Review

Regulation of digestive performance: a proposed adaptive response

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Abstract

Among snakes a correlation exists between feeding habits (frequent or infrequent) and the magnitude by which digestive performance is regulated (modest or large). This paper investigates whether the observed regulation of digestive performance is an adaptation to feeding habits and therefore, a product of natural selection. Using data on metabolic and intestinal responses to feeding for amphibians and reptiles, it is attempted to show the selective advantage and independent origin of either modestly or widely regulating gut performance. In an energetic model, snakes that naturally feed frequently on small meals benefit (from lower energy output) from modestly regulating gut performance as opposed to widely regulating gut performance. Likewise, the model suggests an energetic benefit for infrequently-feeding snakes secondary to the wide regulation of gut performance. This benefit is a function of long spans of fasting with a down-regulated gut (thereby incurring a lower standard metabolic rate) and the occasionally incursion of a costly up-regulation of the gut. In a comparison across several distantly-related lineages of amphibians and reptiles, frequently-feeding species all exhibit small postprandial responses in metabolism and intestinal nutrient transport capacities. In contrast, frogs and snakes that routinely fast for long periods independently experience five- to 30-fold increases in metabolism and intestinal performance with feeding. Among amphibians and reptiles the evidence presented supports the hypothesis that the extent by which the gut is regulated is an adaptive trait that evolved with divergence in feeding habits and energy budgets. In finishing, the foundations, caveats, and suggested future tests of this adaptive hypothesis are presented. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Adaptation; Amphibian; Digestive physiology; Feeding habits; Metabolism; Reptile

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1. Introduction

A familiar concept in animal ecology is that the successful ingestion of energy and the proper allocation of that energy are paramount to an organism's survival, growth, and reproductive fitness, therefore to its overall success. Serving as the functional link between energy intake and energy allocation, the gut has undoubtedly experienced many selective pressures during species evolution. For example, it has been inferred that selective forces gave rise to the ability of herbivore intestines to transport simple sugars at faster rates than they transport amino acids and to the reciprocal trait characteristic of carnivore intestines (Karasov and Diamond, 1988).

In a recent paper, it was suggested that selective forces also underlie the correlation between feeding habits of snakes and the magnitude by which their guts regulate performance (Secor and Diamond, 2000). Snakes which naturally feed infrequently on large meals were found to regulate widely their gut's performance as exemplified by the literal shut down of their digestive tract upon completion of digestion and the rapid up-regulation of gut performance after feeding (Secor and Diamond, 2000). Up-regulation of gut performance appears energetically costly, as indicated by the relative high cost of digestion (known as specific dynamic action or SDA) experienced by infrequently-feeding snakes. Conversely, frequently-feeding snakes maintained elevated gut function following completion of digestion and therefore, experience only minor regulatory responses with feeding and a consequently smaller SDA. This correlation between feeding habits and digestive responses of snakes was tested to be independent of phylogeny (Secor and Diamond, 2000).

It was proposed in the previously noted study that the regulation of digestive performance (either narrowly or widely) is an adaptive response of feeding habits (respectively, for frequent or infrequent feeding). But can this hypothesis be rightfully inferred? In order to claim adaptation by natural selection as the evolutionary mechanism underlying divergent digestive physiology with respect to feeding habits, two criteria must be met (Lauder et al., 1993). First, each trait must have a selective advantage over ancestral or alternative forms of that trait. And secondly, each trait must have evolved in response to a particular selective regime. If the constant or wide regulation of digestive performance are each adaptations, then they should each possess both criteria. The objective of this paper is to attempt to satisfy these two criteria as a means to support or refute the proposed hypothesis of an adaptive digestive response. In order to do this, the available data are used on the digestive responses of frequently-feeding and infrequently-feeding amphibians and reptiles. Presented in this paper are the apparent energetic advantages of each mode of digestive response, the independent occurrence of each digestive response among distantly-related amphibians and reptiles, as well as the foundation, caveats, and future testing of the adaptive hypothesis.

2. Materials and methods

2.1. Data and animal care

Data on digestive responses of amphibians and reptiles were compiled from published studies and from my own unpublished measurements. As previously, the reported species are divided into two generalized categories of feeding habits: frequent feeding and infrequent feeding (Secor and Diamond, 2000). A species was designated as a frequent feeder if it feeds frequent enough during its normal activity season to experience some phase of digestion the majority of the time. Frequently-feeding amphibians and reptiles are considered as those species that feed daily to once every 2 weeks in the wild. An infrequently-feeding amphibian or reptile was designated as one that normally experiences long bouts of digestive quiescence (greater than 1 month) either during its activity season or during periods of estivation (excluding hibernation). The feeding habits of many of the reported species are described by Duellman and Trueb (1986), Secor and Phillips (1997), Secor and Diamond (1999), and Secor and Diamond (2000).

The majority of the data reported in this paper originates from my own studies; therefore, presented in the following are the methods for animal care, the measurements of whole-animal metabolism, and intestinal nutrient transport rates. Readers are referred to the other papers

referenced for a description of the methodologies used in each study.

