Functional Ecology

British Ecological Society

Functional Ecology 2009, **23**, 794–799 doi: 10.1111/j.1365-2435.2009.01565.x

Divergence of visual motion detection in diurnal geckos that inhabit bright and dark habitats

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Summary

1. Recent studies of the sensory drive hypothesis suggest that communicative signals evolve readily whereas change in sensory perception is more constrained by the demands of the physical environment.

2. Here, we find that diurnal *Sphaerodactylus macrolepis* geckos collected from dark, forested habitats were best able to detect motion in very dim light (< 10 lux), whereas geckos collected in brightly-lit coastal areas exhibited optimal motion detection at a much brighter light range 200–300 lux.

3. Motion detection by geckos from both habitat types declined as light intensity increased above 300 lux. These differences were observed after the lizards had been living in a common laboratory environment for 1 full year and are hence unlikely to be due to acclimation effects.

4. Light conditions for optimal visual performance match the light conditions of the natural habitats in which the lizards are found. Our results support the suggestion that visual performance may evolve quickly and that the sensory drive process may be best described as repeated co-evolution between signals and receiver sensory systems.

5. Thus, for animals that inhabit wide ranges of visual habitats, the sensory drive process may potentially act differently on separate visual response properties, resulting in diverse levels of variation and divergence in visual performance and communication systems.

Key-words: divergence, gecko, microhabitat selection, motion detection, sensory drive, visual performance

Introduction

The sensory drive hypothesis predicts that animal communicative signals evolve to match the sensory abilities of receivers, which in turn are shaped by the physical characteristics of the environment in which the animals live (Endler 1992; Boughman 2002; Fuller *et al.* 2005). For example, differences in the visual sensitivity of surf perch match the optical characteristics of the California kelp forest in which they are found. These differences in visual performance also match the differences in color signals used by these fish in sexual signals (Cummings 2004; Cummings 2007). But more recent studies have found evidence that receiver preferences can also evolve quickly. For example, Grether *et al.* (2005) found that the preference of female guppies for orange depends on the abundance of carotenoids in their diet. Similarly, Ryan *et al.* (2007) found differences in the call preferences of female Túngara frogs between populations. Receiver preferences may differ because animals choose to act differently in response to the same sensory input without undergoing any changes in sensory physiology. Alternatively, sensory physiology may be more evolutionarily labile than previously thought and the sensory drive hypothesis may be better described in terms of repeated co-evolution of signal senders and receivers rather than in terms of a unidirectional matching of signals to sensory systems. Here, we test the malleability of sensory systems by comparing how light intensity affects the visual ability of lizards from populations that have evolved in distinctly different light environments. We hypothesize that lizards that inhabit different lighting environments will diverge in visual motion detection ability.

The physical properties of the environment can greatly affect signal detectability (Endler 1992; Wiley 2006). For example, water turbidity influenced by algal blooms reduces visibility and reliability of male sexual signals in stickleback fish (Wong *et al.* 2007). Environments can vary greatly in the quality and amount of light available (Endler 1993; Marchetti 1993; Heindl & Winkler 2003), and as light decreases, visual performance declines (Dusenbury 1992; Warrant 2001). Consequently, we would expect animals that live in habitats

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Fig. 1. Photograph of an adult *Sphaerodactylus macrolepis spanius* male. The photograph was taken by Alejandro Sanchez.

with low light levels (e.g. under dense forest canopies) to evolve increased sensitivity to signal properties at lower light levels than animals that inhabit more brightly-lit habitats (Endler 1992).

Visual environments are often spatially and temporally heterogeneous and characteristics such as background motion, ambient light and structural complexity can greatly affect signal detectability (Endler 1992; Wiley 2006). For example, Jacky Dragons are less able to detect motion signals against a background of wind-blown vegetation than against a still background (Peters 2007). Similarly, crabs from habitats with high environmental motion (within vegetation) habituate to motion more rapidly than crabs that inhabit still, rocky habitats (Tomsic *et al.* 1993). Animals can also use behaviour to buffer themselves from environmental variation (Huey *et al.* 2003). For example, *Anolis* lizards produce more vigorous head-bob displays when signalling in front of a visually noisy background of moving vegetation than when the background is still (Ord *et al.* 2007). Similarly, male golden-collared manakins make their courtship displays more conspicuous to females by clearing leaf litter from the visual background (Uy & Endler 2004). Thus, behavioural adjustments buffer signallers and receivers from selection on communicative traits (Huey *et al.* 2003).

