ECOLOGICAL CONSTRAINTS ON FEEDING AND GROWTH OF *SCAPHIOPUS COUCHII*

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The ecology of the desert toad, *Scaphiopus couchii*, is very precisely regulated by summer rainfall, such that emergence may be less than 20 nights/year. There are estimates in the literature that, at best, *S. couchii* can obtain its entire annual energy requirement from a single, very large meal, comprising of 50% its body weight in lipid-rich termites. However, our field data from the San Simon Valley in southeast Arizona, show that the toads are generalist feeders, taking prey groups which appear in sequence during the short summer season, including a remarkable range of noxious animals (solpugids, scorpions, centipedes and pogonomyrmid ants). Alate termites emerged briefly after the first rains and seldom represented a major component of the diet. On the other hand, beetles and other hard-bodied insects formed a consistent food type throughout the season. Alate termites represented around 24% of the total food items ingested by *S. couchii* and when prey size (length) was taken into account their contribution to the annual intake was around 20%. Beetles, on the other hand, contributed (by size) around 33% to intake, with ants representing around 19% and all other items each representing less than 8%. Differences in prey type, total food ingested and temperature all significantly influenced the weight change of individual toads fed under controlled laboratory conditions. Animals which were fed more frequently grew more rapidly, since weight increases were correlated with food intake. However, for any given intake, increases in weight were significantly lower at high environmental temperatures (31-33°C compared with 20-24°C), presumably due to increasing metabolic demands with temperature. The nutritional quality of the food significantly influenced body weight change and fat body accumulation: toads amassed excessively large fat bodies (representing up to 14% body weight) when fed with lipid-rich mealworms, compared with those fed crickets (fat bodies up to 10% body weight), and toads fed woodlice had virtually no fat bodies after eating an equivalent number of meals. These studies show that the natural prey range of *S. couchii* varies in time and space, and when toads consume high energy foods, weight increase and fat deposition are very efficient. However, the frequent ingestion of other foodstuffs, lower in calorific value, suggests that a greater number of meals are necessary to accumulate the total annual energy requirement. These other prey items may provide essential nutrients that are lacking from lipid-rich foods.

INTRODUCTION

The desert toad, *Scaphiopus couchii*, inhabits some of the most inhospitably-arid regions of America (Mayhew, 1965). In order to survive here, the toads show remarkable behavioural and physiological adaptations to an extreme environment. They escape the hostile conditions for around 10 months of the year by burrowing up to a metre beneath the ground and accumulate tissue urea to increase osmotic potential (McClanahan, 1967; Shoemaker, McClanahan & Ruibal, 1969; Ruibal, Tevis & Roig, 1969). During hibernation, they do not feed and rely wholly on stored energy reserves for survival. Activity is associated with summer monsoons and rainfall is the key factor correlated with emergence (Mayhew, 1965; Ruibal *et al.*, 1969), but temperature is also important: in parts of California where winter rains occur, *Scaphiopus* does not emerge if temperatures are below 10°C (Mayhew, 1962). At summer temperatures, activity sometimes follows light rains which only dampen the soil surface and this may occur several weeks prior to the arrival of

torrential rainfall which typically stimulates breeding (Ruibal *et al.*,1969). Moisture in itself does not stimulate arousal of hibernating toads but the key factor for their emergence is the low frequency vibrations of rainfall on the soil surface (Dimmitt & Ruibal, 1980a). Thus, the toads are able to emerge before the surface water has penetrated the desert soil. Breeding occurs in temporary pools formed from run-off and this is the only time the toads enter large water bodies (Bragg, 1967). In southeastern Arizona, USA, the rains occur fairly predictably each year in July and August (Chew, unpublished; Tocque & Tinsley, 1991).