Animals were obtained either from commercial breeders or were captured in the wild. Each animal was housed individually, maintained at 25°C (amphibians and turtles) or 30°C (lizards and snakes), and fed at 2- to 14-day intervals with water available ad libitum. Prior to experiments, each animal was fasted for 2 (example, frequently-feeding amphibians) to 4 (example, infrequently-feeding snakes) weeks, in order to achieve a post-absorptive state. Next, they were acclimated to 30°C for several days within an environmental chamber. This temperature had been selected for earlier studies (Secor et al., 1994; Secor and Diamond, 2000) because it is the approximate mean field body temperature of digesting sidewinders (*Crotalus cerastes*) and coachwhips (*Masticophis flagellum*) (S.M. Secor, unpublished observations) and therefore, was established as the standard temperature for all subsequent experiments.

For each species, metabolic rate and/or intestinal function and mass were measured from fasting postabsorptive individuals and from fed individuals following their consumption of meals equal to 5–25% of the animal's fasted body mass. Meals consisted of crickets and mealworms for small amphibians and lizards, strips of beef for turtles, and rodents for snakes and larger amphibians and lizards. For each species, the meal size selected represents a substantially large meal for that animal if given the opportunity to feed ad libitum (relative meal sizes are listed in Tables 1 and 2).

2.2. Measurements of metabolism and intestinal nutrient transport

The oxygen consumption rates ($\dot{V}O_2$ in units of ml g^{-1} h^{-1}) were measured at 30°C of fasted individuals for 3–5 days and again for 5–11 days following feeding using closed-system respirometry as described by Secor and Diamond (1997). From these measurements, the following variables were quantified: standard metabolic rate (SMR; as lowest measured $\dot{V}O_2$ during fasting), postfeeding peak $\dot{V}O_2$ (as highest $\dot{V}O_2$ during digestion), and SDA (calculated from the extra O_2 consumed beyond SMR during the duration of significantly elevated $\dot{V}O_2$) quantified as kJ,

kJ/kg, and as a percentage of the energy content of the meal. To calculate these last three variables, an energy conversion was assumed of 19.8 J expended per ml of O_2 consumed and an energetic value of 6.4, 9.5, 7.3, and 8 kJ per gram wet mass, respectively, for cricket, mealworm, beef, and rodent meals (Harwood, 1979; Rubert, 1980; Geesman and Nagy, 1988; Holland et al., 1991; Secor and Diamond, 1995).

Nutrient uptake rates were measured across the intestinal brush-border membrane using the in vitro everted-sleeve technique as described by Karasov and Diamond (1983) and Secor et al. (1994). Intestinal uptake of two or all of the following nutrients; amino acid L-leucine, amino acid L-proline, and sugar D-glucose, were measured from both fasted and fed individuals of each species. As explained previously, uptake rates were quantified from individual 1-cm sleeves of intestine as nmol mg^{-1} min^{-1} (Secor et al., 1994). Total nutrient uptake capacity of the small intestine was calculated for each nutrient as the product of mass-specific uptake rate times small intestinal wet mass (Secor and Diamond, 1995). The magnitude of the post-feeding response of intestinal performance was quantified by dividing for each nutrient its total uptake capacity at 1 day post-feeding by its uptake capacity during fasting.

2.3. Criteria 1 — selective advantage of an adaptive trait

The first criteria suggests that there is an advantage of either maintaining or widely regulating digestive performance, respectively, for frequent or infrequent feeders. To ascertain if there is an energetic advantage of each mode of digestive response, several simple models were constructed that compare time-averaged energy expenditure as a function of feeding interval between a frequently-feeding and an infrequently-feeding snake of similar size. The aforementioned measures of SMR and SDA were used to calculate the average daily expenditure of SMR and SDA for each snake species when feeding at regular intervals of once every 1–8 weeks. Standard metabolic rate represents fasting metabolism, a portion of which is contributed by the continued energy cost of maintaining the digestive system. Specific dynamic action is in part the energy spent to up-regulate gut performance after feeding. These mod-

Table 1

Body mass, meal size (% of body mass), factorial increase in post-feeding $\dot{V}_{O_2}$ (peak $\dot{V}_{O_2}$/SMR), SDA as kJ, kJ/kg, and as a percentage of ingested energy for frequently-feeding and infrequently-feeding amphibians and reptiles

