989, Bonnet et al. 1998). Organisms that efficiently acquire and assimilate resources achieve higher fitness. Resource availability varies across time and space, and species have evolved to exploit variance in food availability to maintain positive energy balance, a requisite for growth and reproduction. For example, organisms may migrate long distances to areas with greater food availability (Gross et al. 1988, Winemiller and Jepsen 1998, Le Boeuf et al. 2000), may store surplus energy for leaner times (Bonnet et al. 1998, Jobling et al. 1998), or may reduce metabolic costs by allowing organs and muscles to atrophy when they are not needed (Piersma and Lindström 1997, Piersma 1998, Secor and Diamond 2000).

Huey et al. (2001) recently asked, ‘‘How often do lizards run on empty?’’ Their study evaluated whether lizards alternate between feast and famine, or continuously maintain positive energy balance. They used the observed proportion of empty stomachs for species as an index of instantaneous energy balance. Individuals with empty stomachs were assumed to be in negative energy balance, relying on reserve energy stores from previous feeding bouts as a substrate for metabolism (Boivin and Power 1990). An individual with food in its stomach is assumed to be gaining energy and therefore in a state of positive energy balance at that moment (Huey et al. 2001). However, it should be pointed out that, in some cases, individuals with measurable stomach contents could be in a state of negative energy balance if the energy content of food does not exceed the individual’s energetic demand at that moment. Detritivores and herbivores have the greatest potential to be influenced by this source of error.

Huey et al. (2001) encouraged compilation of data from other taxa to examine general patterns of energy balance. Here we examine data from teleost fishes, a taxonomically and ecologically diverse group of poikilotherms. We evaluated the proportion of empty stomachs (Huey et al.’s definition of negative energy balance) among fishes from four geographic locations and compared our results to Huey et al.’s (2001) findings for lizards. They found a large sample of lizards ($n_{\text{species}} = 127$; $n_{\text{individuals}} = 18\,223$), on average, to have food in their stomachs. Nocturnal lizards and top-predator species had empty stomachs significantly more often than diurnal lizards and lizards feeding at lower trophic levels. Because fishes show large variations in life history characteristics (Winemiller 1989, Winemiller and Rose 1992) and a diverse array of trophic specializations (Winemiller 1991), they provide an excellent model system to test the generality of Huey et al.’s findings for poikilotherms.

METHODS

Data collection

We report data for percentages of empty stomachs based on 36 875 individual fish from 254 species col-

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lected from Africa (Zambezi River; Winemiller 1996), Central America (Río Tortuguero Basin; Winemiller 1990), South America (Río Orinoco Basin, Winemiller 1990, Peterson 1997; C. A. Layman and D. A. Arrington, *unpublished data*), and North America (Matagorda Bay, Texas, Akin 2001; Kissimmee River, Florida, F. Jordan and D. A. Arrington, *unpublished data*; and Everglades, Florida, Loftus 2000). Like Huey et al. (2001), we did not explicitly evaluate temporal effects. Yet by sampling a large number of individuals, and analyzing the means for a large number of taxa we were able to state the statistical likelihood of possessing an empty stomach for various groups of fishes. We included fishes collected in all seasons, and most species were represented by both juvenile and adult stages. We collected fishes with multiple capture techniques at each site. Capture techniques were highly comparable among our samples, and fishes from each study were collected with the specific aim of dietary analysis. Once collected, fishes were immediately either immersed in an ice-water slurry, or preserved in 15% formalin to prevent decomposition of stomach contents. We made an incision through the abdominal wall of large individuals to expedite preservation of the gut (stopping digestion). Subsequently, we removed stomach contents from recently euthanized or formalin preserved specimens for examination. These techniques preserved stomach contents, intact, at the time of collection. The volume of each diet category was measured or estimated (e.g., Winemiller 1990), but for purposes of our study, we classified specimens merely as having stomachs ''with food'' or ''empty.'' Empty was defined as the absence of any measurable organic material in the stomach. Following Winemiller (1990), the ''stomach'' was defined as the anterior half of the gut, unless a well-defined stomach was present.

We calculated the percentage of individuals of each species collected with empty stomachs. Only those species with ≥10 individuals from a single location were included in our analysis; mean sample size for species analyzed was 145 individuals. Each species was treated as a single record regardless of the number of specimens examined per species. We sampled most species at a single location; however, we collected a few species from more than one location within a region. These individuals were combined and analyzed as a single datum in our analysis. Only a single species (*Belonesox belizanus*) was collected from two disparate geographic regions (Costa Rica and Florida). Because *B. belizanus* is native to Central America and introduced into North America, we treated these two populations as separate entries (species) in our analysis.