During the activity season, the toads occupy shallow temporary burrows in the daytime and emerge on damp nights to forage on desert invertebrates (Ruibal *et al.*, 1969; Dimmitt & Ruibal, 1980a). Breeding and feeding must take place while environmental conditions are favourable for nocturnal emergence and before the return of harsh conditions, when the toads re-enter hibernation. The amount and frequency of rainfall varies from year to year (Tinsley & Tocque, 1995) and

Tinsley (1990) estimated that in southeastern Arizona the toads have a maximum of 20 nights in the year when conditions are suitable for foraging. These environmental constraints severely restrict the period for resource accumulation and growth in desert anurans. *Scaphiopus* typically emerges to feed after long periods of dormancy and starvation. The depletion of stored reserves during hibernation is reflected by the fact that the majority of toads have virtually no fat bodies upon emergence (Seymour, 1973; Tocque, 1993). Nevertheless, a previous study (Dimmitt & Ruibal, 1980b) has determined that the feeding ecology of *Scaphiopus couchii* may be so efficient that the toads can survive one year on a single, albeit very large, meal equalling 55% of the toad's body weight and consisting solely of lipid-rich alate termites. A more realistic estimate was that a toad eating meals of half termites and half beetles, corresponding to 29% its body weight, needed just 2-3 meals to provide the total annual energy requirements.

The present studies were carried out during long-term research on the ecology and parasitology of *Scaphiopus couchii,* in a region of Chihuahuan desert scrub in southwestern Arizona, USA (Tinsley, 1990, 1993; Tocque, 1993; Tinsley & Tocque, 1995 and references therein). The aims were to estimate the overall contribution of alate termites to the toads' annual intake and to measure the effects of different food types and environmental conditions on resource accumulation. This involved analysis of gut contents throughout the entire feeding season and laboratory studies recording the voluntary intake of toads and their growth under different feeding and temperature regimes.

MATERIALS AND METHODS

NATURAL PREY RANGE

Fieldwork was carried out during 1990 and 1991 in one area of the San Simon Valley in southeastern Arizona described by Tinsley & Jackson (1988). Frequent rainstorms occurred throughout July and much of August in both these years, providing ideal circumstances for foraging by desert amphibians. Animals were collected from the desert surface on nightly excursions, along transects covering approximately 50 km. However, in 1990, collections of juvenile toads in particular were concentrated along one stretch of road running from the Arizona / New Mexico border to Portal. After capture, the toads were transferred to the Southwestern Research Station during the same night and maintained in soil-filled terraria. The following day, animals were either dissected (as part of ecological and parasitological studies; e.g. Tocque, 1993; Tinsley & Tocque, 1995) or their stomachs were 'flushed' with water until a food bolus was regurgitated. The stomach contents were weighed and preserved in 70% alcohol until prey items could be analysed. The individual items were identified with the aid of field guides (White, 1983; Borro & White, 1970) and museum specimens of the Southwestern Research Station, and were assigned to size classes based on body length.

LABORATORY FEEDING EXPERIMENTS

Animals collected in the San Simon Valley were transported to the UK by air freight during August and were maintained in soil-filled terraria at relatively low temperatures (15-20°C) until the start of feeding experiments. Prior to feeding, the toads were weighed (after removal of urine by catheter) and randomly assigned to different groups (see below and Table 3). Each toad was maintained individually in a plastic tube partially filled with moist soil and with a perforated base to allow water uptake (Tinsley & Earle, 1983) and moved to a controlled environment room two days before feeding commenced. Groups of toads were fed according to the following regimes :

Experiment 1 : The effect of temperature. Male and female toads were maintained at either 20 or 33°C and fed with laboratory-raised crickets approximately every three days (a total of 16 meals in 51 days).

Experiment 2 : The effects of temperature and feeding rate. Male and female toads were maintained at either 24 or 31°C and fed with laboratory-raised crickets, either once a week (a total of 6 meals in 42 days) or four times a week (a total of 24 meals in 42 days).

Experiment 3 : The effect of food quality. Male and female toads were maintained at 25°C and fed with either laboratory-raised crickets or mealworms or wild-caught woodlice every other day (a total of 28 meals in 56 days).

At each feeding session, individual toads were removed from their soil-filled tubes and transferred to plastic aquaria (50 x 60 x 80 cm), with a number of pre-weighed food items. The animals were then left to feed at their maintenance temperature under lighted conditions (with the exception of animals at 31°C in Experiment 2, which were fed in the dark) for two hours. After this time, the toads were washed to remove any urine, which otherwise burns the delicate skin, returned to their individual tubes and remained undisturbed until their next feed. The food items remaining in each aquarium were recovered and re-weighed to determine the amount eaten by each animal. Several days after the end of the feeding period, each toad was weighed and animals from Experiment 3 were dissected after a further two weeks (during which they were maintained at 10-15°C) to determine fat body weights.

