

A test of optimal foraging and the effects of predator experience in the lizards *Sceloporus jarrovii* and *Sceloporus virgatus*

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Summary

Foraging efficiency of predators can be evaluated by using optimality or profitability models which incorporate prey choice, handling time and pursuit or search time. Optimality of a diet could vary based on the age, sex, size, predation risk, or foraging experience of the predator. This study tested the effects of a predator's age and foraging experience by observing prey capture attempts and success rate, and by calculating diet profitability for adult and neonate *Sceloporus jarrovii* and adult *Sceloporus virgatus*. Prey availability was assessed in order to determine prey preference and profitability. Neonates showed an increased number of prey capture attempts, but success rate was similar for neonates and adults of both species. Total diet profitability of neonates was lower than adults of either species, which could be a result of poor prey choice or gape limitation (although body size showed no direct effect). Overall, the diets of all three groups were less profitable than would be expected based on the types of prey in the environment, although this is likely due to low availability (from the lizard's perspective) of highly profitable items. Lizards seem to be eating prey items in the same proportion as they are found in the environment.

Keywords: optimal foraging, predator experience, prey choice, neonate, *Sceloporus*.

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Introduction

Optimal foraging theory

The Optimal Foraging Theory states that given a diverse selection in prey choice, a predator will spend minimal energy capturing prey to maximize nutritional intake over time. When an organism has a high level of food intake based on a highly efficient foraging strategy (such that intake exceeds metabolism) it will receive rewards to its fitness: an increase in weight or nutritional reserves in breeding adults, which may lead to increases in clutch size, egg or offspring size, or offspring fitness. Therefore, high-foraging efficiency, or optimal foraging, has a long-term selective advantage; those organisms that live longer and are healthier due to good foraging practices will have increased fitness (Emlen, 1968; Schoener, 1971). When prey densities are low, predators must spend an increased amount of time foraging, which may require higher energy expenditure, which in turn requires more energy intake (Norberg, 1977).

Natural selection is expected to act on all of the following factors in order to result in a highly efficient, or optimal, foraging strategy: search time, pursuit time, handling time and prey choice. However, optimal foraging strategies are only needed in an organism if there are costs to sub-optimal foraging. Potential costs to inefficient foraging are increased vulnerability to predators (Downes, 2001), decreased time and energy available for reproduction (Schoener, 1971), or the loss of available time to eat a highly valuable prey item when the time was spent eating a low value prey item instead (Schoener, 1974). Organisms may choose food based on high biomass per unit time, caloric value, nutritional value, or ease of capture and handling in order to maximize efficiency (Schoener, 1971).

Prey preference is observed when predators deviate from random sampling, which could be caused by active choice, non-random prey distribution in space and time, prey escape, and predator satiation level (Chesson, 1978). Emlen (1966) and Schoener (1971) suggested that there are a number of assessments that can be used to predict prey choice. If prey densities are high and prey with high caloric values are abundant, predators should be specialists. As high value prey become more scarce, predators should shift toward generalist feeding behaviour, eating nearly all prey items encountered, in order to maximize total food intake and efficiency (Emlen, 1966, 1968; Schoener, 1971, 1974; Estabrook & Dunham, 1976; Chesson, 1983). If the

cost of eating a prey item is less than that of waiting and eating nothing, then the predator should eat any prey item encountered (Schoener, 1974).

It is important to note that predator choice readily change based on environmental fluctuations in relative abundances of various prey (Emlen, 1966). Once the high value prey item increases in relative abundance in the environment, predators should switch back to being specialists on the high value prey item (Chesson, 1983). In addition, a satiated predator should behave more as a specialist than a starved predator (Emlen, 1966). Natural selection should favor an increase in specialization unless environmental heterogeneity (spatially or temporally) encourages long-term generalization if high-quality resources are readily available (Emlen, 1968).

Optimal foraging models all assume that predators are capable of making optimal decisions while foraging (Marten, 1973). Thus, an optimally foraging predator must be capable of determining nutritional value of its various prey, as well as their relative abundances. These skills are not necessarily inherent in a vertebrate predator, but may have to be learned over time (Jaeger & Rubin, 1982; Roughgarden, 1995). Predatory learning at an early age has lasting effects on food choice later in life (Punzo, 2003). In addition, pursuit time and prey capture success rate may be dependent on predatory experience, prey size, mobility and density (Schoener, 1971; Eifler & Passek, 2000). Handling time and technique may also vary based on the age of a predator because handling and foraging efficiency increase with experience (O'Connell & Formanowicz, 1998; Krause, 2001). Lack of predatory experience may then result in decreased energetic or caloric intake which could lead to a decrease in fitness or juvenile survivorship (Paulissen, 1987).