Species		Body mass (g)	Meal size (%)	Peak $\dot{V}_{O_2}$/ SMR	SDA (kJ)	SDA (kJ/kg)	SDA (% of ingested energy)	Source
Frequently-feeding								
Amphibians								
Caudata	*Tarchica granulosa*	13.3	8.8	2.1	1.2	89	11.8	Secor et al.[a]
	T. torosa	11.0	7.5	2.9	1.0	92	13.5	Secor et al.[a]
	Plethodon jordani	4.3		1.8				Feder et al., 1984
Anura	*Rana catesbeiana*	296	15	4.6	59.8	202	16.8	Secor and Diamond[b]
	Hyla regilla	2.4	10	2.6	0.2	64	9.8	Secor et al.[a]
	H. cadaverina	3.4	10	2.8	0.2	63	9.9	Secor et al.[a]
	Bufo marinus	75	15	3.5	14.2	187	15.6	Secor and Diamond[b]
Reptiles								
Testudines	*Sternotherus odoratus*	61	5	2.1	3.7	61	17	Secor and Diamond, 1999
	Chelydra serpentina	101	11.3	3.4	18.0	178	22	Secor and Diamond, 1999
	Trachemys scripta	356	5.2	2.7	27.1	76	21	Secor and Diamond, 1999
	Chrysemys picta	7.7		3.2				Sievert et al., 1988
	Kinixys spekii	640		1.6–2.0			14–23	Hailey, 1998
Sauria	*Gambelia wislenzeii*	28	21	2.8	7.3	261	20	Secor and Diamond[b]
	Sceloporus merriami	4.5	6		0.6	133	4	Beaupre et al., 1993
	Angolosaurus skoogi	65	7	1.8				Clark and Nicolson, 1994
Serpentes	*Coluber constrictor*	223	25	5.4	68.9	309	15	Secor and Diamond, 2000
	Elaphe guttata	285	25	3.7				Secor and Diamond[b]
	Lampropeltis getula	188	25	7.0	56.0	298	14	Secor and Diamond, 2000
	Masticophis flagellum	273	25	5.9	70.4	258	13	Secor and Diamond, 2000
	Nerodia fasciata	180	25	3.5				Secor et al.[a]
	Pituophis melanoleucus	732	25	8.0	211	288	14	Secor and Diamond, 2000
	Natrix maura	30	10–14	3.4	2.4–4.6		12–24	Hailey and Davies, 1987
	Thamnophis sirtalis		25	4–5			13–18	Bear, 1992

Table 1 (*Continued*)

Species		Body mass (g)	Meal size (%)	Peak $\dot{V}_{O_2}$/ SMR	SDA (kJ)	SDA (kJ/kg)	SDA (% of ingested energy)	Source
Infrequently-feeding								
Amphibians								
Anura	*Pyxicephalus adspersus*	225	15	8	59.9	266	22.2	Secor and Diamond[b]
	Ceratophrys ornata	149	15	8.7	37.8	254	21.1	Secor and Diamond[b]
Reptiles								
Sauria	*Varanus albigularis*	8100	9.3	9.9	1260	156	23	Secor and Phillips, 1997
Serpentes	*Boa constrictor*	346	25	18.5	232	670	33	Secor and Diamond, 2000
	Crotalus cerastes	161	25	9.9	73.3	455	21	Secor and Diamond, 2000
	C. durissus	93	30	5.2	13.5	145	12	Andrade et al., 1997
	Lichanura trivirgata	163	25	15.9	58.2	357	18	Secor and Diamond, 2000
	Python molurus	736	25	17.7	428	581	30	Secor and Diamond, 2000

[a] S. Secor, L. Kats, and J. Diamond, unpublished observations.

[b] S. Secor and J. Diamond, unpublished observations.

Table 2

Body mass, meal size (% of body mass), and factorial increases in intestinal uptake capacity of the amino acids L-proline and L-leucine and of the sugar D-glucose 1 day after feeding for frequently-feeding and infrequently-feeding amphibians and reptiles

Species		Body mass (g)	Meal size (%)	Factorial increase in			Source
				L-proline uptake	L-leucine uptake	D-glucose uptake	
Frequently-feeding							
Amphibians							
Caudata	*Tarchica granulosa*	12.6	10	1.8	2.2	1.0	Secor et al.[a]
	T. torosa	10.8	10	1.1	1.0	2.5	Secor et al.[a]
Anura	*Rana catesbeiana*	315	20	1.3	1.8	3.1	Secor and Diamond[b]
	R. pipiens	29	10	2.5	1.6	4.5	Secor and Diamond[b]
	Hyla regilla	2.2	10	1.7		2.0	Secor et al.[a]
	H. cadaverina	2.4	10	1.4		2.2	Secor et al.[a]
	Bufo marinus	74	20	1.6	1.8	2.0	Secor and Diamond[b]
Reptiles							
Testudines	*Sternotherus odoratus*	64	5.5	1.2	1.0	1.9	Secor and Diamond, 1999
	Chelydra serpentina	79	10	1.0	1.0	2.2	Secor and Diamond, 1999
	Trachemys scripta	325	5.9	1.3	1.2	2.0	Secor and Diamond, 1999
Sauria	*Gambelia wislenzeii*	28	25	1.3	4.5	1.4	Secor and Diamond[b]
	Sceloporus occidentalis	9.0	6.5	1.3	1.0	1.6	Secor and Diamond[b]
Serpentes	*Coluber constrictor*	170	25	1.6	1.4	1.9	Secor and Diamond, 2000
	Elaphe guttata	215	25	3.7	1.6		Secor and Diamond[b]
	Lampropeltis getula	220	25	2.4	2.6	2.2	Secor and Diamond, 2000
	Masticophis flagellum	329	25	2.0	2.2	2.3	Secor and Diamond, 2000
	Nerodia fasciata	143	25	1.9	2.4		Secor and Diamond[b]
	Pituophis melanoleucus	741	25	1.8	1.5	1.9	Secor and Diamond, 2000
Infrequently-feeding							
Amphibians							
Anura	*Pyxicephalus adspersus*	240	20	5.3	4.6	10.1	Secor and Diamond[b]
	Ceratophrys ornata	190	20	5.5	6.3	10.0	Secor and Diamond[b]
Reptiles							
Serpentes	*Boa constrictor*	375	25	7.2	9.7	9.4	Secor and Diamond, 2000
	Crotalus cerastes	128	25	5.0	13.0	17.0	Secor and Diamond, 2000
	Lichanura trivirgata	236	25	6.0	4.6	8.3	Secor and Diamond, 2000
	Python molurus	724	25	12.0	12.1	29.3	Secor and Diamond, 2000