RESULTS

PREY SELECTION IN THE DESERT ENVIRONMENT

The range of prey items found in the combined sample of stomach contents from 158 animals collected in 1990 and 1991 shows the opportunistic nature of *S. couchii* feeding (Table 1). The toads were typically generalist insectivores with a wide range of genera ingested but arachnids were also a major food source.

TABLE 1. The total contribution of different prey types to the nutrition of *Scaphiopus couchii* during the entire feeding season (data collected in July/August, 1990 and 1991).

Prey item Order & Family	Common name used in text	% of total food items ($n = 2180$)	% toads eating item ($n=158$)	Mean No. items ingested	Mean length of food item (cm)	[a]Relative contribution to annual intake (%)
Insecta						
Coleoptera:	Beetles:					
Carabidae	Ground	0.83	8.23	1.38	0.75	0.82
Cicindelidae	Tiger	0.05	0.63	1.00	0.75	0.05
Curculionidae	Weevil	1.74	17.09	1.41	0.58	1.33
Elateridae	Click	2.71	7.59	4.92	0.77	2.74
Eucnemidae	False-click	0.05	0.63	1.00	0.75	0.05
Scaribidae	Scarab	17.20	59.49	3.99	0.70	15.83
Pairs elytra		11.70	49.37	3.27	0.70	10.78
Unknown		0.83	8.23	1.38	0.90	0.98
Diptera	Flies	0.28	3.80	1.00	0.56	0.20
Hemiptera	Bugs	1.42	17.09	1.15	0.80	1.50
Homoptera	Hoppers	0.32	4.43	1.00	1.00	0.42
Hymenoptera:						
Scolioidae	Ants					
alates		5.92	13.92	5.86	0.78	6.07
workers		5.73	18.35	4.31	0.36	2.72
heads only		11.83	40.51	4.03	[b]0.62	9.66
Apoidae	Bees	0.41	3.80	1.50	0.75	0.41
Isoptera:	Termites					
alates		24.27	8.86	37.79	0.61	19.49
workers		1.51	1.90	11.00	0.25	0.50
Lepidoptera	Caterpillars	2.52	17.72	1.96	1.95	6.47
Neuroptera	Lacewings	0.14	1.90	1.00	1.00	0.18
Orthoptera:						
Gryllidae	Crickets	3.94	37.97	1.43	1.42	7.37
Phasmatidae	Stick-insects	0.55	7.59	1.00	1.25	0.91
Mantidae	Mantids	0.14	1.90	1.00	1.25	0.23
Insect larvae		0.09	1.27	1.00	1.00	0.12
Arachnida						
Araneida	Spiders	1.65	15.19	1.50	0.53	1.15
Acarina	Mites	0.83	5.70	2.00	0.75	0.82
Chelonethida	Pseudoscorpions	0.05	0.63	1.00	0.25	0.02
Phalangida	Harvestmen	0.05	0.63	1.00	0.25	0.02
Scorpionida	Scorpions	0.23	3.16	1.00	2.75	0.83
Solpugida	Solpugids	2.75	29.11	1.00	1.72	6.23
Chilopoda	Centipedes	0.28	3.80	1.00	5.75	2.08
Reptilia						
Teiidae	Whiptail lizard	0.05	0.63	1.00	-	-

[a] calculated from the average length and the relative occurrence of individual food items.
[b] calculated as the average length of all ants

Beetles (scarabs and weevils in particular) formed the most substantial prey and were eaten by 83.3% of toads and represented 35.1% of food items. Ants, Orthoptera (particularly crickets) and solpugids were ingested by 57.9, 44.7 and 29.1% of toads (representing 23.5, 4.6 and 2.8% of food items), respectively. Several other food groups were also eaten by over 15% of toads: these were caterpillars, bugs and spiders. Alate termites were only eaten by 8.9% of toads but they represented 24.3% of food items since they were consumed in large numbers: a maximum of 200 items ingested per animal (average 37.8 termites/toad). Some prey types, such as, worker termites, lacewings, mantids, pseudoscorpions, harvestmen and some beetles were consumed rarely (by less than 2% of toads) which reflected either their low abundance or chance encounters. The most interesting of these occurrences was the ingestion of a hatchling whiptail lizard (*Cnemidophorus* sp.) by one animal. A range of particularly noxious animals was ingested by *S. couchii*, including, solpugids, scorpions, centipedes and pogonomyrmid ants.