A test of optimal foraging

Two diurnal, insectivorous lizard species, *Sceloporus jarrovi* (Yarrow's Spiny lizard) and *Sceloporus virgatus* (the Striped Plateau lizard), were studied to test foraging differences between different age and size classes. These lizards work as ideal models in this situation because they are ambush predators of varying sizes and ages, but still have a high degree of diet similarity and are present in the same habitat (Watters, 2008, 2009). Adult *S. jarrovi* are much larger (70.6 ± 8.2 snout vent length (SVL)) than neonates of the same species (29.9 ± 4.5 SVL), whereas adult *S. virgatus* are intermediate in size (50.6 ± 6.4 SVL) between the two age classes of *S. jarrovi* (Watters,

2006). By incorporating both species in the study I aimed to tease apart those differences in foraging and prey choice that are based on age and experience rather than size differences among lizards.

This study addressed a variety of questions, based on the premise that neonates are less experienced predators. In general, if there were costs to inefficient foraging for natural selection to act upon, I would expect to see evidence in the level of optimality in the diet of the *Sceloporus* lizards, as tested by a prey profitability model. If there are no costs to inefficient foraging, it may be more likely that the lizards do not show highly profitable diets (i.e., their diets are not approaching the profitability values possible in this system). If optimal foraging is occurring in this lizard community, it may only be seen in adults of *S. jarrovi* and *S. virgatus* because neonates of *S. jarrovi* have not yet gained the predatory skills required to forage efficiently. The neonates may not be able to evaluate prey availability or value. I expected this would lead to a decrease in total diet profitability and fewer high profitability items in the diet of *S. jarrovi* neonates as compared to adults of both species. This same lack of predatory experience should also lead to a decrease in prey capture success, resulting in an increase in prey capture attempts (to make up for the lost items).

Materials and methods

Study sites

My study occurred in boulder-strewn dry creekbeds in the vicinity of the Southwestern Research Station (SWRS; owned by the American Museum of Natural History), located outside Portal, Cochise County, Arizona. The research plots were located within the boundaries of two Forest Service campgrounds, Herb Martyr, or HM (31.8724167°N, 109.2352667°W, 1787 m), and John Hands, or JH (31.8782333°N, 109.22295°W, 1714 m). Vegetation in the area was typical of the pine-oak forest in the sky-islands of Arizona and New Mexico (for a complete description of the study site, see Watters, 2008).

Behavioural observations

From late May to late July in 2004 and 2005, 29–60 individuals of each lizard group (adults of *S. jarrovi*: $N_{2004} = 51$; $N_{2005} = 38$, neonates of *S.*

jarrovii: $N_{2004} = 29$; $N_{2005} = 35$, and adults of *S. virgatus*: $N_{2004} = 59$; $N_{2005} = 60$) were captured by hand-held noose, individually marked via paint marks and toe clips, and the following measurements were taken: SVL, head length, head width and gape width. Head length was defined as the tip of the snout to the posterior edge of the skull. Head width was the widest point on the skull, just behind the jaw. In contrast, the gape width was the distance between the right and left jaw articulation. Each day, marked lizards were observed at a 1 m distance, in half hour increments per lizard. All behavioural observations occurred between the hours of 0800–1200 h and 1400–1700 h in order to coincide with observed peak foraging activity (Simon, 1976; Phelan & Niessen, 1989). Observed lizards were chosen opportunistically; observers walked up and down the field site until they viewed a marked lizard, which was then observed for 30 min (unless that same lizard had already been observed within the last 7 days), after which, the observer repeated the process with the next marked lizard. No individual lizards were observed more than four times total throughout the season.

We recorded the number of prey capture attempts, number of successful prey captures, time between captures, time spent in pursuit, handling time, and relative size and type of prey captured (description and taxonomic classification), in addition to general (non-foraging) behaviours (Watters, 2008, 2009). All timed behaviours were rounded to whole seconds. A total of 352 30-min behavioural observations occurred (2004: 174; 2005: 178), which resulted in the following sample sizes for individual prey items eaten (both years combined): adult *S. jarrovii*: $N = 111$, neonate *S. jarrovii*: $N = 80$, and *S. virgatus*: $N = 76$.