We might expect evolutionary shifts in sensory ability and/or strong reliance on behavioural buffering mechanisms to occur especially in species that inhabit wide ranges of physical environments where they confront strong, variable, natural selection. For example, *Sphaerodactylus macrolepis* geckos (Fig. 1) inhabit habitats ranging from dense rainforest to dry coastal desert across Puerto Rico. *Sphaerodactylus* differ greatly from other geckos in that they are very small (as small as 16 mm in snout-to-vent length), diurnal, and communicate using visual motion displays consisting of body motions such as head bobs, push-ups and tail waves (Regalado 1997, 2003). Furthermore, *Sphaerodactylus* eyes and all cone retinae seem especially adapted to diurnal activity and motion detection (Roll 2000). Thus, the wide spread *S. macrolepis* provides a unique opportunity to test for divergence in visual performance and microhabitat selection. We hypothesize that (i) *S. macrolepis* are active in microhabitats within the available range that maximize visual performance and that (ii) *S. macrolepis* from different photic environments will exhibit differences in motion detection performance.

Materials and methods

STUDY SPECIES

We collected 32 adult *S. macrolepis* from two distinctly different types of habitats in Puerto Rico: (i) the humid and densely vegetated montane rain forest of the Cordillera Central mountains in the center of the island (10 males, 2 females), and (ii) the dry, scrub vegetation habitat along beaches of the North and Eastern coast of the main island and of small satellite islands off the Eastern coast (9 males, 11 females). Based on morphological differences, lizards from the Cordillera Central Mountains represent two sub-species (*S. macrolepis spanius* and *S. macrolepis mimetes*) (Fig. 1). The lizards from the dry, scrub habitats represent three sub-species (*S. macrolepis grandisquamis* from the north eastern coast of the main island, *S. macrolepis inigoi* from Vieques island and *S. macrolepis macrolepis* from Culebra island) (Schwartz & Henderson 1991). For small lizards, the geographic distances, including the stretch of water between the main island and the satellite islands, between the sites are a considerable barrier to gene flow. Although we do not know whether these subspecies represent monophyletic populations, it seems likely that lizards from the two different habitat types are genetically distinct. The lizards were transferred to our laboratory at Indiana University and maintained under lab standard conditions (12 h light cycles, full spectrum, fluorescent lighting). We kept all the lizards under the same light intensities (300–400 lx) for 1 full year before measuring their visual abilities. The lab light intensities are relatively high for these animals and are similar to the light environments the lizards experience in coastal habitats.

HABITAT LIGHT AND MICROHABITAT SELECTION

During the month of August, 2005, we collected light data from the two habitat types inhabited by *S. macrolepis*. We only collected data on sunny days in which the sky was clear and no clouds were present. We used a digital illuminance meter (Minolta Camera Co., Ltd., Japan) to record light intensity to the nearest tenth of a lux.

We collected two types of habitat light data from each sampling area: from available microhabitats at each site and from microhabitats where a lizard was observed on the substrate at each site. *Sphaerodactylus macrolepis* inhabit the ground substrate (e.g. leaf litter) underneath tree and vegetation canopy shade. The lighting on the habitat substrate at all the sites we sampled consisted usually of a heterogeneous, shaded and lit mosaic. For the 'available' samples, we collected light data during three time periods at all sites (07.00–10.00 h, 12.00–15.00 h and 16.00–19.00 h EST). We walked through each area and recorded light intensity at 30 positions along a 15-m transect. At each position, we laid down a 1 m × 1 m grid, placed the light meter on the surface of the substrate in the centre of each of the four quadrats of the 1 m × 1 m grid and recorded the mean of the four readings. During the day, *S. macrolepis* are typically active on the surface of the leaf litter substrate commonly interacting with conspecifics and foraging on the leaf litter substrate (S. Nava, personal observation). For example, we frequently observed male *S. macrolepis* display head bobs to each other and forage for small invertebrates,

such as termites, on the surface of the leaf litter. For the 'observed' samples, we collected data during the same three day time periods as our 'available' data collection. We walked slowly through a different 15-m transect at each site, laying down the same 1 m × 1 m grid at each spot in which an active gecko was observed on the surface of the substrate. Again, we took 4 light readings and recorded the mean.