From the combined data, the average contribution (by size) of different prey types to the intake of *S. couchii* during the entire feeding season has been estimated (Table 1). In total, beetles represented 32.6%, alate termites 19.5%, ants 18.5%, crickets 7.4%, caterpillars 6.5% and solpugids 6.2% of the overall prey intake.

A total of 81 toads was collected along Portal road throughout July and August, 1990, which provided an indication of the change in prey availability over the entire feeding season (Table 2a,b). The prey types eaten most frequently (scarabs, crickets, ants, spiders, weevils and solpugids) were found consistently throughout the two month feeding season (ingested by at least 55%, 30%, 20%, 13%, 13% and 12.5% of toads, respectively). However, alate termites were confined to the first week following the onset of the summer rains (in the second week of July), when they represented a major food source and were consumed by 33% of toads. Another group of toads ($n = 12$) was also collected in the second week of July, less than 5 km away, but not a single animal had eaten termites. No alate termites were ingested during the subsequent five weeks of *S. couchii* activity. Similarly, alate ants were eaten in abundance following the first rains and decreased dramatically thereafter. Flies, bees, mites, pseudoscorpions and mantids also decreased in occurrence after the first week of rain. By contrast, caterpillars, lacewings and unidentified beetles were ingested in increasing numbers and by a greater proportion of toads as the summer season progressed.

FOOD INTAKE AND GROWTH UNDER LABORATORY CONDITIONS

The effects of varying prey type, as well as feeding rate and temperature, on weight changes and resource accumulation were investigated under controlled laboratory conditions. There was no consistent difference between the intake and weight changes of male and female toads. In some groups, males consumed more and increased in weight more than females and in others the reverse occurred. Therefore, the sexes have been combined for the following analysis (Table 3). The total intake of laboratory-raised crickets increased as the number of meals eaten increased: overall means of 7.8, 21.2, 38.3 and 41.2 g of food were ingested by toads fed 6, 16, 24 and 28 meals, respectively. There was a corresponding increase in the average weight change of the animals with increasing intake : 2.4, 5.2 12.5 and 17.5 g, respectively.

The influence of feeding rate and temperature. In Experiment 2, toads were fed either 6 or 24 times over the same time period. There was little obvious effect of these different feeding rates on the efficiency of food conversion, since animals increased in weight by 1 g after eating around 3.0 and 2.6 g of food, respectively, at 24°C and 3.8 g in both groups at 31°C. However, intake varied considerably between individuals and temperatures. In Experiment 1, the toads fed at 33°C ate more than those fed at 20°C (Table 3) whereas in Experiment 2, the toads ate less at the higher temperature (presumably because they were fed in the dark). Therefore, since toad size varied as well as intake, the efficiency of food conversion at different temperatures was analysed as the relationship between intake and weight change relative to initial body weight (Fig. 1). In both Experiments 1 & 2, for any given intake, toads showed smaller weight increases at the higher temperature. Multiple analyses of covariance (with intake as the covariate), showed that weight changes were significantly different between the temperatures in both experiments ($F = 4.76$, $P < 0.05$ and $F = 8.39$, $P < 0.01$, respectively). The difference between temperatures was more pronounced as the toads ate more. This was especially true in Experiment 2 (Fig. 1b) for which there was no significant difference between weight changes at the different temperatures in toads fed once a week ($F = 0.24$, $P > 0.6$; Fig. 1).

The influence of prey type. Toads fed with mealworms ate around the same weight of food as those fed with crickets over the same period (Experiment 3) but woodlice were not readily eaten by *S. couchii* (see Table 3). Weight changes were slightly greater in toads eating mealworms compared with those eating crickets but there was wide individual variation in intake, such that some toads trebled in weight during the eight week period. The animals eating woodlice did not, on average, increase in weight despite eating a mean of 11.5 g of food (Table 3). In fact, half these toads lost weight during the experiment. The relationship between relative intake and weight change (Fig. 2) shows that mealworms were converted to body weight more efficiently than crickets (MANCOVA: $F = 9.74$, $P < 0.01$) and woodlice provided a very poor diet for the toads compared with crickets (MANCOVA: $F = 10.88$, $P < 0.01$).