As part of the analysis of foraging behaviour, prey capture attempts and percent capture success were analyzed by lizard group (adult *S. jarrovii* = jA, neonate *S. jarrovii* = jN, *S. virgatus* = vA) using a three-way ANOVA with year and site as fixed factors. The number of capture attempts was square root transformed and the percent capture success was arcsin (square root) transformed for analysis. These analyses, and all other ANOVA and ANCOVA in this study, were completed using Systat 10.0 (SPSS).

In 2005, a total of 15 handling time experiments were conducted on marked adults of *S. jarrovii* ($N = 2$) and *S. virgatus* ($N = 10$), and neonate *S. jarrovii* ($N = 3$). Large prey items such as dragonflies, caterpillars, and butterflies or moths were captured by sweep nets, placed within 25 cm of a lizard during its normal foraging period, and the behaviour of the lizard

was recorded. Legs and/or wings were disabled on the insects so that pursuit time and prey escape were not factors. If the lizard did not attempt to eat the insect within one minute, the insect was removed and that lizard was not tested again that day, as it may have been satiated (Parmerlee & Guyer, 1995; Shafir & Roughgarden, 1998). Handling times from these experiments were compiled with those from the 30-min observations, in order to obtain a more complete set of foraging behaviour to determine prey profitability.

Arthropod sampling methods and analysis

Once a week per site, I set out two sticky traps and two pitfall traps located at designated locations along a linear transect down the length of the dry creekbeds within each site, every 20 m (HM: $N = 10$ locations, JH: $N = 16$ locations), to estimate prey abundance and relative availability of arthropod prey items. The sticky traps were built from 10 cm by 15 cm Masonite® boards covered with a thin layer of plastic sheeting and Tanglefoot™ insect trapping adhesive (similar methods used by Ballinger & Ballinger, 1979; Simon & Middendorf, 1985; Bullock et al., 1993). The pitfall traps consisted of two stacked small (9 oz.) plastic cups sunk flush into the ground, with approx. 2 cm depth of soapy water, to prevent insects from escaping. Both types of traps remained active at each site for eight hours (approx. 0900–1700 h) when the lizards were likely foraging (Simon, 1976; Phelan & Niessen, 1989). Each evening, traps were collected and returned to the laboratory at SWRS.

Soon thereafter, arthropods collected on or in the traps were counted, given descriptions, and representative samples were stored in 1.5-ml vials (or 45-ml vials for larger organisms) in 75% ethanol for further identification. From the sticky traps, arthropods were removed by dissolving the glue with a non-toxic solvent, Histo-Clear II™. Samples were sorted and identified in a laboratory on the University of New Hampshire campus in the winter following collection (Bland & Jaques, 1978; Milne & Milne, 1980; Roth, 1985; Jackman, 1997). Length and width measurements were taken from the preserved samples, which were incorporated into calculations for profitability. Data from both types of traps were pooled for analysis.

Diet analysis

I used a simple prey choice optimality model to determine which lizard group had a more profitable foraging strategy (Schoener, 1971, 1979; Pough &

Andrews, 1985):

$$P_i = \frac{E_i}{h_i + S_i},$$

where E_i represents the energy gained (in calories) from eating prey $_i$. Handling time (h_i) is the time spent subduing and swallowing prey $_i$. S_i represents the time spent in pursuit of prey $_i$. The energy input gained from each prey item is estimated using the equation:

$$E_i = C_a \times l^\tau,$$

where C_a is the caloric constant for that type of insect, l is the length of the insect (see insect sampling methods above), and τ , in the case of insects, is a constant equal to approx. 2 (Schoener, 1971, 1974). Caloric values were obtained from a literature review of estimates of insect caloric values from previous studies using bomb calorimetry (Cummins & Wuycheck, 1971; Moulder & Reichle, 1972; Craig et al., 1979; Torok, 1981; Krebs & Avery, 1985; Oyarzun et al., 1996). When multiple values were available, a mean caloric value was calculated. Both average profitability per lizard group diet and average profitability per taxon were calculated and rank transformed for analysis. Profitability per lizard group was analyzed by a three-way ANOVA, with year and site as fixed blocking factors and post-hoc Tukey's tests. Additional analyses were done using log-transformed body size measurements (SVL, head length, head width, gape width) as covariates in order to separate out any effects of profitability due to body size alone.