We tested for differences between time periods using ANOVA. We first tested for effects of time-of-day and a possible interaction between habitat type and whether the light samples were taken from randomly chosen sites or areas in which a lizard had been observed. We then used a two-way ANOVA to test for differences between habitat types and between available and observed light data. We used residual plots to confirm that the data did not need to be transformed and conducted all statistical analyses in SAS (2007), using the GLM repeated-measures function.

MOTION DETECTION

For *Sphaerodactylus* and for most lizards, motion is used for prey, predator, and mate detection and communication (Fleishman 1992; Regalado 1997, 2003). In the visual periphery, motion is the most effective stimulus for the visual grasp response (Fleishman 1992). The visual grasp response is a reflex shift of eye position placing an image on the central fovea when something of importance (e.g. a prey item or conspecific) is detected in the periphery (Ingle 1982; Wallman 1975). We measured the latency to the visual grasp response to a motion stimulus under various light intensities (from relatively dim to bright). We tested lizards under six light levels: 10 lx, 100 lx, 200 lx, 300 lx, 400 lx and 500 lx that represent the range of natural light conditions in which these lizards are found in Puerto Rico (see below). We chose the order of testing at random, testing all of the lizards at a single light treatment before proceeding to the next light level. We did not test a lizard more than two times in one day. During each trial, we placed a subject lizard in the test arena (a 14·5 × 8·5 × 8 cm container with three opaque white sides and one clear side for viewing) under the test lighting for a 10-min acclimation period. During the acclimation period, we ensured that the test lizard's gaze was forward by lightly tapping the wall of the test arena in front of the lizard once. After the acclimation period, we presented a spinning stimulus flag (3.4° visual angle) in the lizard's visual periphery (~45° and ~15 cm from the lizard) for 30 s. From the clear viewing side, behind a cloth blind with a small viewing hole, we observed the test lizard and used a stop watch to record the latency to a positive visual grasp response. We scored a positive response if the focal lizard exhibited a shift of eye position towards the direction of the stimulus flag. The motion stimulus was a flat, circular flag (9 mm in diameter) diametrically painted black and white. We spun the stimulus flag at 3 Hz using a small, silent DC (1–6V) geared motor. The DC motor was wrapped in felt cloth to control for any noise or vibrational cues during testing. During preliminary trials in which we spun the DC motor shaft without the stimulus flag, we did not observe any positive responses, thus precluding nonvisual cues as the cause for positive responses. Three hertz was selected as the presentation frequency because this is a common frequency of head bob communicative displays used by *S. macroplepis* geckos (R. Regalado, personal communication). A full-spectrum light, suspended 50 cm above the test arena floor, illuminated the arena and was regulated by a standard voltage divider. Light intensities for each trial were measured using the same digital illuminance meter used to collect microhabitat light data. Temperature of the experimentation container was constant for all light treatments, 26 °C.

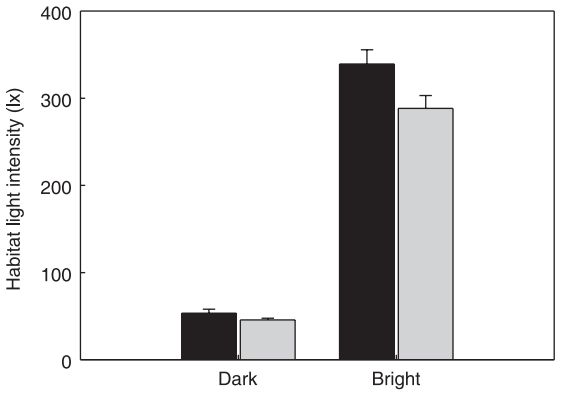

Fig. 2. Light intensity for the dark and bright habitat types where geckos were collected on Puerto Rico. Dark bars represent the mean light intensity from available microhabitats. Grey bars represent the mean light intensity of microhabitats where a gecko was observed. Error bars represent one standard error.

We analysed motion detection data using repeated-measures ANOVA, including factors for habitat type and light treatment. This analysis compares the behavioural response of lizards from light and dark habitats simultaneously across all six light treatments, while taking into account that we measured each individual repeatedly. We then used *post hoc* univariate analyses to compare lizards at each light treatment. We used residuals to ensure that ANOVAs conformed to the usual assumptions of homoscedasticity and normality.