Data analysis

Similar to Huey et al. (2001), we did not attempt a formal phylogenetic analysis, because relationships among these diverse taxa are not highly resolved. Although fishes reveal considerable variation in trophic specializations within lower taxonomic units (i.e., family, genera; Winemiller 1991, but see Harvey and Pagel 1991), we explored phylogenetic patterns by averaging percentages of empty stomachs for species within taxonomic orders within separate geographic regions (Table 1). We provide our complete data set for future phylogenetic analysis should a robust higher level phylogeny become available (see the Appendix).

Each species was categorized a priori based on documented diel feeding behavior (i.e., nocturnal or diurnal) and trophic group: detritivore (including algivores), invertivore, omnivore, and piscivore. Although species often consume a continuum of prey types (Winemiller 1990), we assigned our species to four trophic groups in search of generalities characteristic of these broad classifications. Assignment to trophic group was based on published records and documented stomach contents of these species. To evaluate the effect of meal size on the likelihood of possessing an empty stomach we further divided piscivores based on mode of prey capture (biters vs. engulfers). Biters are piscivores that frequently shear off a portion of their prey (e.g., piranhas, *Serrasalmus* spp.), and engulfers consume their prey whole (e.g., largemouth bass, *Micropterus salmoides*).

Empty stomach percentage data were non-normal and heteroscedastic; therefore data were arcsine square-root transformed. If transformation did not cause data to meet assumptions for parametric analysis, we performed a nonparametric test. We used a Mann-Whitney *U* test to test for differences in percentages of empty stomachs between diurnally and nocturnally feeding fishes. We used a three-dimensional contingency table (Zar 1996) to test for independence among diel feeding behavior, trophic group, and empty stomach percentages. To provide a relative measure of the likelihood of possessing an empty stomach more or less frequently than an ''average'' fish species, we divided species into two groups based on those with percentages of empty stomachs ≤16.2%, the mean for all fishes, and those with percentages >16.2% (Table 2). This test is similar to a test of overall interaction effect using two-way ANOVA. We evaluated effects of trophic group and geographic location on the percentage of empty stomachs using a two-factor ANOVA. We tested for differences in the percentage of empty stomachs between piscivores classified as biters or engulfers using a Mann-Whitney *U* test.

We believe our data and analyses are robust to potential biases associated with stomach-contents analysis. Investigator bias was minimized by the simplicity of our evaluation (i.e., binary classification as stomachs with food or empty). Presence or absence of stomach contents is a function of ingestion rate and evacuation rate; therefore, sampling regime can influence stomach-contents data (Bowen 1996). However, effect of feeding patterns on proportions of empty stomachs should be lessened, because gastric evacuation is not instan-

TABLE 1. Presence or absence of food in the stomachs of fishes was associated with taxonomic groups and geographic regions.

Region and order	N_{species}	$N_{\text{individuals}}$	Empty stomachs (%)	
			Mean ± 1 SE	Range
Africa				
Osteoglossiformes	5	224	6.4 ± 3.3	0.0–16.9
Cypriniformes	4	147	8.3 ± 4.6	0.0–21.1
Characiformes	2	213	28.1 ± 28.1	0.0–56.2
Siluriformes	8	721	27.0 ± 7.5	0.0–64.4
Cyprinodontiformes	1	65	1.54	
Synbranchiformes	1	10	40.0	
Perciformes	14	1366	31.5 ± 8.74	0.0–78.9
Neotropics				
Clupeiformes	1	20	35.0	
Characiformes	78	12 232	11.9 ± 2.0	0.0–79.4
Siluriformes	25	3103	16.4 ± 3.5	0.0–56.7
Gymnotiformes	9	688	15.2 ± 4.5	0.0–36.1
Atheriniformes	1	238	2.1	
Cyprinodontiformes	8	1853	9.6 ± 7.2	0.0–59.6
Gasterosteiformes	1	248	28.6	
Synbranchiformes	1	81	14.8	
Perciformes	33	5602	18.7 ± 3.5	0.0–68.8
Pleuronectiformes	3	134	8.3 ± 2.3	4.8–12.5
Tetraodontiformes	1	10	0.0	
North America				
Semionotiformes	2	566	4.6 ± 5.9	40.0–51.9
Amiiformes	1	93	19.4	
Elopiformes	1	10	40.0	
Clupeiformes	3	1635	7.4 ± 4.4	0.0–15.2
Cypriniformes	3	68	18.2 ± 2.7	15.0–23.5
Siluriformes	4	468	21.3 ± 1.4	18.4–25.0
Esociformes	1	22	50.0	
Mugiliformes	1	517	17.6	
Atheriniformes	3	719	22.1 ± 8.8	6.7–37.2
Cyprinodontiformes	14	2276	13.3 ± 4.6	0.3–58.2
Gasterosteiformes	1	16	12.5	
Perciformes	23	3436	15.3 ± 2.5	0.0–4.23
Pleuronectiformes	2	94	22.0 ± 18.0	4.1–40.0