Profitability was calculated for all prey taxa present in the diet and was based on behavioural observations, as these observations provided both handling time and pursuit time for prey items. Behavioural observations were pooled for both 2004 and 2005 to increase sample size. Any prey type that was not eaten at least twice was excluded from analysis. Average profitability was calculated for each prey taxon, but was not tested for statistical differences due to small sample sizes and was used only for subjective comparisons. As a final means of comparison between the profitability of each prey taxon and that prey taxon's prevalence in the lizard's diet, all profitability values were converted to proportions of the total profitability value of all available prey. If we were to assume that this new profitability calculated for each prey type represents the proportion that the lizards ought to eat them in order to be foraging at an optimal level, we can then compare what they

actually ate to this theoretically optimal level and also to the proportion of those taxa in the environment.

In order to make comparisons between the lizards' diet and the prey availability in the environment, I used a Mann–Whitney U -test to determine if the distribution of arthropods in the environment was the same as the distribution in the lizards' diets. If there were no statistical differences, then it is assumed that the lizards are eating prey in the same proportion as they are found in the environment; they are eating randomly. This analysis was completed using the statistical software, MedCalc 11.1 on the same eight prey taxa that were used in the profitability analysis.

Results

The number of capture attempts per observation period was significantly higher for neonate *S. jarrovii* than either adult group (Figure 1, $F_{2,341} = 4.15$, $p = 0.02$). There were no significant site ($F_{1,341} = 2.80$, $p = 0.10$) or year ($F_{1,341} = 0.24$, $p = 0.63$) differences in number of capture attempts. The percent of successful prey captures was uniformly high for all lizard groups ($F_{2,132} = 0.81$, $p = 0.45$), with no site differences ($F_{1,132} = 0.10$, $p = 0.92$), although there were significant year differences ($F_{1,132} = 5.74$, $p = 0.02$); prey capture success was consistently higher in 2005 (Figure 2).

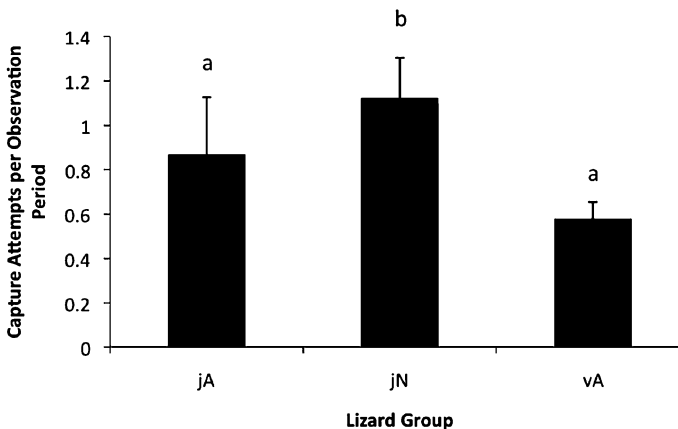


Figure 1. A comparison of foraging attempts per observation for all lizard groups. More foraging attempts were made by neonate *Sceloporus jarrovii* ($N = 75$) than by adult *S. jarrovii* ($N = 133$) and adult *S. virgatus* ($N = 144$). Error bars represent ± 1 standard error. Different letters above bars indicate significant difference at $p \leq 0.05$ between lizard groups.

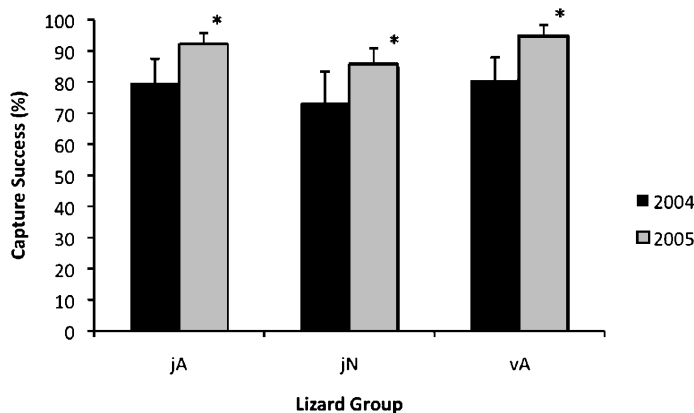


Figure 2. A comparison of percent capture success by lizard group and year. For the lizard groups, percent capture success was similarly high (jA: $N = 111$, jN: $N = 80$, vA: $N = 76$). The study year 2005 ($N = 125$) showed a higher success rate than 2004 ($N = 142$). Error bars represent ± 1 standard error. An asterisk (*) over a bar indicates significance at $p \leq 0.05$ within the lizard group.