TABLE 2 (a). The prey intake of *Scaphiopus couchii* (*n* = 81) collected from Portal Road over the entire feeding season in 1990, represented as the percentages of total prey items eaten.

Prey item		Occurrence of prey (% total prey items)			
		7-13 July (*n* = 766)	14-29 July (*n* = 318)	3-13 Aug (*n* = 123)	14-22 Aug (*n* = 114)
Insecta					
Coleoptera:					
	Carabidae	0.0	0.0	0.81	0.0
	Cicindelidae	0.0	0.31	0.0	0.0
	Curculionidae	0.52	2.2	2.44	7.89
	Elateridae	0.13	15.09	1.63	0.0
	Eucnemidae	.013	0.0	0.0	0.0
	Scaribidae	12.14	31.45	24.39	30.7
	Pairs elytra	2.61	16.35	22.76	16.67
	Unknown	0.0	0.63	3.25	3.51
Diptera		0.39	0.31	0.0	0.0
Hemiptera		0.52	3.14	2.44	0.88
Homoptera		0.26	0.0	1.63	1.75
Hymenoptera:					
	Scolioidae				
	alates	15.14	0.31	0.0	0.0
	workers	2.87	5.98	2.44	3.5
	heads only	18.54	7.86	4.88	3.51
	Apoidae	0.91	0.0	0.0	0.0
Isoptera:					
	alates	32.25	0.0	0.0	0.0
	workers	3.79	0.0	0.0	3.51
Lepidoptera		0.26	6.6	11.38	10.53
Neuroptera		0.0	0.0	0.81	1.75
Orthoptera:					
	Gryllidae	1.31	3.14	6.5	7.89
	Phasmatidae	0.13	0.63	0.0	0.0
	Mantidae	0.26	0.31	0.0	0.0
Insect larvae		0.0	0.0	0.81	0.88
Arachnida					
Araneida		1.83	1.89	4.88	1.75
Acarina		1.83	0.0	0.0	0.0
Chelonethida		0.13	0.0	0.0	0.0
Scorpionida		0.0	0.63	0.81	0.0
Solpugida		0.91	3.14	7.32	5.26
Chilopoda		0.13	0.0	0.81	0.0

Accumulation of stored reserves. Animals from Experiment 3 were dissected to determine the weight of fat body accumulated after feeding with different food types. Despite the fact that toads ate, on average, similar weights of crickets and mealworms (Table 3), the fat bodies of those fed mealworms were considerably heavier (Table 4): animals eating crickets had fat bodies weighing to up to almost 10% of their body weight but those fed lipid-rich mealworms had fat bodies weighing up to 14% of their body weight. The amount of fat body amassed was positively correlated with intake (R^2 = 0.69, F = 15.4, P < 0.01 and R^2 = 0.59, F = 7.10, P < 0.05, for crickets and mealworms, respectively) but the efficiency of fat accumulation was almost three times greater in toads eating mealworms compared with those eating crickets (Table 4). Toads eating woodlice did not accumulate fat and probably utilised previously stored fat body during the experiment.

TABLE 2 (b). The prey intake of *Scaphiopus couchii* collected from Portal Road over the entire feeding season in 1990, represented as the percentages of toads ingesting each prey item.

