

SHORT COMMUNICATIONS

TESTING THE USE OF VISUAL CUES OF A MONOCULAR PREDATOR, THE VEILED CHAMELEON (*Chamaeleo calypttratus*) DURING PREY SELECTION

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During foraging, animals often feed selectively and choose to pursue or ignore a prey item based on a specific set of pre-determined criteria (Shine and Sun, 2003). Lizards are no exception to this rule, and at present continue to gain popularity for their use as model organisms in ecological studies (Shafir and Roughgarden, 1998). Although chemoreception has been implicated in some species (Cooper, 2000; Kaufman et al., 1996), well developed visual systems remain essential for accurate prey recognition during foraging (Janzen et al., 1995). Attempts to isolate which discriminatory cues are correlated with prey selection are restricted to only a few recent studies (Kaufman et al., 1996; Diaz and Carrascal, 1993). As with other visual predators, the underlying assumption is that lizards should utilize a combination of fundamental visual cues including prey movement, color, size, and shape to discriminate between equally accessible prey items (Ibrahim and Huntingford, 1989).

Chameleons (family Chamaeleonidae) are excellent model systems for studying prey choice behavior for two reasons. First, they are unique for being the only terrestrial vertebrates that forage using monocular vision and independent lateral eye movement. Second, these animals possess lateral eye movement over a total range of 180° horizontally and 90° vertically (Haker et al., 2003). By switching between saccadic eye movements in the left and right eyes, these animals are able to detect prey in two separate visual fields (Pettigrew et al., 1999). This is of great benefit during prey choice experiments as prey can be introduced simultaneously into each visual field. This also provides advantages for sit-and-wait foragers such as chameleons, since they draw little attention to themselves by maintaining their head in a stationary position during prey detection.

The objective of this study is to determine if chameleons discriminate between prey items that differ in movement and size during prey choice behavior. We conducted three separate prey choice experiments on veiled chameleons (*Chamaeleo calypttratus*) to test the influence of these visual cues. The first experiment tested the effect of prey mobility, while the second experiment tested the effect of prey size. The third experiment tested the capacity of chameleons to undergo prey-switching based on these visual cues, once already engaged in fixation on an initial prey target. We hypothesized that prey mobility and size are two visual cues used by chameleons during prey selection and that mobile and larger prey should be preferred. Our predictions are based on the principle of retinal movement detection in amniotes (Fleishman, 1992), and the assumption that larger prey should offer a more visible target to predators (Brooks and Dodson, 1965 as cited in Li et al., 1985). When encountering sequential prey items, as in the case of the third experiment, we predicted that chameleons should direct their attention towards the larger prey items since they should be most easily detected.

For each experiment, six captive bred, juvenile veiled chameleons (SVL = 96.8 ± 4.22 mm) were used as subjects. Chameleons were obtained from a commercial supplier (Reptilia Inc., Vaughan, Ontario, Canada) and housed in the environmentally controlled Hagen Aqualab at the University of Guelph. Chameleons were kept in separate 10 L terraria and maintained on a 12L:12D photoperiod in a room with high humidity, fluorescent lighting, and incandescent lights. Daily basking temperatures remained between 30 – 33°C, with nightly lows of 20°C. To minimize distress to subjects, all terraria were separated with cardboard dividers.

Chameleons were fed a diet of 8 – 12 southern brown crickets (*Acheta domestica*) (mean body length =

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8.7 ± 2.4 mm) and water daily two weeks prior to and following experimental trials. Crickets were also introduced as prey items during testing because they are common in the diets of chameleons in captivity and in the wild (Pleguezuelos et al., 1999). Crickets were obtained from an active breeding culture in the Hagen Aqualab, where they were fed ground Meow-mix ad libitum.

Chameleons were individually handled each day for two weeks prior to the 16 day test period. This allowed animals to become accustomed to handling and facilitate their transfer from their housing terraria to the experimental terrarium during experimental trials. One week prior to testing, chameleons were transferred daily to the experimental terrarium and presented with crickets to allow them to acclimate to feeding under test conditions.