Results

HABITAT LIGHT AND MICROHABITAT SELECTION

The average light intensity of available microhabitats from the montane habitats was less than 100 lux with a range from 8–170 lux, whereas the average light intensity of the available microhabitats from the coastal habitats was 340 lux, with a range from 54–665 lux (Fig. 2). We found no evidence of an interaction effect between habitat type and whether light measures were from observed or available microhabitats ($P > 0{\cdot}05$), and we found no significant differences between light samples taken at different time periods of day ($P > 0{\cdot}05$). We thus did not include these factors in subsequent analyses. Differences between the lighting in the two habitat types were significant ($F = 287$, df = 1, 358, $P < 0{\cdot}0001$). In both habitat types, we also found active lizards in microhabitats with slightly lower light than the available environment (Fig. 2, $F = 6{\cdot}1$, df = 1, 358, $P = 0{\cdot}01$). These results show that geckos from both habitat types not only inhabit different lighting regimes (i.e. bright vs. dark) but also seem to prefer microhabitats that were slightly darker than what was randomly available.

MOTION DETECTION

Sphaerodactylus macrolepis from 'bright' habitats exhibited a u-shaped response profile, with the best motion detection at

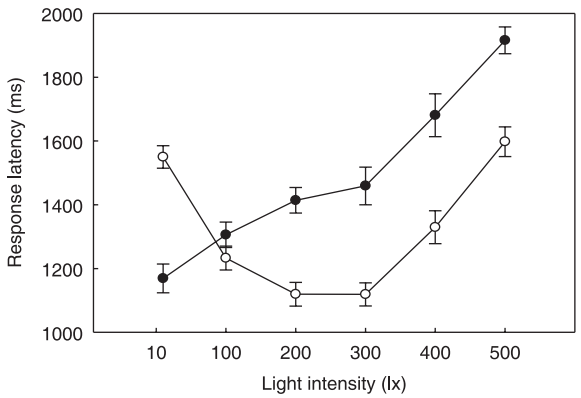

Fig. 3. Mean motion detection response profiles for *Sphaerodactylus macrolepis.* Closed circles represent lizards from the 'dark' habitats and open circles represent lizards from the 'bright' habitats. Error bars represent one standard error.

an intermediate light intensity, 200–300 lux (Fig. 3). In contrast, *S. macrolepis* from the montane, forest 'dark' habitats had a linear response profile, with better motion detection in very low light (10 lux, Fig. 3). Lizards from both habitats had poor motion detection in very bright light (> 300 lx).

The motion detection profiles of lizards from the two habitat types differed in shape (see Fig. 3); this difference was statistically significant, yielding a significant interaction between treatment lighting and habitat type ($F = 18{\cdot}4$, df = 5, 85, $P < 0{\cdot}0001$). We found a significant main effect also for habitat type ($F = 5{\cdot}42$, df = 1, 17, $P = 0{\cdot}03$) and for light treatment ($F = 45{\cdot}9$, df = 5, 85, $P < 0{\cdot}0001$). When we used *post hoc* tests to examine effects at each light treatment, we found significant differences between motion detection of lizards from light and dark habitats at nearly all light treatments (Table 1). Only at 100 lx was there no difference between lizards from light and dark habitats ($F = 0{\cdot}22$, df = 1, 17, $P = 0{\cdot}64$).

Results for males and females were similar, and we did not find significant sex differences at any treatment level ($P > 0{\cdot}05$, results not shown). Thus, we did not include sex as a factor in subsequent analyses. Additionally, in 17 lighting trials geckos did not respond at all to the stimulus flag during testing; we excluded those trials from statistical analyses. All lizards responded to at least four lighting treatments.

Discussion

We found that lizards are more likely to be active in microhabitats that had light levels closer to levels where their motion detection was maximally sensitive, than the average light level of the habitat. *Sphaerodactylus macrolepis* lizards from bright habitats responded faster to motion in bright light and lizards from darker habitats responded more rapidly to motion in dim light. Thus, visual performance of *Sphaerodactylus* geckos that live in extremely different lighting habitats seems to be both evolutionarily and behaviourally (via habitat selection) modified.