Prey item		Occurrence of prey (% toads eating each item)			
		7-13 July ($n = 24$)	14-29 July ($n = 23$)	3-13 Aug ($n = 20$)	14-22 Aug ($n = 14$)
Insecta					
Coleoptera:					
	Carabidae	0.0	0.0	5.0	0.0
	Cicindelidae	0.0	4.4	0.0	0.0
	Curculionidae	12.5	26.1	15.0	28.6
	Elateridae	4.2	17.4	10.0	0.0
	Eucnemidae	4.2	0.0	0.0	0.0
	Scaribidae	75.0	91.3	55.0	71.4
	Pairs elytra	45.8	78.3	40.0	50.0
	Unknown	0.0	8.7	10.0	14.3
Diptera		12.5	4.4	0.0	0.0
Hemiptera		16.7	39.1	10.0	7.1
Homoptera		8.3	0.0	10.0	14.3
Hymenoptera:					
	Scolioidae				
	alates	66.7	4.4	0.0	0.0
	workers	45.8	21.7	10.0	21.4
	heads only	62.5	52.7	20.0	28.6
	Apoidae	16.7	0.0	0.0	0.0
Isoptera:					
	alates	33.3	0.0	0.0	0.0
	workers	8.3	0.0	0.0	7.1
Lepidoptera		8.3	21.7	50.0	35.7
Neuroptera		0.0	0.0	5.0	14.3
Orthoptera:					
	Gryllidae	41.7	30.4	30.0	50.0
	Phasmatidae	4.2	8.7	0.0	0.0
	Mantidae	8.3	4.4	0.0	0.0
Insect larvae		0.0	0.0	5.0	7.1
Arachnida					
Araneida		41.7	13.0	20.0	14.3
Acarina		29.2	0.0	0.0	0.0
Chelonethida		4.2	0.0	0.0	0.0
Scorpionida		0.0	8.7	5.0	0.0
Solpugida		12.5	39.1	35.0	21.4
Chilopoda		4.2	0	5	0

DISCUSSION

For any terrestrial amphibian, activity and foraging take place only when environmental conditions are suitable: generally when it is wet and warm enough for emergence (Poynton & Pritchard, 1976; Toft, 1980; Galatti, 1992). For a desert anuran, such as *Scaphiopus couchii,* the occurrence of these conditions is more limited than for most other amphibians. It has already been determined that *S. couchii* ingests a wide range of invertebrate prey but takes advantage of the mass emergence of alate termites, enabling efficient accumulation of lipid reserves (Dimmitt & Ruibal, 1980*b*). Our data confirm the generalist nature of *S. couchii* feeding patterns, with a wide range of prey types being ingested (Table 1). However, the collection of gut contents throughout the entire feeding season has shown that the prey ingested varies throughout the activity season, presumably reflecting variations in invertebrate abundance. Some prey types were eaten consistently throughout the two month feeding season (scarabs, crickets, ants, spiders, weevils and solpugids)

TABLE 3. Food intake and weight changes of *Scaphiopus couchii* maintained at different temperatures and feeding regimes. Values show means (with standard deviation in parentheses) and range for percent weight change.

Expt. No.	n	Total No.of meals	Duration of feeding (days)	[a]Food type	°C	Starting body weight (g)	Total weight of food eaten (g)	Change in body weight (g)	Percent weight change (%)
1	8	16	51	Cr	20	21.9 (6.2)	24.3 (10.6)	5.3 (2.8)	9-38
	8	16	51	Cr	33	22.6 (6.6)	28.8 (12.5)	6.2 (3.4)	13-60
2	10	24	42	Cr	24	20.3 (4.2)	41.8 (12.8)	15.9 (5.7)	43-123
	10	24	42	Cr	31	21.7 (5.2)	34.9 (9.5)	9.2 (2.7)	31-58
	10	6	42	Cr	24	21.2 (4.0)	8.8 (5.0)	2.9 (3.1)	-12-37
	10	6	42	Cr	31	24.7 (6.6)	6.9 (3.7)	1.8 (2.0)	1-33
3	9	28	56	Cr	25	21.0 (6.8)	41.2 (15.5)	17.5 (6.8)	25-204
	8	28	56	Mw	25	21.1 (4.5)	43.0 (14.9)	24.9 (9.4)	63-217
	6	28	56	Wl	25	21.8 (6.8)	11.5 (6.0)	0.3 (2.9)	-14-30