Experiment 1 tested the prediction that chameleons prefer mobile prey over stationary prey items. This was tested by simultaneously presenting live (mobile) and freshly killed (stationary) crickets of approximately the same size (body length ~10 mm) to chameleons.

Experiment 2 tested the prediction that chameleons prefer large prey over small prey items. This prediction was tested by simultaneously presenting large (body length ≥ 10 mm) and small (body length ≤ 5 mm) live crickets to individual chameleons. All animals in experiments 1 and 2 received two trials in each visual field.

Experiment 3 tested the prediction that chameleons should continue to pursue or switch to the larger prey item from a smaller item when engaged in a period of fixation. Prey items varied in both size and their time of introduction. This was tested by first presenting one initial large (body length ≥ 10 mm) or small (body length ≤ 5 mm) live cricket to chameleons in one container. Upon fixation on the initial prey item, a second cricket opposite in size was introduced into the same container.

All animals received 4 trials in each visual field, with two large and two small initial prey items.

During each experimental trial chameleons were transferred by hand onto a 50 cm long central perch in the experimental terrarium. To minimize distress, all interior walls were occluded with cardboard to eliminate external distractions and the reflection of the chameleon in the glass. Crickets were presented by hand in open, transparent, plastic containers (diameter 11.5 cm; height 8 cm) 30 cm from the beginning of the perch. If crickets escaped the trial was stopped and immediately re-run. Chameleons were allowed a maximum of 20 min to make a prey choice. A choice was confirmed by the tongue shoot and ingestion of a prey item. If no choice was made after 20 min, the trial was assumed uninformative and was not counted.

To analyze our data, χ^2 -tests were used for each experiment to assess a prey choice preference between pairs of prey. Each experiment was performed equally in the left and right visual fields of subjects to account for an eye bias during prey detection, and was analyzed using a Fisher's exact test. Pseudo-replication was used for all experiments because of the cost of obtaining chameleons and the limited lab space available to house them for the duration of the test period.

The results of our study reveal three main findings. First, experiment 1 demonstrated a significant preference towards mobile prey compared to stationary prey (Table 1: $\chi^2 = 6.545$; $df = 1$; $P = 0.011$). Secondly, experiments 2 and 3 provided evidence that large prey items are preferred over smaller items during prey selection. Experiment 2 showed a significant visual preference towards larger crickets, where large crickets were chosen 91.6% of the time during paired comparisons (Table 1: $\chi^2 = 16.67$; $df = 1$; $P < 0.001$). Thirdly, experiment 3 showed significant evidence that veiled chameleons favor larger prey items, regardless of their time of

TABLE 1. Results of the Prey Choice Experiments of Veiled Chameleons

Experiment	Number of successful paired comparisons from 24 trials (<i>N</i>)	Number of prey selected in each comparison	Eye bias
Experiment 1	22	Mobile 17	Absent
Mobility		Stationary 5, $P = 0.011$	$P > 0.613$
Experiment 2	24	Large 22	Absent
Size		Small 2, $P < 0.001$	$P = 1.000$
Experiment 3a	24	Large primary 22	Absent
Prey-switching		Small secondary 2, $P < 0.001$	$P > 0.478$
Experiment 3b	23	Small primary 2	Absent
Prey-switching		Large secondary 21, $P < 0.001$	$P > 0.217$

Note. χ^2 -tests were conducted to assess a prey choice preference between pairs of preys. A Fisher's exact test was used to test for the presence of an eye bias during prey detection. Two chameleons made no choice during experiment 1, and one chameleon made no choice during experiment 3b.

introduction. When large crickets were presented as primary prey items, chameleons fixated upon them and showed little interest towards the secondarily introduced smaller prey (Table 1 — 3a: $\chi^2 = 16.67$; $df = 1$; $P < 0.001$). Conversely, when larger crickets were introduced secondly, chameleons demonstrated prey-switching from the smaller prey to the larger prey item on 21 of 23 occasions (Table 1 — 3b: $\chi^2 = 15.70$; $df = 1$; $P < 0.001$). Table 1 shows no correlation between the left and right visual fields of chameleons and their prey preference for the 3 experiments ($P > 0.2$; Fisher's exact test).