In the arthropod samples, the most abundant taxa for the combined data from 2004 (108 total items) and 2005 (182 total items) were: Diptera (26%), Heteroptera (21%), Hymenoptera (non-ant) (12%), Coleoptera (11%), Chelicerata (7%) and Lepidoptera (6%). The remaining 14 taxa identified in the samples were found in relative abundances less than 5% and many were only found in one of the two years (Table 1).

Profitability per prey taxon was calculated for those taxa that were caught at least twice (Figure 3), but was not analyzed for statistical differences due to small sample sizes. In order to determine the level of diet profitability, the average profitability for each lizard group was calculated by pooling the profitability of each of the items in the observed diets for both years. Average profitability varies significantly by lizard group, with adult *S. jarrovi* having the highest profitability per diet, followed by adult *S. virgatus*, and then neonate *S. jarrovi*. Neonates had a significantly lower profitability level than adults of either species ($F_{2,228} = 15.53$, $p < 0.001$). There was also a significant year difference in profitability ($F_{1,228} = 15.15$, $p < 0.001$) (Figure 4). The analysis of covariance completed on all body size measurements showed no statistical significance (Table 2). When comparing the percentage of prey profitability to that seen in the lizards' diets and the environment, we observe that for the two years of data combined, very few of the most profitable items (Lepidopteran adults and larvae, Odonata and Orthoptera) were

Table 1. The total abundance and proportion of each prey type in the arthropod trap samples.

	2004		2005		Total	
	No.	%	No.	%	No.	%
Chelicerata	11	10.19	9	4.95	20	6.90
Coleoptera	10	9.26	24	13.19	34	11.72
Dictyoptera	1	0.93	0	0	1	0.35
Diplura	0	0	1	0.55	1	0.35
Diptera	26	24.07	50	27.47	76	26.21
Formicidae	3	2.78	9	4.95	12	4.14
Heteroptera	22	20.37	40	21.98	62	21.38
Hymenoptera	12	11.11	23	12.64	35	12.07
Isopoda	2	1.85	1	0.55	3	1.03
Isoptera	1	0.93	0	0	1	0.35
Lepidoptera	5	4.63	11	6.04	16	5.52
Mecoptera	2	1.85	0	0	2	0.69
Odonata	0	0	4	2.20	4	1.38
Orthoptera	3	2.78	5	2.75	8	2.76
Plecoptera	0	0	1	0.55	1	0.35
Siphonaptera	2	1.85	0	0	2	0.69
Thysanoptera	1	0.93	0	0	1	0.35
Thysanura	1	0.93	0	0	1	0.35
Unidentified larvae	5	4.63	3	1.65	8	2.75
Trichoptera	1	0.93	1	0.55	2	0.69
Sum	108		182		290	

eaten; instead, the less profitable Diptera, Formicidae and Isoptera made up most of the diet for all lizard groups (Figure 5). In addition, a comparison of the percentage of those same prey taxa that were present in the arthropod trap sample revealed no statistical differences between the samples and the diet of the three lizard groups (Table 3, Figure 5).

Discussion

Previous studies have shown that neonates eat more often than adults due to the necessary energy expenditures from rapid growth to adulthood and establishment of territories for the first time (Nagy, 2000; Watters, 2009). With that in mind, we may expect a higher percentage of foraging attempts in neonates as compared to adults, as was observed in this study. However,