[a] S. Secor, L. Kats, and J. Diamond, unpublished observations.
[b] S. Secor and J. Diamond, unpublished observations.

els serve to illustrate the energetic benefits of each mode of digestive response for each feeding habit.

2.4. Criteria 2 — similar responses exist within a particular selective regime

The fulfillment of this criteria requires that each mode of digestive response has evolved independently within distant lineages in response to frequent and infrequent feeding. Among different lineages of amphibians and reptiles, available data was tabulated and analyzed on the magnitudes of post-feeding responses for frequent and infrequent feeders. The data presented include; factorial increase in postprandial metabolic rate (peak $\dot{V}O_2$/SMR), SDA quantified as kJ, kJ/kg, and as a percentage of ingested energy [SDA coefficient of Jobling and Davies (1980)], and factorial increases (1-day value divided by fasting value) in intestinal uptake capacity of L-leucine, L-proline, and D-glucose.

3. Results

3.1. Criteria 1 — selective advantage of an adaptive trait

Fig. 1 illustrates three separate models which compare the time-averaged partial daily energy expenditure (sum of SMR and SDA) of a frequently-feeding snake that experiences modest regulation of digestive response and an infrequently-feeding snake that experiences a large digestive response, when each snake feeds at regular intervals of once every 1–8 weeks. Feeding at intervals of once every 1–4 weeks, the average daily expenditure of SMR and SDA of the frequently-feeding *Lampropeltis getula* is less than that of the infrequently-feeding *Boa constrictor* (Fig. 1a). The former species experiences non-significant post-feeding changes in intestinal performance, whereas the latter species significantly up-regulates intestinal performance with feeding (Secor and Diamond, 2000 and Table 2). Conversely, at feeding intervals of 5 weeks or more, the trend reverses, and it is the *B. constrictor* with the lower averaged daily cost of SMR and SDA compared to *L. getula*. This pattern is repeated
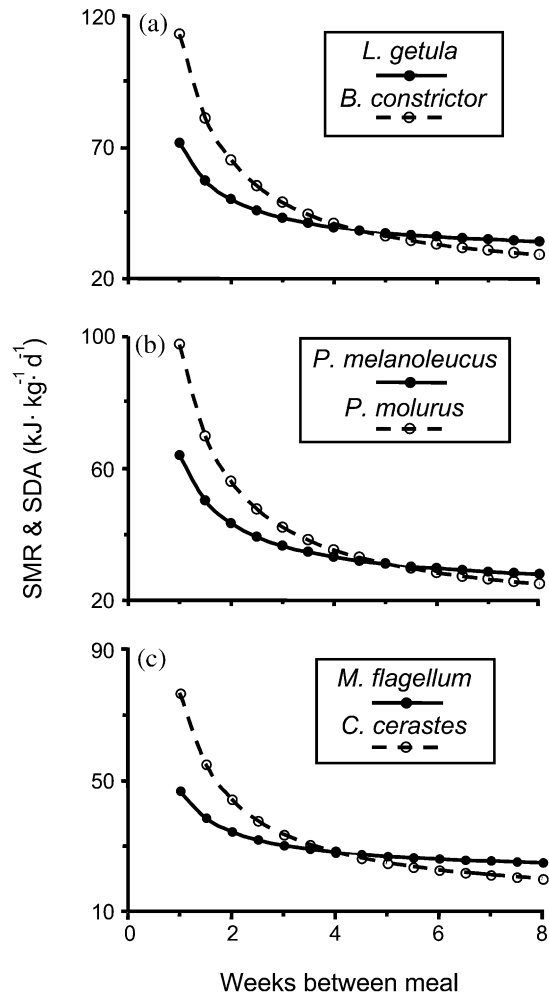