Our data unequivocally demonstrates that veiled chameleons use visual cues during prey selection and prefer mobile and large preys. There are several possible explanations for such preference; the simplest being that mobile and larger objects are easier to detect. The visual system of reptiles, birds, and mammals are equipped with both continuous saccadic eye movement and a greater density of receptors in the center of their retina (Fleishman, 1992), also known as a horizontal visual streak (Hassni et al., 1997). As a result, these animals are known to be able to respond strongly to motion in their visual periphery (Fleishman, 1992). Thus, at the simplest level we suggest that the preference towards moving prey objects is a likely consequence of the structural design of the retina of these chameleons. However, in some instances chameleons also consumed the stationary item immediately following the consumption of the mobile prey. We expect that this behavior is mainly attributed to the continuous saccades of amniotic vertebrates which transform stationary visual stimuli into retinal moving images that trigger neurons specialized in pattern recognition (Burghagen and Ewert, 1983). This implies that the shape of the prey item may also be of importance during prey detection. Therefore, the hierarchical preference of chameleons for mobile objects, followed by stationary objects may be best explained by easier retinal detection of moving objects compared to stationary ones.

The motion detection system of chameleons can also account for the results of experiment 2. The more conspicuous movement displays of larger prey items should be more easily detected by the horizontal visual streak during saccadic eye movement. Irrespectively of retinal structure, our results remain consistent with other studies on lizard ecology. Strong preferences towards larger prey items have been displayed during studies of active foragers such as the monitor and lacertid lizards (Kaufman et al., 1996; Diaz and Carrascal, 1993). Within the class Amphibia, research has also shown that the green treefrog (*Hyla cinerea*) chooses its prey based on size

cues when foraging among similar-looking insects of different sizes that exhibit similar behavior patterns (Freed, 1988).

The high resolution of receptor cells in the center of the retina (Fleishman, 1992) of chameleons appear to largely account for the results of our first two experiments. In spite of this, when we consider the obvious prey-switching towards larger prey items when already fixated on an initial prey, as in the case of experiment 3, alternative explanations must be examined. We suggest that chameleons may be evaluating the profitability of each item, and accordingly, associating greater energetic return with prey size. Under the assumptions of the classical prey model by Charnov (1976) that predators are omniscient and perfect optimizers, we could infer that chameleons are able to associate larger prey with higher profitability and nutrient intake (Charnov, 1976 as cited by Berec, 2003). Optimal foraging theory (OFT) predicts that a predator should consume prey item 1 only if the energy gained per unit time by consuming 1 is greater than the average expected energy gained per unit time by skipping 1 and searching for a better prey item (Paulissen, 1987). In agreement with OFT, chameleons were quick to display prey-switching behavior towards larger prey items when the primary prey item was small, but conversely when initially provided with a large prey, switching behavior was absent. Based on the assumptions of the classical prey model, we cannot overlook the possibility that chameleons may be optimal foragers.

Although the use of visual senses is well documented in reptiles, particularly in lizards, it has been primarily associated with intraspecific communication (Zuri and Bull, 2000). Chameleons are arboreal lizards that spot their prey visually (Ott and Schaeffel, 1995) and here we have tested two visual cues associated with their prey choice. The data shows that prey mobility and size are prevalent cues that trigger prey choice between equally accessible prey items. In addition, our results suggest that chameleons may display optimal foraging behavior by switching towards larger prey targets when previously engaged in fixation. These results indicate that chameleons use similar visual cues as other visual predators when choosing their next meal. Understanding prey selection and how these animals associate visual cues during predator-prey interactions helps to predict the diet of these lizards in their natural environment.

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