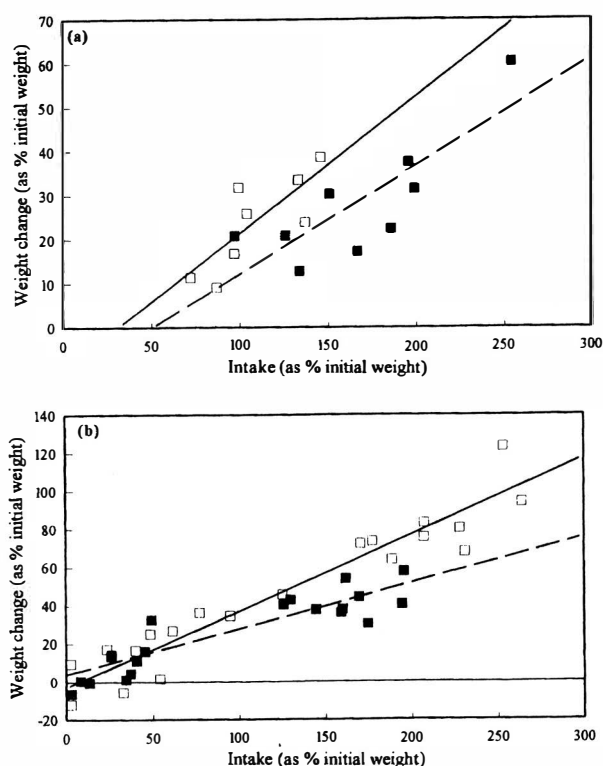[a] Cr = crickets; Mw = mealworms; Wl = woodlice

FIG. 1. The effect of temperature on the weight change of *Scaphiopus couchii* fed (a) 16 meals in 51 days at 20°C (open squares, solid line $R^2 = 0.94$, $F = 103$, $P < 0.001$) or 33°C (filled squares, dashed line $R^2 = 0.92$, $F = 97.6$, $P < 0.001$) and (b) 6* or 24 meals in 42 days at 24°C (open squares, solid line $R^2 = 0.91$, $F = 173$, $P < 0.001$) or 31°C (filled squares, dashed line $R^2 = 0.65$, $F = 32.7$, $P < 0.001$). * toads fed 6 meals consumed equivalent to less than 100% their body weight.
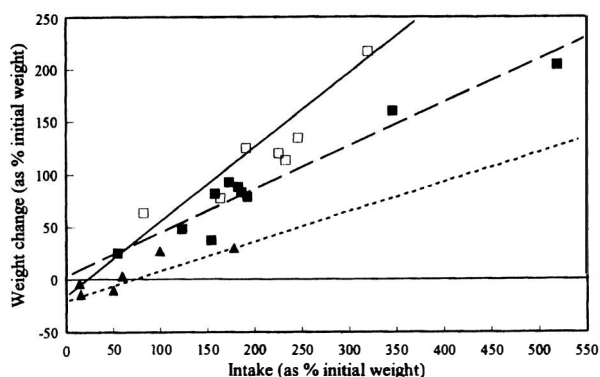

FIG. 2. The effect of food quality on the weight change of *Scaphiopus couchii* fed with crickets (open squares, solid line $R^2 = 0.98$, $F = 494$, $P < 0.001$), mealworms (filled squares, dashed line $R^2 = 0.98$, $F = 293$, $P < 0.001$) or woodlice (filled triangles, dotted line $R^2 = 0.59$, $F = 7.3$, $P < 0.05$) at 25°C.

but others increased in abundance with time (caterpillars, lacewings and unidentified beetles); and some were present only after the first rains and decreased dramatically afterwards (alate ants, mites, bees, pseudoscorpions and mantids). This was also true for alate termites which were ingested only in the second week of July in 1990 and not at all in the following 5 weeks of toad activity.

The opportunities for feeding on high energy foodstuffs are a direct result of localised thunderstorms which stimulate insect reproductive flights: both temporal and spatial constraints influence the ingestion of alate termites by *S. couchii*. Thus, the toads cannot rely on the presence of such prey items to ensure that they eat a few high energy meals. Harder-bodied inver-

TABLE 4. Variation in fat body accumulation by *Scaphiopus couchii* fed with different food types.