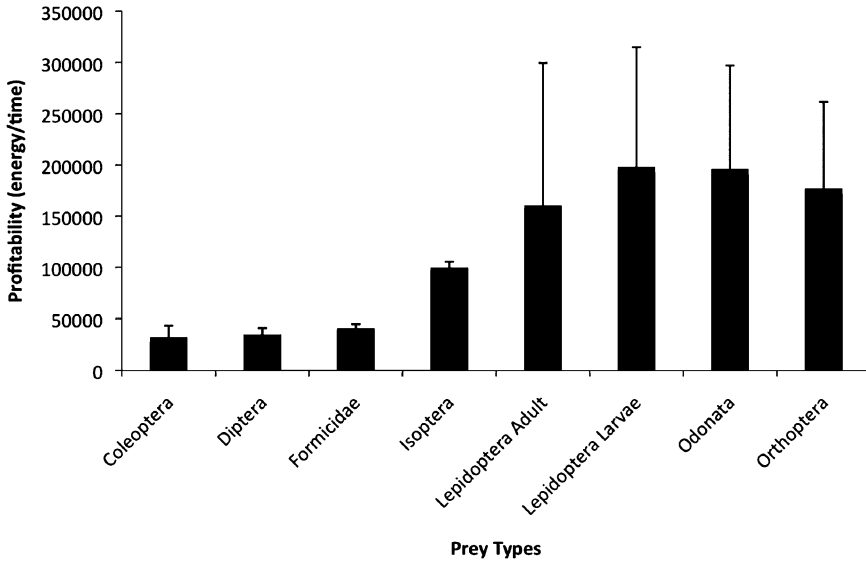


Figure 3. A comparison of profitability (energy/time or kcal/sec) by prey taxon for both years combined. Sample sizes: Diptera ($N = 59$), Formicidae ($N = 117$), Coleoptera ($N = 7$), Isoptera ($N = 35$), Lepidoptera adult ($N = 9$), Lepidoptera larva ($N = 4$), Odonata ($N = 10$) and Orthoptera ($N = 5$). Error bars represent ± 1 standard error.

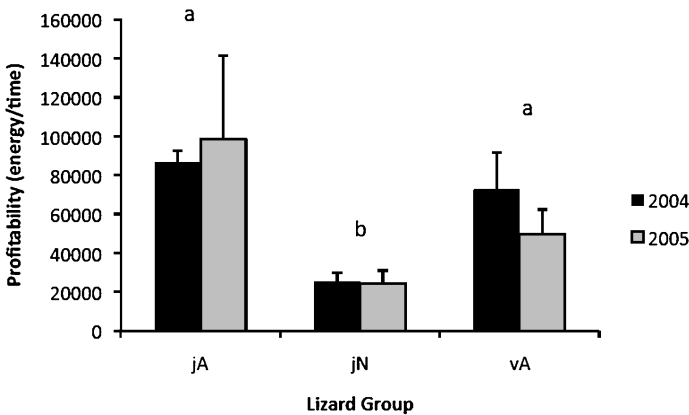


Figure 4. A comparison of profitability (energy/time or kcal/sec) by lizard group and year. Neonates of *Sceloporus jarrovii* ($N = 62$) had a decreased profitability level in their diet as compared to adults of *S. jarrovii* ($N = 116$) and *S. virgatus* ($N = 62$) adults. Profitability levels were higher overall in 2005 (2004: $N = 114$, 2005: $N = 126$). Years are shown separately due to a significant difference in profitability across lizard groups. Error bars represent ± 1 standard error. Different letters above bars indicate significant difference at $p \leq 0.05$ between lizard groups.

Table 2. Results of ANCOVA using body size measurements (log-transformed) as covariates for the analysis of lizard group vs. profitability.

		df	F-ratio	p-value
SVL	Model	2	0.32	0.73
	Covariate	1	0.61	0.44
	Error	244		
Head length	Model	2	0.18	0.83
	Covariate	1	1.61	0.21
	Error	244		
Head width	Model	2	0.14	0.87
	Covariate	1	0.64	0.42
	Error	244		
Gape width	Model	2	0.38	0.68
	Covariate	1	0.26	0.61
	Error	244		