Fig. 1. Daily-averaged energy expenditure of summed standard metabolic rate (SMR) and specific dynamic action (SDA) as a function of feeding interval (weeks) for the snakes *Lampropeltis getula* and *Boa constrictor* (a), *Pituophis melanoleucus* and *Python molurus* (b), and *Masticophis flagellum* and *Crotalus cerastes* (c). Frequently-feeding *L. getula*, *P. melanoleucus*, and *M. flagellum* exhibit modest regulatory spans of digestive performance, whereas infrequently-feeding *B. constrictor*, *P. molurus*, and *C. cerastes* significantly up- and down-regulate their intestinal performance with each meal. Note in all figures that the frequently-feeding species possess lower averaged energy expenditures on SMR and SDA at feeding intervals less than 4 weeks, presumably because of not paying the high cost of up-regulation that infrequently-feeding species incur. In contrast, at feeding intervals greater than 5 weeks, it is the infrequently-feeding species with the lower averaged expenditures, due to a lower SMR between meals and only occasionally having to incur their relatively high SDA.

twice more in comparing the average daily SMR and SDA as a function of feeding interval between

the frequently-feeding *Pituophis melanoleucus* and the infrequently-feeding *Python molurus* (Fig. 1b) and between the frequently-feeding *Masticophis flagellum* and the infrequently-feeding *Crotalus cerastes* (Fig. 1c). Both *P. melanoleucus* and *M. flagellum* with their modest post-feeding responses have a lower average SMR and SDA at inter-meal intervals of 1–4 weeks, whereas *P. molurus* and *C. cerastes* which both up and down regulate their guts with each meal have the lower combined SMR and SDA at meal intervals greater than 5 weeks. In all three models, the lines cross at an inter-meal interval of 4–5 weeks.

Thus, the benefit to a snake of modestly regulating digestive performance is a lower time-averaged cost of SMR and SDA (a portion of its total daily energy expenditure) when feeding frequently. In contrast, infrequent feeders experience the relative benefits of widely regulating digestive performance in terms of lower cost of SMR and SDA (in comparison to narrowly regulating gut performance) when feeding infrequently.

3.2. Criteria 2 — similar responses exist within a particular selective regime

Table 1 presents postprandial metabolic responses of 23 frequently-feeding and eight infrequently-feeding amphibian and reptile species. The factorial increase in postprandial $\dot{V}_{O_2}$ (peak $\dot{V}_{O_2}$/SMR) experienced by the frequent feeders averaged 3.6 ± 0.4 (range $= 1.6$–8, $N = 22$), an increase that was significantly (ANOVA, $F = 46.9$, $P < 0.0001$) less than that measured from the infrequent feeders (mean $= 11.7 \pm 1.7$, range $= 5.2$–18.5, $N = 8$). The overall cost of digestion (SDA) quantified as kJ per kg for frequent feeders (172 ± 24 kJ/kg, $N = 15$) was less (ANOVA, $F = 10.2$, $P = 0.004$) than half that experienced by the infrequent feeders (361 ± 68 kJ/kg, $N = 8$). Likewise, SDA for the frequent feeders ($N = 18$) was equivalent to $15.0 \pm 1.0\%$ of the ingested energy, 50% less (ANOVA, $F = 12.0$, $P = 0.002$) than that of the infrequent feeders ($22.5 \pm 2.3\%$ of ingested energy, $N = 8$). For each of these parameters of the postprandial metabolic response, there is very little overlap in species values between frequent and infrequent feeders.

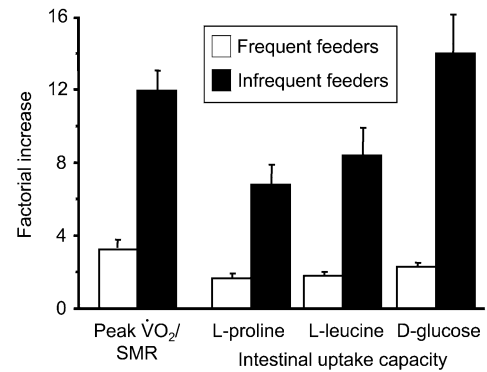Table 2 presents the factorial increase at 1 day post-feeding in intestinal uptake capacity for L-

Fig. 2. Mean factorial increase in postprandial metabolic rate (peak $\dot{V}_{O_2}$/SMR) and intestinal uptake capacity (1 day post-feeding) of L-proline, L-leucine, and D-glucose for frequently-feeding (open bars) and infrequently-feeding (closed bars) amphibians and reptiles. Note that the factorial increases are significantly greater (ANOVA, all *P*-values < 0.0001) for infrequent feeders than for frequent feeders. The error bars represent 1 S.E.

leucine, L-proline, and D-glucose for 18 frequently-feeding and six infrequently-feeding amphibian and reptile species. Frequent feeders exhibit modest postprandial responses, elevating uptake capacities of L-leucine, L-proline, and D-glucose by respective factors of 1.8 ± 0.2, 1.7 ± 0.2, and 2.2 ± 0.2 (Fig. 2). In contrast, infrequent feeders elevated intestinal uptake capacities of L-leucine, L-proline, and D-glucose by factors of 8.4 ± 1.5, 6.8 ± 1.1, and 14.0 ± 3.3, respectively (Fig. 2). For all three nutrients, factorial increases in intestinal uptake capacity with feeding was always greater (ANOVA, *F*-values ranging from 37.1 to 61.5, all *P*-values < 0.0001) for the infrequent feeders than for the frequent feeders. The emerging pattern from these intestinal measurements is that frequently-feeding amphibians and reptiles experience a doubling of intestinal performance with feeding, whereas infrequent-feeding species characteristically increase intestinal nutrient uptake performance by 10-fold.

