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A Hierarchical View of Gecko Locomotion: Photic Environment, Physiological Optics, and Locomotor Performance

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Synopsis Terrestrial animals move in complex habitats that vary over space and time. The characteristics of these habitats are not only defined by the physical environment, but also by the photic environment, even though the latter has largely been overlooked. For example, numerous studies have examined the role of habitat structure, such as incline, perch diameter, and compliance, on running performance. However, running performance likely depends heavily on light level. Geckos are an exceptional group for analyzing the role of the photic environment on locomotion as they exhibit several independent shifts to diurnality from a nocturnal ancestor, they are visually-guided predators, and they are extremely diverse. Our initial goal is to discuss the range of photic environments that can be encountered in terrestrial habitats, such as day versus night, canopy cover in a forest, fog, and clouds. We then review the physiological optics of gecko vision with some new information about retina structures, the role of vision in motor-driven behaviors, and what is known about gecko locomotion under different light conditions, before demonstrating the effect of light levels on gecko locomotor performance. Overall, we highlight the importance of integrating sensory and motor information and establish a conceptual framework as guide for future research. Several future directions, such as understanding the role of pupil dynamics, are dependent on an integrative framework. This general framework can be extended to any motor system that relies on sensory information, and can be used to explore the impact of performance features on diversification and evolution.

Introduction

Behaviors such as locomotion and prey capture are complex phenotypes that emerge from the integration of parts and systems within an organism, often causing quantitative phenotypic traits to co-vary with one another (Kane and Higham 2015). In terrestrial systems, these behaviors are executed in complex environments that vary in numerous ways, including physical structure, temperature, and photic environment. Although the former two factors have been examined extensively with respect to locomotor performance (Huey and Hertz 1982; Schmitt 1994; Higham et al. 2001; Bergmann and Irschick 2006; Lammers et al. 2006; Foster and Higham 2012), the photic environment has largely been ignored. In actuality, structural challenges in the environment

are encountered in all photic environments. Given the importance of visual sensory information for motor tasks (Gibson 1958), the photic environment has likely shaped the evolution of locomotion and also the ability to cope with shifts in light level.

Sensorimotor integration involves the nervous system forming functional and anatomical links between motor commands and the associated sensory feedback (Murphy et al. 2017). Of the sensory modalities, vision is often implicated in the accurate and effective motion of vertebrates. Vision is critical for a number of behaviors such as feeding (Fouts and Nelson 1999; New et al. 2001; Rice and Westneat 2005; Kane and Zamani 2014) and predator avoidance (Webster and Webster 1971; Meager et al. 2006). The visual scene is continuously changing in

real environments, and this change is translated to the visual cortex. This “optic flow” (Lee 1980) includes all of the information about the displacement of the animal (kinematics), including speed and direction. The role of optic flow in locomotor control has been studied primarily in flying animals (Srinivasan et al. 1996; Bhagavatula et al. 2011), but is important for all vertebrates that move and avoid collisions in their environment (Varraine et al. 2002).

Not surprisingly, most research involving vision and terrestrial locomotion has focused on human locomotion (Patla et al. 1991; Patla 1997; Patla and Vickers 2003; Marigold and Patla 2008; Jansen et al. 2011). Although informative, we have yet to explore the role of vision in a number of interesting terrestrial systems that experience variation in photic environment. There has been a recent push to incorporate ecologically-relevant situations when considering vertebrate locomotion and feeding (Russell and Johnson 2007, 2014; Higham et al. 2015; 2019; Niewiarowski et al. 2016; Clemente et al. 2019), but the photic environment has not been sufficiently incorporated (Birn-Jeffery and Higham 2016b).

Many groups of vertebrates, such as lizards, exhibit a range of diel activity patterns, the preferred activity time during the 24 h cycle, providing a range of photic conditions that can strongly influence the visual system. Among the geckos, species with a diurnal lifestyle have evolved from a nocturnal ancestor multiple times (Gamble et al. 2015; Schmitz and Higham 2018), thus providing an outstanding system in which to examine questions related to sensorimotor integration.

How have geckos managed to repeatedly make this transition between a primarily nocturnal and diurnal lifestyle? Each evolutionary transition provides an opportunity to study how vision and locomotor behavior evolved in response to changes in light levels. Investigating multiple shifts in diel activity in both directions (nocturnal \leftrightarrow diurnal) in a phylogenetic context should enable us to distinguish the factors common to all transitions from factors unique to each individual lineage, helping us determine how evolutionary patterns are coupled with environmental change.

Our study is a first step in approaching gecko vision and locomotion in an integrative framework (Fig. 1). Here we review the factors that influence light conditions (photic environment) in different terrestrial systems including vegetation density and canopy structure, total intensity, and vision-limiting atmospheric conditions such as fog. We then review

how the eyes of geckos have evolved in response to their primary photic environments over long temporal scales, and how geckos may be able to respond to rapidly changing light conditions. After introducing the role of vision in motor-driven behaviors, we focus on what is known about gecko locomotion, especially in relation to differences in light conditions. New data highlight the importance of the photic environment on locomotor performance. Using what is known about optics and locomotion/feeding, we identify how photic environment should be associated with movement patterns. Overall, we emphasize the important influence of integrating sensory and motor information in order to understand how animals successfully execute tasks that are important for survival.