Notes: Unweighted mean percentage of empty stomachs among species within taxonomic orders and geographic regions. The overall mean percentage of empty stomachs for all species was 16.2%. Taxonomic orders follow Nelson (1994).

taneous (Anderson 1998, 1999). Fish life history stage and size should affect ingestion rates and presence of prey in stomachs (Bowen 1996).

RESULTS AND DISCUSSION

Mean percentage of empty stomachs was low across all fishes sampled (percentage empty = 16.2 ± 1.2% [mean ± 1 SE]) but ranged considerably for individual species (0–79.4% empty). A large sample of lizard species yielded similar results (mean percentage empty = 13.9% and 12.2% for desert and tropical species, respectively; range = 0.0–65.6% empty; Huey et al. 2001). Evaluation of all fish species ($n_{\text{species}} = 254$) indicated a strongly right-skewed distribution with modal peaks between 0.1% and 10.0% empty (Fig. 1). On average, most fishes possessed food in their stomachs.

Phylogenetic patterns

Although we did not conduct a formal phylogenetic analysis, some taxonomic and geographic patterns were associated with presence or absence of food in the stomachs of fishes (Table 1). Cyprinodontiforms from all three regions had empty stomachs less frequently than the mean percentage of empty stomachs for all fish species (16.2%). Siluriformes consistently had empty stomachs more frequently than the mean for all species. Characiforms, however, varied considerably in the percentage of empty stomachs among regions, with African characiforms' (28.1 ± 28.1%) stomachs more frequently empty than Neotropical characiforms (11.9 ± 2.0%). North American cypriniforms (18.2 ± 2.7%) had empty stomachs more often than African cypriniforms (8.3 ± 4.6%). Similarly, perciforms varied considerably in the percentage of empty stomachs among regions (Africa 31.5 ± 8.7% [mean ± 1 SE], Neotropics 18.7 ± 3.5%, North America 15.3 ± 2.5%). African and Neotropical perciforms had empty stomachs more frequently, and North American perciforms were empty less frequently than the overall mean for all species. Within perciforms, cichlids did not reveal a common trend in the percentage of empty stomachs among the three regions (Africa 31.5 ± 8.7%; Neotropics 18.8 ±

TABLE 2. Based upon a chi-square analysis, frequencies of empty stomachs were differentially distributed in relation to time of feeding and trophic classification.

Empty stomachs (%)	Trophic group			
	Detritivore	Omnivore	Invertivore	Piscivore
Diurnal				
≤16.2	18	45	58	16
>16.2	4	8	15	34
Nocturnal				
≤16.2	4	1	18	5
>16.2	0	2	18	8

Notes: To provide a relative measure of the likelihood of possessing an empty stomach more or less frequently than an ''average'' fish species, species were divided into two groups based on those with percentages of empty stomachs ≤16.2%, the mean for all fishes, and those with percentages >16.2%.

Mutual independence $X^2_{0.05,10} = 84.7$; $P < 0.001$.

Partial independence $X^2_{0.05,7} = 123.2$; $P < 0.001$. Time is not independent of proportion of empty stomachs and trophic classification.

Partial independence $X^2_{0.05,9} = 65.9$; $P < 0.001$. Trophic classification is not independent of time and proportion of empty stomachs.

Partial independence $X^2_{0.05,7} = 53.7$; $P < 0.001$. Proportion of empty stomachs is not independent of trophic classification and time.