Therefore, regardless of taxa, frequently-feeding amphibians and reptiles appear to exhibit a generalized pattern of relatively modest postprandial responses in metabolism and gut performance. Conversely, frogs and snakes that routinely experience long bouts of digestive quiescence are characterized by much larger increases in metabolism and gut performance when they feed.

4. Discussion

An adaptation is defined as a trait that enhances fitness and which arose historically as a product of natural selection for its current biological role (Lauder, 1996). It is suggested that the extent by which digestive performance is regulated is an adaptive phenomena of feeding habits. If this is the case, it can be inferred that the physiological trait being expressed is superior (in maximizing fitness) over alternative traits and that similar physiological traits have arisen independently in conjunction with a specific feeding regime. Illustrated using several snake species is the potential selective advantage (in terms of energy conservation) of either modestly or widely regulating gut performance when feeding frequently or infrequently, respectively. Also, across several amphibian and reptile lineages was found the apparent occurrence of each mode of digestive physiology within comparable feeding regimes. As it may be premature to assert the adaptiveness of digestive response based on these preliminary analyses, the following will discuss the potential foundation of an adaptive response of digestion, caveats of the approach, and future tests of the adaptive hypothesis.

4.1. Adaptive digestive response

The three models presented in Fig. 1 illustrate the potential energetic advantage of modestly regulating gut function for frequently-feeding snakes and widely regulating gut function for infrequently-feeding snakes. In all three models, snakes which modestly regulate gut performance (*Lampropeltis*, *Masticophis*, and *Pituophis*) have a lower combined average SMR and SDA [significantly (*P*-values < 0.05) so by paired comparison at 1- to 2-week feeding intervals] when feeding at intervals of once every 3 weeks or less compared to infrequent feeders. For these frequently-feeding snakes paying the constant cost of elevated gut performance (thereby incurring a higher SMR) appears energetically advantageous compared to paying the high cost of gut up-regulation with each frequent meal. Each of these snakes feed in the wild once every week or two (Secor and Diamond, 2000) and thereby, benefit energetically from constantly maintaining gut function. But to what extent is energy saved over the long term? Integrating the model of *M. flagellum* and *C.*

cerastes with actual field measurements from Secor and Nagy (1994), *M. flagellum* when feeding at its normal rate of once every 1.5 weeks is found to allocate 41% of yearly energy expenditure to SMR and SDA. If this snake shifted its digestive and metabolic physiology to that of *C. cerastes* while maintaining a 1.5-week feeding cycle, its yearly energy expenditure would be projected to increase by 15% (largely resulting from frequent high SDAs). For an adult snake, this increase in its yearly energy budget (approx. 750 kJ) would have to be met by the ingestion of an additional 10 lizard meals (calculated from Secor and Nagy, 1994).

These same three models show that snakes which widely regulate gut performance (*Boa*, *Crotalus*, and *Python*) have an apparent energetic advantage when feeding at intervals of once every 5 weeks or more. At such feeding intervals, their low SMR (a partial function of their down-regulated gut) expressed over their extended bouts of fasting offsets their occasional high cost of gut up-regulation. In a paired comparison at a feeding interval of once every 8 weeks, the average combined SMR and SDA of the three infrequent feeders are significantly less ($P = 0.04$) by $16.5 \pm 4.1\%$ than the values for the three frequent feeders. In a similar approach of integrating the model with the field study of Secor and Nagy (1994), at a feeding interval of 7 weeks, *C. cerastes* would be projected to experience an increase in yearly energy expenditure of 17% if it adopted the digestive and metabolic physiology of *M. flagellum*. For an adult *C. cerastes* this increase in its yearly energy budget (approx. 300 kJ) would have to be balanced by the ingestion of two additional rodent meals.

An analogy to consider in reference to infrequent feeding and the wide regulation of gut performance is that while stopped at a train crossing and waiting for a long, slow train to pass, you may turn off your car's engine. Your decision is based on the common knowledge that the gas saved from not having your engine idling for several minutes should offset the extra gas that will be used to restart your car's engine after the train has passed. Conversely, an analogy to frequent feeding and maintaining gut performance is that you routinely keep your car's engine idling while stopped at a stop light. You would not save any gas if you had to restart your car's engine immediately after turning it off.