The constraints imposed by terrestrial photic environments

The most obvious, but dramatic, shift in photic environment for a terrestrial animal is the change in light level between daytime and nighttime. In fact, light levels throughout a 24-h cycle can span up to nine orders of magnitude. Therefore, animals that are active during the day will experience very different demands than animals active at night.

Daytime ambient light levels can vary substantially among habitats due to a number of factors, such as canopy cover in a forest (Pringle et al. 2003; Nava et al. 2009), cloud cover, and level of fog. The light environment in a forest is not only heterogeneous, but is constantly in flux. As discussed by Endler (1993), forest geometry is complex, but can be divided into four categories according to the light level. Forest shade areas, as well as small gaps, receive little light, whereas large gaps and woodland shade receive much more light. Forests and woodlands differ in the structure of the canopy, with the former having a dense and light-restricting canopy and the latter having crowns that are separated, leaving spaces in which light can penetrate (Endler 1993). Therefore, a species that occupies woodlands will experience a very different photic environment than one occupying forests. For six species of Puerto Rican anoles, four distinct light habitats have been identified: full shade, partial shade, no shade, and forest canopy (Fleishman et al. 1997). Interestingly, the spectral sensitivity of all six species peaked in the range 550–560 nm, which is comparable to the reflectance spectrum of green vegetation (550 nm). Therefore, it appears that the visual system is tuned to the environment. In addition, populations of a species can differ dramatically in their

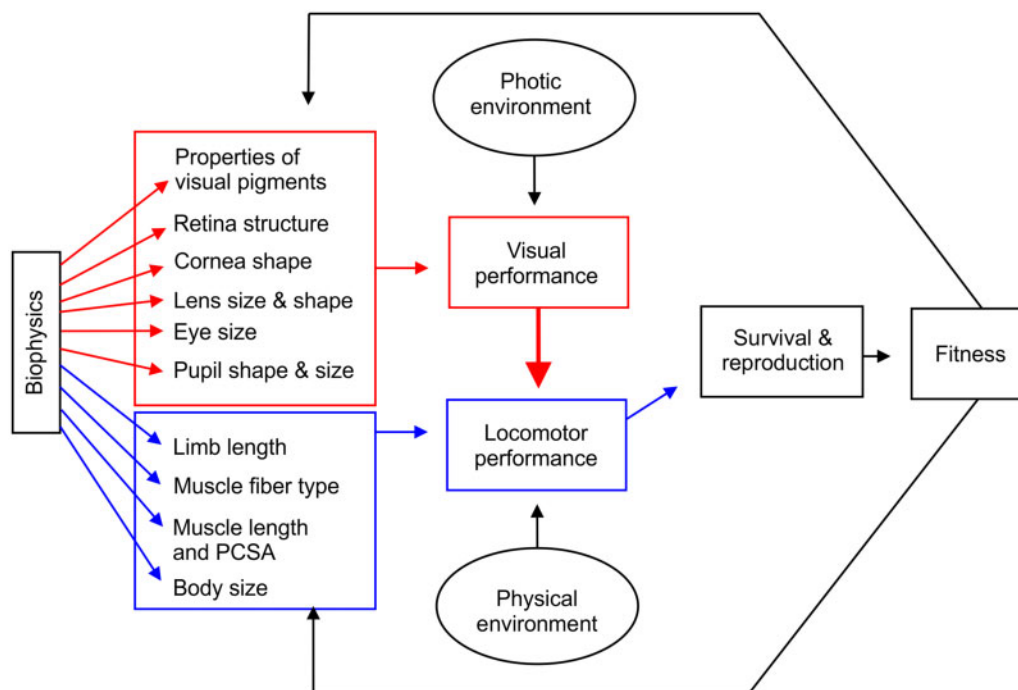


Fig. 1 An integrative framework for studying the links between the visual system, locomotor performance, and fitness in terrestrial vertebrates. Both the visual and locomotor systems are driven by a series of subordinate traits. In addition, locomotion is influenced strongly by visual performance, and should not be studied without information regarding the photic environment. Finally locomotion relies on attributes of the physical environment, such as obstacles, temperature, inclines, roughness, etc. Ultimately, fitness will emerge from the ability to survive and reproduce, which is dependent on context-specific locomotor performance. Fitness will then drive the evolution of lower level traits.

habitat, with some living in a forest and some living in an exposed area. For example, *Sphaerodactylus macrolepis* geckos in Puerto Rico occupy two distinct types of habitat: a densely vegetated montane rain forest and a dry, scrub vegetation along beaches (Nava et al. 2009).

Atmospheric visibility is generally limited by the presence of small airborne particles, droplets, or aerosols. Clouds are essentially a collection of small water droplets that will, depending on the type of cloud, reflect and absorb a significant amount of solar radiation (Liou 1976). Thick nimbostratus and cumulonimbus clouds, for example, will reflect 80–90% of light. Thus, clouds will disrupt and reduce the ambient light available for terrestrial vertebrates as they move in their habitat.