4.7%; North America 9.8 ± 6.1%), but instead showed trends in proportion of empty stomachs in relation to trophic niche and provision of brood care (see *Results and discussion: Trophic classification* and *Parental care*). Because fishes, particularly cichlids (Greenwood 1974, Kaufman and Leim 1982, Stiassny and Jensen 1987), display a radiation of diverse feeding mechanisms, it might be expected that phylogeny would not constrain the proportion of empty stomachs. In contrast to results from lizards (Huey et al. 2001), the proportion of time spent with food present in the stomachs of fishes apparently is not strongly associated with phylogeny.

Nocturnal vs. diurnal fishes

Percentages of empty stomachs differed significantly between nocturnally and diurnally feeding fishes (Mann-Whitney $U = 4415$, $P < 0.02$). As in lizards (Huey et al. 2001), nocturnal fishes were collected with empty stomachs more frequently (18.9 ± 2.2%) than diurnal fishes (15.4 ± 1.1%), although both diurnal and nocturnal fishes had modal peaks of empty stomachs at 10% (Fig. 1). A possible explanation for this pattern is that most species in our data set were collected during daylight hours, and thus skewed the proportion of empty stomachs for nocturnal species. Yet this explanation may be unlikely, because differences between diurnal and nocturnal fishes were partially constrained by trophic classification.

Trophic classification

We found a significant interaction among diel feeding behavior, trophic classification, and proportions of empty stomachs among fishes (Table 2). The null hypothesis of mutual independence was rejected ($\chi^2 = 84.7$, df = 10, $P < 0.001$). Thus, we tested the null hypothesis of partial independence of trophic classification from diel feeding behavior and proportions of empty stomachs. This hypothesis was rejected ($\chi^2 = 65.9$, df = 9, $P < 0.001$); fishes in different trophic classifications are distributed differently in relation to time of feeding and likelihood of empty stomachs (Table 2). Diurnally feeding piscivores were collected more frequently with empty stomachs than nocturnal piscivores, and nocturnal detritivores were less likely to have empty stomachs than diurnal detritivores. Nocturnal omnivores and invertivores had empty stomachs more frequently than their diurnal counterparts (Table 2).

We observed a significant interaction in proportions of empty stomachs among trophic classifications and geographic locations (Fig. 2; ANOVA, $F_{6,242} = 3.3$, $P < 0.005$). Detritivores and omnivores had lowest proportions of empty stomachs, with invertivores intermediate between detritivores and piscivores for all locations (Fig. 2). Piscivores had highest proportions of empty stomachs at each location (Fig. 2), and African piscivores had empty stomachs more frequently than piscivores from either the Neotropics or North America. Again, we included juveniles and adults together in our analysis. We expect the greatest potential effect of including juvenile fishes in our analyses was to reduce the average proportion of empty stomachs in species that undergo ontogenetic diet shifts from insectivory to piscivory (e.g., *Micropterus salmoides*, largemouth bass). Thus, inclusion of juveniles in our analyses may have resulted in a conservative estimate of proportions of empty stomachs for piscivores.

Fish that consume food with low metabolizable-energy content forage more frequently to procure their specific daily ration than those consuming energy-rich food items (Brett and Groves 1979, Bowen et al. 1995).

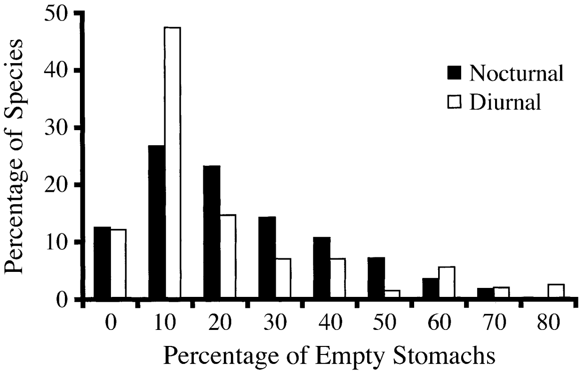

FIG. 1. On average, most fishes possessed food in their stomachs. Nocturnal fishes, however, were collected with empty stomachs more frequently than diurnal fishes, though both groups had modal peaks of empty stomachs at 10%. Percentages of diurnal and nocturnal fishes among bins (0% = 0, 10% = 0.1–10.0%, 20% = 10.1–20.0%, and so on) representing percentage of empty stomachs are presented.