Two components of their metabolism contribute to infrequently-feeding amphibians and reptiles experiencing larger factorial scopes of $\dot{V}_{O_2}$ and greater overall SDA than frequently-feeding species. First, infrequent feeders appear to possess lower SMR (relative to body mass) than frequent feeders. For eight snakes previously studied, the SMR of the infrequent feeders was significantly less (by an average of 55%) than the SMR of the frequent feeders (Secor and Diamond, 2000). Secondly, infrequent feeders normally experience higher rates of $\dot{V}_{O_2}$ during digestion (for a given meal size) than frequent feeders (Secor and Diamond, 2000). Understandably, more energy is expended to up-regulate a dormant gut than a gut that has maintained its activity and structure. While the specific costs of gut up-regulation have not been quantified, it is presumed that there is an added cost in producing and secreting gastric acid and digestive enzymes, in up-regulating intestinal nutrient transporters, and in growing new tissue from a down-regulated dormant gut.

The dichotomy in the magnitude of postprandial gut up-regulation among frequently and infrequently feeding amphibians and reptiles is largely generated by infrequent feeders' low rates of transport capacities during fasting. During fasting, infrequently-feeding snakes and frogs possess intestinal uptake capacities that are 11–50% of those of frequently-feeding snakes and frogs (Secor and Diamond, 2000; S. Secor and J. Diamond, unpublished observation). Apparently the distinct feature among infrequently-feeding snakes and frogs (*Ceratophrys* and *Pyxicephalus*) is the functional down-regulation and atrophy of their intestines upon the completion of digestion. This sets the stage for their dramatic up-regulation of intestinal uptake capacity which includes a doubling of intestinal mass and a 3- to 10-fold increase in the activities of intestinal nutrient transporters (Secor and Diamond, 2000). Frequent feeders maintain elevated gut activity following the completion of digestion and therefore, experience only minor increases in uptake capacities with feeding. The increases that they do experience are largely the result of an increase in intestinal mass, whereas any increase in nutrient transporter activities is typically non-significant.

For amphibians and reptiles the regulation of digestive response may only be adaptive when occurring with another trait. A common thread that binds all of these species is their relatively low rate of energy expenditure compared to endotherms (Pough, 1983). Therefore, the possession of a relatively small energy budget may be a necessary prerequisite of evolving a lifestyle that can include long periods of digestive quiescence and hence, the capacity to widely regulate gut performance. For these low-energy species it is envisioned that a valuable component of their daily energy expenditure is devoted to tissue maintenance. The down-regulation of an unused tissue at appropriate times, such as the gut during extended bouts of fasting, would allow a significant amount of energy to be saved and thus, become available for activity, growth, and reproduction. In contrast, for animals with high energy requirements (birds and mammals), fasts are relatively short and any energy saved from a down-regulated gut may be insignificant compared to the cost of their other physiological systems and processes (i.e. thermoregulation, cellular ion exchange, activity, etc), thereby reducing any adaptive incentive to down-regulate tissues. Therefore, an adaptive capacity to widely regulate gut performance may only exist among low-energy species (i.e. ectotherms) and be excluded from endotherms. Of course, the argument could be made for an extension of an adaptive down-regulation of the gut to hibernating birds and mammals. Hibernation, and thus, fasting is characterized by atrophy of the gut as exemplified by an 80% reduction in intestinal mucosal mass experienced by hibernating 13-lined ground squirrels (Carey, 1990). Such a response would similarly provide the benefits of reducing maintenance costs during an extended period of digestive quiescence.

4.2. Caveats of the hypothesis

Any proposal that a trait has evolved as an adaptation is bound to be met with an air of skepticism (Gould and Lewontin, 1978). There are three potential sources (data, phylogeny, and target of selection) of concern regarding the hypothesis that regulation of gastrointestinal performance is adaptive. The first concern is the data at hand and its treatment. Obviously feeding habits of animals are not dichotomized simply as frequent and infrequent feeding, but rather exist along a continuum of feeding frequencies. By dichotomizing these species either as 'frequent feeders' or 'infrequent feeders' (the ends of the

continuum), rather than assigning them along a continuum of feeding frequencies, the strength of any correlated trends may be underestimated. This approach was taken in order to establish two distinct feeding regimes that would facilitate the analysis of the variation in digestive responses.

Another potential concern is the variation in relative meal sizes (5–25% of body mass) among species analyzed. It was felt that if the intestine was going to significantly up-regulate performance, it would do so in response to a large digestive load; therefore, each individual was fed a large meal (relative for that species) in an attempt to generate intestinal up-regulation (if it was to occur). For some species, a meal equal to 5% of body mass is a large meal when given the opportunity to feed ad libitum, whereas for other species, a large meal is one equivalent to 25% or more of body mass. Intraspecifically, meal size can be an important determinate of SDA parameters (Andrade et al., 1997; Secor and Diamond, 1997), therefore suggesting that the variation in meal size may partially explain the interspecific dichotomy in metabolic response as presented earlier. Although this is quite possible, the dichotomy in the metabolic response is obvious among frequently and infrequently-feeding snakes digesting meals equaling 25% of body mass.