Table 1. *F* values, degrees of freedom (df), and *P* values for ANOVAS comparing motion detection response of lizards from dark vs. light habitats

Light treatment (lx)	*F*	df	*P*-value
10	31·27	1, 17	< 0.001
100	0·22	1, 17	0.642
200	13·23	1, 17	0.002
300	8·99	1, 17	0.008
400	12·19	1, 17	0.003
500	8·91	1, 17	0.008

Visual sensory performance is suggested to play a key role in driving the vast diversity of visual signals used in communication (Endler 1992). The sensory drive model predicts that when a population of animals moves into a new habitat or its existing habitat changes, the sensory capabilities of individuals from that population may also evolve, and in turn guide the evolution of communicative signals and behavioural preferences (Endler 1992). Thus, divergence in sensory ability and signal properties is predicted when populations occupy different environmental conditions (Boughman 2002, Endler 1992). For example, Fuller *et al.* (2005) found considerable genetic and environmental variation in the visual system (i.e. opsin expression) of bluefin killifish, demonstrating that despite their complexity, sensory systems are readily evolvable systems subject to both natural and sexual selection. Our results support the idea that visual performance is subject to local adaptation and divergence and, that the sensory drive process can occur repeatedly between populations occupying divergent environmental conditions.

Visual properties associated with terrestrial communication systems, especially colour, have been shown to vary little between closely related species and populations. For example, numerous studies on terrestrial animals have shown habitat-related differences in signal coloration (Gomez & Thery 2004; Uy & Stein 2007), but little or no divergence in color sensitivity (Fleishman *et al.* 1997; Hart *et al.* 2000; Jordao *et al.* 2007). *Anolis* lizard species, for instance, exhibit great diversity of dewlap coloration and habitat lighting, but there is little evidence of environmentally tuned spectral sensitivity and differences between closely related species (Fleishman *et al.* 1997; Loew *et al.* 2002), but see Leal and Fleishman (2002). On the other hand, environmental tuning of visual ability can occur in contexts outside of intraspecific communication, such as foraging. For example, Sumner and Mollon (2000) show that the retinal spectral sensitivities of several species of primates are optimal for detecting fruit or young leaves within the vegetation.

In terrestrial animals, temporal response properties may potentially be more evolutionarily labile than spectral response properties. For example, Jenssen and Swenson (1974) found a positive correlation between average habitat light intensity and motion detection performance of seven closely related species of *Anolis* lizards, but see Fleishman *et al.* (1995). Similarly, Frankenberg (1981) showed interspecific differences in

optomotor response in geckos that are active at different times of the day. Motion sensitivity that is environmentally tuned may be common in many terrestrial taxa (e.g. jacky-dragon motion sensitivity to moving vegetation) (Peters *et al.* 2007), perhaps because in many terrestrial environments, light intensity tends to be more discrete and less variable (e.g. under a dense forest canopy vs. an open desert scrub). In general, motion detection operates under a wide range of environmental conditions (e.g. vegetation motion, background complexity and light intensity). The ability to detect and respond to motion in many animals depends greatly on differences between the stimulus brightness and its background and the overall light availability greatly affects performance (Srinivasan 1985; Borst & Egelhaaf 1989).

For diurnal animals, motion detection typically improves with light availability. As overall light intensity increases, retinal integration time shortens resulting in improved ability to detect and respond to moving objects (Fleishman *et al.* 1995). However, in our own study, motion detection declined as light intensity increased in dark-habitat geckos, and even bright-habitat geckos were less able to detect motion as light increased above 300 lx (approximately the brightness of a well lit office). Gecko visual systems have undergone enormous evolutionary shifts in eye and retinal morphology and physiology. Although most gecko species are nocturnal, they are derived from diurnal ancestors and their retinae consist only of cone photoreceptor cells. Retinal organization and morphology vary greatly between nocturnal and diurnal geckos. For example, nocturnal gecko species have lost their fovea and have relatively high photoreceptor densities which enhance overall sensitivity (Roll 2001). On the other hand, the diurnal *Sphaerodactylus*, which exhibit cone pattern organization similar to that of predaceous fish that depend on motion detection for prey detection (Wagner & Ali 1978), have developed new temporally located foveae associated with high peripheral sensitivity (Roll 2001). Additionally, the retinal outer segments of the diurnal *Sphaerodactylus* are relatively smaller in size than those of nocturnal geckos, thus limiting *Sphaerodactylus* visual sensitivity under low light levels (Roll 2000). In a study comparing motion detection between geckos with different activity times (diurnal, nocturnal, crespusular), Frankenberg (1981) found that the diurnal geckos did better under high light intensities. However, our results suggest that despite retinal adaptations to a diurnal lifestyle, *Sphaerodactylus* from bright and dark environments are still better able to detect motion in relatively dim light. Thus, these findings point toward a historical or genetic constraint on visual performance given that diurnal *Sphaerodactylus* geckos have evolved from nocturnal ancestors.