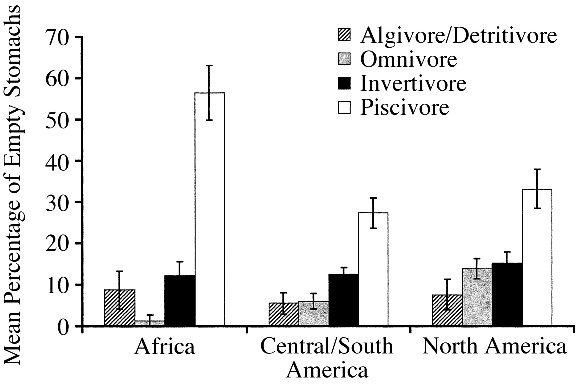

FIG. 2. Mean percentages of empty stomachs are significantly associated with trophic classifications and to a lesser extent geographic locations. African piscivores, many of which exhibit parental care, had disproportionately high percentages of empty stomachs. Error bars indicate ± 1 SE.

Detritivores and omnivores had lowest proportions of empty stomachs, which indicates they experienced negative energy balance infrequently according to Huey et al.'s (2001) definition. Observed stomach contents for these individuals, however, may have contained less labile energy than the amount required for maintenance costs, thus, resulting in net negative energy balance. Detritivores and omnivores had empty stomachs less frequently than other trophic groups (Fig. 3A), and these fishes probably increase their feeding interval to compensate for low per-unit-time energy gain (Bowen et al. 1995). Furthermore, herbivorous fishes have lower gross conversion efficiencies than invertivorous or piscivorous fishes because of the large nondigestible fraction in their diet (Brett and Groves 1979). Though more frequent occurrence of empty stomachs among piscivores could be due to stochastic variation in encounter rate and successful capture of few large prey (Breck 1993), an alternative explanation is that consumption of small numbers of large, high-quality food items permits individuals to rely on stored energy and forgo foraging for longer periods of time (Bowen et al. 1995, Secor and Diamond 2000).

Piscivores have rapid gastric-evacuation rates (Anderson 1998, 1999) and high percentages of empty stomachs that indicate frequent short-term negative energy balance. Nonetheless, increased proportions of empty stomachs do not imply net negative energy balance over the long term (Jobling et al. 1998, Secor and Diamond 2000). High frequencies of empty stomachs in snakes have been associated with consumption of large, high-quality food items and reliance on stored energy (Secor and Diamond 2000). To test this idea in fishes, we compared piscivores by mode of ingestion, biters vs. engulfers. Biters had empty stomachs significantly less often than engulfers that tended to consume larger prey items over less-frequent intervals (Fig. 3B; Mann-Whitney $U = 42.5$, $P < 0.001$).

An intraspecific analysis of four Arctic charr (*Salvelinus alpinus*) morphospecies with distinct trophic classifications yielded empty stomach proportions very similar to those obtained for species with the same trophic classifications in our interspecific analysis (Malmquist et al. 1992). Stomach contents were examined from three invertivorous and one piscivorous charr morphs over four seasons. Mean percentage of empty stomachs among invertivorous morphs (n = 748 individuals, mean percentage empty stomach = 11.0%) was similar to that of our diurnal invertivores (10.5 ± 1.4% [mean ± 1 SE]). The proportion of empty stomachs for the diurnal piscivore morph (n = 52, mean percentage empty stomachs = 28.9%) was similar to that of our diurnal piscivores (35.2 ± 3.5%; Table 2). Arctic charr findings strengthen our contention that trophic position, and not phylogeny, affects the proportion of time fishes spend with food items present in their stomach.

Parental care

Among fish species with highest percentages of empty stomachs (>50%; Fig. 3A), a disproportionate num-