A second pitfall stems from the fact that among the presented taxa, closely-related species share more recent evolutionary histories and thus, more traits in common than distantly-related species. Feeding habits, for example, tend to be conserved within a taxa, therefore implying that the mode of digestive physiology expressed is potentially pre-determined phylogenetically. The question that arises is: What component of the relationship between digestive response and feeding habits is due to phylogeny and what component is due to an adaptive phenomena? Previously, a significant correlation was reported for eight snake species between feeding intervals and the magnitude of postprandial responses conducted using a phylogenetic independent contrast analysis, thus implying that the relationship was independent of phylogeny (Secor and Diamond, 2000). No attempt was made to undertake a similar phylogenetic analysis to include all species of this study due to the historical breadth of anurans, salamanders, turtles, lizards, and snakes and to the bias in the number of frequent feeders compared to infrequent feeders. Certainly, the future addition of more species (especially infrequent feeders) and the employment of a phylogenetic analysis would resolve the question of 'Is it phylogeny or adaptation'?

Thirdly, digestion involves a very integrative and complex set of processes. For example, the up-regulation of intestinal nutrient uptake capacity includes at least, a cascade of transcriptional and/or translational events, cellular positioning of membrane transporters, hypertrophy of intestinal epithelial cells, and the possible lengthening of intestinal microvilli; therefore, it is difficult to identify the specific characters of digestion that underlie the proposed adaptive response. Unknown in this scenario is the target(s) of selection: Is it a single trait, a small set of traits, or a suite of interlinked traits? Also, those traits which are linked phenotypically to adaptive traits and thus, are simply 'hitching a ride' in the course of evolution have not yet been identified. Conceivably, selection is acting upon those traits which have the biggest impact on energy conservation and performance, possibly including transporter activities and cellular growth.

4.3. Future tests of hypothesis

Whereas the actions of natural selection in the evolutionary development of digestive physiology can not be directly demonstrated or tested, the continued collecting of more data shall serve in elucidating the presence or absence of a causal relationship between feeding habits and digestive response. Drawing from aforementioned caveats, the following areas of future study are suggested.

4.3.1. Comparative studies that reduce the confounding influence of phylogeny

In the Secor and Diamond (2000) study on snakes, four snake families were represented, but all frequent feeders were of the single family Colubridae, thus introducing potential phylogenetic bias (resolved in that study with phylogenetic analysis). Ideally, intrafamiliar comparisons between frequent and infrequent feeders would be preferable in the testing of the proposed hypothesis. Such natural comparisons do exist. For example: (1) within the snake family Elapidae there are many frequently-feeding species and the infrequently-feeding death adder *Acanthophis* (Shine, 1991); (2) among varanid lizards which range from small frequently-feeding species to

large species that routinely experience long fasting bouts (King and Green, 1999); and (3) frogs of the family Ranidae and Leptodactylidae, each possessing frequently-feeding species and species that estivate without eating for months during the dry season (Duellman and Trueb, 1986).

4.3.2. Using known feeding and fasting habits of fishes, birds, and mammals to further test the hypothesis

Predictions of the regulatory response of digestive performance can be drawn and tested for animals with known feeding habits. Besides amphibians and reptiles, the feeding habits of fishes also vary greatly from species that feed frequently on small meals to infrequently-feeding abyssal fishes that consume meals exceeding their own size (Moyle and Cech, 1988). In contrast to the characteristic frequent feeding by endotherms, relatively long periods of fasting are experienced by egg-brooding penguins, weaned elephant seals, migrating birds, and several large carnivores that periodically gorge themselves on large meals (Mech, 1970; Schaller, 1972; Reiter et al., 1978; Biebach, 1990; Williams, 1995). Examining the physiological responses to fasting and re-feeding among other taxa with documented feeding and fasting regimes can support or refute the hypothesis of an adaptive response of digestive performance.

4.3.3. Measure other potentially selective traits of digestion and metabolism

To date, only the response of intestinal nutrient uptake capacity and whole-animal metabolism to digestion and fasting has been investigated. The former response is a direct indicator of a potentially adaptive phenomena, whereas the latter is simply a consequence of the magnitude of the former response. Studies that would be fruitful in supporting and explaining the adaptive hypothesis include; comparing the underlying molecular mechanisms (potentially the target of selection) of intestinal down and up-regulation between frequent and infrequent feeders and measuring the response of other organ systems that are functionally and energetically coupled to digestion. Previously found among infrequently-feeding snakes were significant post-feeding increases in stomach, pancreas, liver, and kidney masses and a reciprocal decrease in the masses of

these organs with fasting, indicative of a more integrated response.

4.3.4. Cost of maintaining and regulating the gut

The hypothesis of an adaptive digestive response is founded on the selective incentive of conserving energy by either maintaining digestive performance for frequent feeders or regulating gut performance for infrequent feeders. Whereas the models (Fig. 1) suggest an energetic advantage of each digestive physiology, the specific cost of intestinal up-regulation, which includes the activation of nutrient transporters, the production of enzymes, and cellular hypertrophy, has not been quantified, nor was the specific cost involved in the constant maintenance of intestinal function. Indeed, these measurements would serve to determine if there is a strong energetic foundation for the divergence of digestive physiology.

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