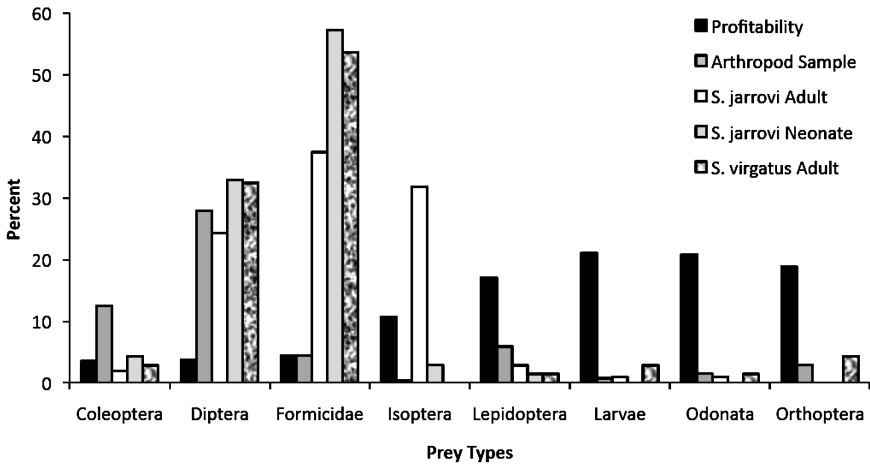


Figure 5. The proportion of each prey taxon’s profitability relative to the total profitability of all prey taxa compared to the proportion of the prey taxon in the diet of all three lizard groups and the prey available in the environment (pooled for both years).

percent capture success was fairly consistent across all lizard groups, with all groups achieving a mean success rate over 80%. This fact, combined with the increased number of prey capture attempts in neonates, implies that they are eating more prey items overall, as compared to adults of both species. I expected that neonates would show a decrease in capture efficiency, due to

Table 3. Results of the Mann–Whitney *U*-test comparing the proportion of prey taxa in arthropod samples and the lizards' diet.

	Year	<i>t</i> -statistic	<i>p</i> -value
<i>S. jarrovii</i> adult	2004	71.5	0.22
	2005	85.0	1.00
<i>S. jarrovii</i> neonate	2004	71.0	0.22
	2005	76.5	0.44
<i>S. virgatus</i> adult	2004	84.5	0.93
	2005	82.5	0.80

Each year and lizard group were analyzed separately.

their lack of predatory experience, and that handling time would be affected by the age and experience of the predator, resulting in a decreased ability to maintain control of the prey item (O'Connell & Formanowicz, 1998; Krause, 2001). Since there was no decrease in prey capture success for neonates, it suggests that the ability to handle food items may not be greatly affected by experience. The particular prey items eaten may have affected this result, because some prey items are difficult to handle and subdue due to their own mobility (Schoener, 1971; Eifler & Passek, 2000). If the neonates are primarily eating small prey with limited mobility (i.e., Formicidae make up 25–75% of their total diet; Watters, 2008), there may be no penalty from lack of predator experience on prey capture success.

If we assume that the ability of a predator to evaluate prey profitability is based on age and experience, then neonates should have a diet with the lowest profitability value. If, however, profitability of the diet is impacted more by the size of the prey items, then the body size of the predator will be a better predictor of the profitability of the diet. Results of this study show that the neonates have a significantly lower profitability than adults of either *S. jarrovii* or *S. virgatus*. The decreased profitability of the neonate diet was expected based on their lack of predatory experience, possibly leading to poor food choices (Jaeger & Rubin, 1982). In this particular study, body size did not play a direct role in profitability; therefore, the decreased efficiency in the diet can be linked to their predatory inexperience. Although, it is possible that small body size may still have influenced the decreased level of profitability because the highly profitable prey items were all fairly large (prey length > 10 mm) and perhaps the neonates simply did not attempt or

were unable to ingest these large prey items (<7% of neonate diet; Watters, 2008). This in turn, kept handling times low for neonates, since they were only preying on small items. It appears then that choosing to eat small, easy to handle, low energy food items resulted in a low profitability value for neonates.

Adult *S. jarrovii* had a higher level of profitability in their diet, which was expected based on their adult predatory experience and the requirements for their larger body size. Norberg (1977) predicted that the larger predators with the higher biomass to support would need to be more efficient than smaller predators. In addition, larger predators are more likely to have larger niche breadths (Costa et al., 2008), which would include prey items with a wide variety of profitability values. Adult *S. virgatus* also had a more highly profitable diet than the neonates. None of the diets were highly profitable, especially when compared to the profitability levels possible. It was clear that the diet of all three lizard groups was composed mainly of low profitability items, with only a few items of the high profitability prey eaten in fairly isolated incidents. Although it is tempting to conclude that the lizards were not foraging optimally, it is important to take prey availability and other factors into consideration before making this assumption. From the arthropod sampling of both years we know that the highly profitable items (Lepidoptera adults and larvae, Odonata and Orthoptera) make up a very small percentage of the prey base. In contrast, the low profitability items (Coleoptera, Diptera and the under-sampled Formicidae) are more common in the environment. It is clear the lizards are eating prey items at random, based on their occurrence in the environment, and prey choice is not occurring.