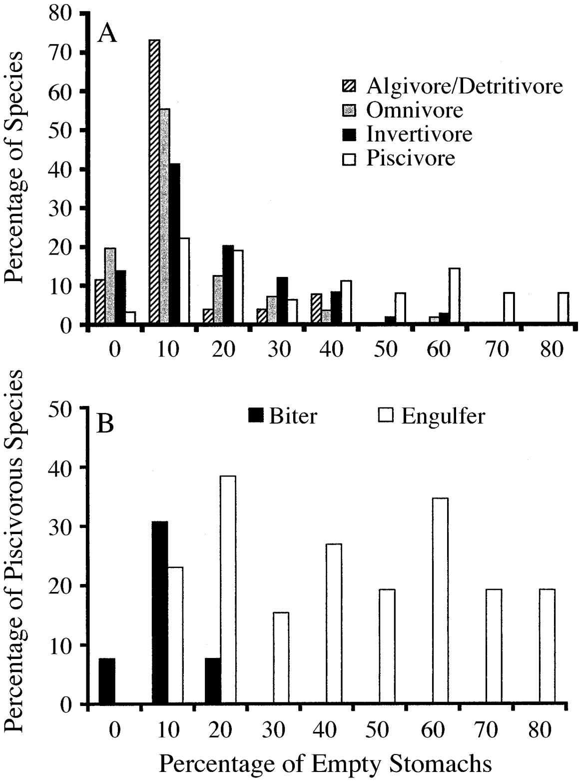

FIG. 3. Distributions of the percentage of fish species according to (A) trophic classifications and (B) piscivore feeding behavior arranged in bins representing percentages of empty stomachs 0% = 0, 10% = 0.1–10.0%, 20% = 10.1–20.0%, and so on. Detritivores and omnivores had empty stomachs less frequently than invertivores and piscivores, and the latter had empty stomachs more frequently than other trophic groups. Piscivores that consume pieces of their prey (biters) had empty stomachs significantly less often than engulfers that consume prey whole.

ber provide parental care (mouth brooding or other forms of brood guarding). Fishes often exploit resource-rich but transient conditions for growth and energy storage, then use energy stores as metabolic substrate during periods of negative energy balance associated with migration, spawning, brood guarding, or extreme physical stress as during confinement to drought refuges (Keenleyside and Bietz 1981, Loftus and Kushlan 1987, Winemiller 1989, Jobling et al. 1998, Winemiller and Jepsen 1998). The only omnivore in our sample with a high percentage of empty stomachs ($>50\%$) was *Hoplosternum littorale*, a nest-guarding callichthyid catfish that shows strongly seasonal patterns of feeding, visceral fat deposition, and reproduction (Winemiller 1987). Among invertivores, two of the three species with $>50\%$ empty stomachs were cichlids with parental care (*Sargochromis giardi* and *Aequidens diadema*). Fifty-six percent of piscivores with $>50\%$ empty stomachs ($n = 18$) provide parental care. In many cases (e.g., mouth brooding), brood care is associated with reduction in foraging.

CONCLUSIONS

Most fishes have food in their stomach over short-term intervals. In fishes, trophic classification and life history characteristics (i.e., parental care) were consistently and strongly associated with percentages of empty stomachs. To achieve positive energy balance, feeding intervals of fishes are adjusted relative to energy content, particle size, and conversion efficiency of their food (Brett and Groves 1979, Bowen et al. 1995). Piscivores appear to be the only trophic group with a high proportion of empty stomachs, with species consuming prey whole and those with parental care having highest proportions. Taxonomy and geography seemed to be associated with proportion of empty stomachs in our analysis, though the effect of phylogeny does not appear as strong in fishes as in lizards (Huey et al. 2001). Future research based on taxonomic groups with well-resolved phylogenies should further evaluate, in greater detail, the effect of phylogenetic relatedness on possession of empty stomachs.

Organisms able to allocate surplus energy into storage (e.g., lipids) can defray costs associated with reproduction (i.e., migration, courtship, brood care) or enhance survivorship during times of physiological stress. Patterns of resource acquisition influence the variability of life history strategies (Ricklefs 1991, Glazier 2000), and our results reveal a potential influence of feeding frequency and energy balance on life history evolution. Future research should directly evaluate the influence of food quality (energy density), meal size, and feeding frequency on potential and realized fitness (including measurement of energy allocated to reproduction). Furthermore, relationships between food quality, energy storage, maintenance of energy balance, and the evolution of complex life histories should be examined.

Further research is needed to evaluate the influence of phenotypic flexibility on bioenergetics of fishes. Several snake and bird species minimize metabolic expenditure on nonessential body machinery by varying organ size and functionality based on immediate needs (Piersma and Lindström 1997, Piersma 1998, Secor and Diamond 2000). Phenotypic flexibility may reduce time-averaged metabolic costs and enhance the individual's ability to meet long-term nutritional requirements. This flexibility may be particularly important for maintenance of long-term energy balance in species that perform long-distance migrations, such as salmon (Salmonidae) and eels (*Anguilla* spp.), and species that cease feeding while brood guarding.

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APPENDIX

Our data set for the 36 875 individual fishes, organized by species (n = 254), used in this analysis is available in ESA's Electronic Data Archives: *Ecological Archives* E083-038-A1.