Because of their diminutive size and extraordinarily high rates of evaporative water loss, *Sphaerodactylus* are vulnerable to heat stress and desiccation, and as a result are generally restricted to humid, leaf litter microhabitats under the shade of trees (Nava *et al.* 2001; Hensley *et al.* 2004; Steinberg *et al.* 2007). Microhabitat preferences for ectotherms, especially tiny ones, are greatly influenced by physiological functions, such as heat regulation and water balance (Huey 1991; Wolf & Walsberg 1996; Chown & Nicholson 2004). *Sphaerodactylus macrolepis* are commonly observed on the surface of the floor substrate under tree or vegetation shade (S. Nava, personal observation). But instead of finding *S. macrolepis* always in deep shade, we found them mostly in microhabitats that were only slightly darker than what was randomly available. *Sphaerodactylus macrolepis* may spend much of their time completely under the leaf litter to avoid desiccation. However, when they emerge on the surface of the leaf litter to forage or to interact with conspecifics, they are almost always found under light levels where their ability to detect motion is optimized. Fuller *et al*. (2005) cautioned that the correlation between environmental characteristics and visual properties may be exaggerated by animals choosing visual environments that match their visual capabilities (i.e. behavioural adjustment via microhabitat selection). Yet, our results show that the difference between optimal light for animals from the dark and bright habitats was much greater than the difference between lighting of available and selected habitats, suggesting that the divergence of motion detection ability is a result of differences in environmental lighting between the two habitat types and microhabitat preferences.

The differences in motion detection ability we observed between lizards from the two habitat types may stem from various shifts in their visual pathways (from presensory to processing). For example, differences in photoreceptor densities and retinal physiology may lead to differences in motion detection ability (Hornstein *et al.* 2000). However, little is known about the genetic bases and mechanisms that control motion vision systems. It is possible that differences in the visual morphology/physiology associated with motion vision may have a genetic basis. Alternatively, developmental/environmental mechanisms may also contribute to the differences in visual performance we measured. The developing visual system of young animals is expected to be subject to plasticity effects from the visual/photic environment. Thus, future studies need to be conducted to test hatchling and/or juvenile geckos from each habitat type to observe the effects of developmental plasticity. Our study shows that within one species across extremely different light environments (dark vs. bright), the latency to detect motion exhibits considerable variation. Thus, the sensory drive process can potentially work differentially on separate visual properties (i.e. spectral, temporal and spatial) and may lead to diverse levels of variation in visual performance in animals living in different habitats.

In the present study, we find that lizards from dark and bright habitats diverge in their motion detection abilities and that the light conditions for optimal motion detection approximately match the light conditions of the natural microhabitats that the lizards occupy. Our results support the suggestion that sensory systems are evolutionarily labile systems that may evolve quickly and that rather than a unidirectional matching of signals to sensory systems, the sensory drive process may be best described in terms of repeated co-evolution of signal senders and receivers.

Acknowledgements

We thank Stephanie Dowdy-Nava, Juan Daza and Luis Diaz for help with field assistance, data collection and animal care. We also thank Nilda and Mike Arocho for their hospitality and lodging in Puerto Rico. Thanks are also due to Mayté Ruiz, Cuauhcihuatl Vital, Duncan Irschick, and three anonymous referees for useful comments and suggestions on earlier versions of this manuscript. We thank Alejandro Sanchez for the gecko photograph. We thank the Departamento de Recursos Naturales y Ambientales de Puerto Rico for permission to collect and transport lizards. M.C. was supported as a research intern in the NSF-funded REU summer program in Animal Behavior at Indiana University's Center for the Integrative Study of Animal Behavior. The research was also supported through a predoctoral fellowship from the National Eye Institute to S.N. The research here was approved by the Bloomington Institutional Animal Care and Use Committee, Indiana. This research adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research, the legal requirements of the USA and all institutional guidelines.

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Received 12 September 2008; accepted 17 February 2008
Handling Editor: Duncan Irschick