One of the predictions of optimal foraging theory is that when prey density is low, predators should be generalists, eating any food item available to them (Emlen, 1966, 1968; Schoener, 1971; Estabrook & Dunham, 1976; Chesson, 1983; Simon & Middendorf, 1985). As the highly profitable items decrease in quantity, they become less profitable for the lizards to eat and predators should switch to the next profitable prey item (Cooper et al., 2007). By doing this, predators are guaranteed a meal and no time or energy are wasted searching for that highly profitable item (Emlen, 1966; Diaz & Carrascal, 1990). Previous research has shown that the time frame of this study (late May through July) is a period of generally low arthropod abundance prior to the onset of the monsoon rains, which do not begin until middle to late July

and continue into August (Ballinger & Ballinger, 1979; Simon & Middendorf, 1985). The arthropod samples in this study clearly show that the high profitability items were in low abundance, making the low profitability items more attractive as a food source (Emlen, 1966; Simon & Middendorf, 1985). Therefore, despite the fact that the lizards do not appear to be eating the most profitable items available to them, they may still be foraging optimally.

Isoptera, another low profitability item, were a unique case because all foraging events were on one day when winged reproductive individuals covered the ground; in this case, the termites were a short-term resource that was exploited to the fullest extent by all lizards observed that day. This example demonstrates the lizards' ability to change with a fluctuating environment to capitalize on a highly abundant resource that was available only temporarily (Emlen, 1966). In addition, since such little effort was required to catch these prey items (personal observation), a lizard would be considered highly inefficient if it ignored this resource.

It is also possible that the lizards in this system are not foraging optimally because there are no real costs to inefficient foraging upon which selection for optimal foraging would act. Predation did not seem to be a major concern, because the majority of lizards in this study spent the entire half hour observation period immobile, basking on rocks in the sun, and seemingly in full view of any potential predators (Watters, 2009). The energy levels required for small, largely sedentary, ectothermic vertebrates may be low and only the bare minimum is required to maintain their basal metabolic rate (Stamps et al., 1981; Diaz & Carrascal, 1990). If the lizards are energy maximizers that need to intake a specific number of calories per day (and any calories above this minimum may increase growth or reproduction), eating any prey item that comes into their foraging range may in fact be the most efficient strategy, as every item results in a net caloric increase. When there are no costs associated with eating any item that comes within range, it is expected that the forager will eat the item instead of eating nothing (Schoener, 1974). During the course of this study, only a few items were encountered by lizards but were not eaten. These "ignored" items, however, were either flying near the lizard, making them difficult to catch, or were crawling near the lizard's tail and may not actually have been seen (personal observation). Other than these few exceptions, lizards seemed to eat all potential prey items.

Researchers have also suggested that for lizards which are energy maximizers, the best strategy may be to eat more small prey items instead of

a few large prey items (Cruz-Neto et al., 2001). When food abundance was low, the *S. jarrovi* in this study and previous studies tended to eat more of the small prey items, thereby becoming more specialized (Ballinger & Ballinger, 1979; Simon & Middendorf, 1985). In other lizard species, individuals became specialists on ants when overall prey densities were low (Stamps et al., 1981). In addition, the type of energy used in foraging may be a more useful predictor of prey choice than caloric gain alone. This is particularly relevant with large or struggling prey items when anaerobic metabolism is necessary for ingestion (Cruz-Neto et al., 2001). Nutrient content, chitin content, prey defense, and water content are other currencies that may also have significant impacts on prey choice, but are not considered in a straight-forward energy maximization model like profitability (Diaz & Carrascal, 1990). Also, it may not be possible for lizards to even evaluate the profitability of prey items (Diaz & Carrascal, 1993). When there are so many factors that may be involved, besides the caloric value, handling time and pursuit time used in the model, profitability may not be a truly representative indicator of the level of optimality shown in a forager.

Conclusion

On the surface, it is not immediately apparent that the *Sceloporus* lizards used in this study are foraging optimally, due to the low profitability values of their diets. However, their diets do follow other optimal foraging predictions such as eating low profitability items more often if they are more common than high profitability items and even taking advantage of short-term resources, such as an Isopteran reproductive event. In addition, neonate *S. jarrovi* are foraging less optimally than adults of both of species, indicating that predatory experience, along with size, does play a role in optimal foraging, although it did not impact prey capture success rate.

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