Food Type	N°of meals	Duration of feeding (days)	°C	Intake (as % of initial body weight)	Fat body weight (as % of final body weight)	[a] Mean fat body accumulation efficiency (%)
Crickets (n = 9)	28	56	25	54 - 519	2.6 - 9.8	3.7
Mealworms (n = 9)	28	56	25	82 - 320	6.1 - 14.2	10.6
Woodlice (n = 5)	28	56	25	14 - 178	0.02 - 0.09	0.2

[a] calculated as fat body weight (g) as a percentage of intake (g)

tebrate prey (particularly beetles but also ants, crickets and solpugids) are more reliable in occurrence throughout the summer but these represent an inferior energy source (Dimmitt & Ruibal, 1980b). The toads may ingest one or two meals composed of large numbers of alate termites in the first week of the summer season but thereafter intake consists of foodstuffs with lower calorific values. Over the entire feeding period, alate termites represented around 24% of the total number of food items ingested. Given their smaller size, compared with beetles and crickets for instance, their actual contribution to nutrition may be less than this. Based on prey length, it is estimated that alate termites contribute 19.5% to the entire annual intake of *S. couchii*, with beetles, ants, crickets, caterpillars and solpugids contributing 32.6, 18.5, 7.4, 6.5 and 6.2%, respectively. However, the calorific and nutritive value of the different prey cannot be determined from the present study. The occurrence and distribution of termite swarms is likely to vary from year to year since environmental conditions promoting their, and other invertebrate, emergence also vary considerably from year to year (Tinsley & Tocque, 1995). These annual variations are also evident in the natural growth patterns of *S. couchii*, presumably because of variations in prey abundance and foraging opportunities (Tocque & Tinsley, submitted).

Varying the quality of prey items significantly influenced resource accumulation by *S. couchii* under controlled laboratory conditions, as did varying environmental temperature. However, the efficiency with which food was converted to body weight seemed to be regardless of feeding rate, since weight changes were proportional to total food intake whether toads were fed once or four times a week. The fact that there was a significant decrease in weight changes as temperature increased is to be expected for an amphibian in which the metabolic rate increases with environmental temperature (McClanahan, 1967; Seymour, 1973). Presumably a greater proportion of absorbed energy is utilised for maintenance at higher temperatures (31-33°C) than at lower temperatures (20-24°C). Bush (1963) found that *Bufo fowleri* did not amass more lip-

id at 31°C compared with 21°C but did convert more food to lean tissue. It seems unlikely that this was the case for *S. couchii*, since the conversion of food to body weight was significantly lower at higher temperatures than at lower temperatures (Fig. 1). In the present study, animals were continuously maintained at the same temperature during the feeding period but under natural conditions the toads feed at cooler night time temperatures (average 20°C) and remain in temporary burrows during higher daytime temperatures (average 34°C) (Ruibal et al., 1969; Tocque & Tinsley, 1991). It is not known how fluctuating daily temperatures would affect metabolic energy demands, digestion efficiency or resource accumulation.

By far the greatest influence on weight changes and the accumulation of fat bodies, was the type of the food ingested. Toads fed crickets and mealworms, at 25°C, ate similar amounts of food but weight increases were greater in animals fed mealworms, and fat body was amassed three times more efficiently than by toads eating crickets. Woodlice, on the other hand, proved to be an inferior food source: animals eating them did not increase in weight and virtually no fat was accumulated. A similar relationship between food quality and weight change has been observed in juvenile *Bufo woodhousei*, for which lipid-rich mealworms produced the greatest growth (Claussen & Layne, 1983). In juvenile *B. bufo*, feeding with mealworms leads to excessive fatness since lipid deposition predominates over protein deposition (Jørgensen, 1989). The lipid content (wet weight) of mealworms may be as high as 16% compared with 10-11% in crickets and beetles (Dimmitt & Ruibal, 1980b). However, mealworms are known to be low in digestible calcium (Mattison, 1993). Fat reserves, which provide all the energetic needs of spadefoot toads during their long hibernation (Seymour, 1973, Dimmitt & Ruibal, 1980b), may be accumulated more effectively when the toads feed on lipid-rich food but it is not known how a nutrient imbalance may adversely effect the growth of other tissues, such as gonad or bone.

The desert environment provides only a short summer season during which conditions are suitable for

Scaphiopus couchii activity and feeding. Erratic environmental conditions during this period limit the occurrence of high energy foodstuffs in both time and space and other harder-bodied prey are ingested consistently throughout the feeding season. The toads show an exceptional ability to accumulate their annual energetic reserves in the form of excessively large fat bodies when ingesting lipid-rich foods. However, the opportunistic nature of feeding and the ingestion of a large variety of prey is likely to provide other essential nutrients which may be lacking from a diet restricted to alate termites.

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