In addition to cloudy conditions, fog will also impact the photic environment. The collection of suspended water droplets near the earth's surface, resulting in fog, reduces horizontal visibility by reducing brightness contrast between an object and its background, and by scattering and absorbing the light due to the presence of the droplets (Houghton 1931; Gultepe et al. 2007; Cronin et al. 2014). That said, most of the impacts of fog on visibility are a result of scattering (Cronin et al. 2014).

As noted by Cronin et al. (2014), fog is the only situation in which the atmosphere becomes an attenuating medium at ecologically relevant distances. Foggy conditions persist in some areas of the world, such as the coastal deserts in Namibia (Olivier 1995), northern Chile and Peru (Rundel 1978). Terrestrial animals that live in these areas must deal with drastic changes in photic environment over both space and time. In addition to the reduction in light, fog will also alter light conditions by scattering, having impacts on contrast and acuity. Therefore, locomotion is likely to be impacted by foggy conditions, although this is poorly understood.

Physiological optics of gecko eyes

The challenge of vision across a large range of different light levels is met by the visual system through a combination of different optical, physiological, and neuronal components that jointly interact to produce images in dim and bright habitats (Warrant 1999; Land and Nilsson 2012). Changes in light levels over evolutionary time, caused by, for example, diel activity patterns, have emerged as a major influence on the diversification of eyes (Walls 1942; Land and Nilsson 2012). Vertebrates exposed to more or

less abrupt changes in light levels encounter a somewhat different challenge: the ability to see well over a large range of light levels in quick succession from another. Short term changes in the light environment at the order of a few seconds or less, such as locomotion through different microhabitats in a forest, can be at least partially dealt with by pupil dynamics and cone photoreceptor adaptation. Changes in light intensity between day and night can be navigated by the presence of the duplex retina consisting of rods and cones, which, in combination, allow vision in very dim and very bright environments (Fain et al. 2010). Remarkably, geckos do not appear to have the advantage of a duplex retina, as their photoreceptor mosaic only consists of (modified) cones (Walls 1942).

For accurate and effective locomotion, geckos will need appropriate light sensitivity, spatial visual acuity, and temporal visual acuity, which altogether combine to a detailed optic flow field with information of the displacement of the animal relative to its environment. Visual light sensitivity and spatial acuity control the quality of the static retinal image of the visual scene, while temporal acuity controls at which rate the visual scene is sampled over time, translating stationary images into information about relative speed, distance, and direction. Given that both spatial and temporal acuity are linked in a trade-off with sensitivity (Land and Nilsson 2012), geckos should evolutionarily benefit from a compromise that satisfies all requirements. If true, nocturnal geckos should have high light sensitivity but maintain spatial and temporal acuity to see sufficient detail and track motion, while diurnal geckos should have less sensitive eyes with high spatial as well as temporal acuity.

Exact determinations of visual performance require behavioral tests, yet such tests are difficult to perform in non-human vertebrates (but see Temple et al. [2013]) and very sparse for geckos (Frankenberg 1981; Nava et al. 2009). However, models based on physiological optics facilitate approximations of the main qualities of detailed spatial vision (Land 1981; Warrant 1999, 2004; Land and Nilsson 2012). The details of the models are beyond the scope of this review, but we emphasize that equivalent visual performance, be it light sensitivity, spatial visual acuity, or temporal visual acuity, can be achieved through various combination of visual system components.

Most geckos tend to have large eyes for their body size (Werner 1969) and mostly appear to be visually guided, which is sensible given that large eyes are metabolically expensive (Niven and Laughlin 2008).

Larger eyes improve visual performance (Land and Nilsson 2012), even though the specific effects on acuity and sensitivity depend on how the individual components of the visual system are scaled up. In addition, large eyes, all else being equal, increase the distance from which specific targets such as obstacles, prey, and predators can be seen, with important consequences for locomotion (Nilsson et al. 2014; MacIver et al. 2017).

Behavioral ecology is likely the key driver of eye size evolution within geckos, with diel activity pattern being primary. Nocturnal species of geckos often have larger eyes for a given body size than diurnal gecko species (Werner and Seifan 2006; Schmitz and Higham 2018). Other ecological factors that might be important for eye size evolution are habitat structure, including habitat clutter (Schmitz and Higham 2018) or whether the gecko is scansorial or cursorial (Werner and Seifan 2006). It is clear that there are multiple axes of eye diversification among geckos, and more work should tease apart the details of the actual photic environment and visual systems with all its components, not just eye size, to account for the trade-offs between spatial acuity, temporal acuity, and visual light sensitivity.

Diel activity pattern also strongly influences the eye shape of geckos. The corneas, fully dilated pupils, and rounded but not quite spherical lenses of the eyes of nocturnal geckos tend to be proportionately large (Denton 1956; Hall 2008, Roth et al. 2009; Schmitz and Motani 2010), which should increase the visual light sensitivity of eyes (Land 1981; Warrant 1999). In turn, nocturnal geckos are capable of almost fully closing their pupils in bright light, shrinking their large, rounded or slightly elliptical pupil to a series of very small pinhole apertures (Frankenberg 1979; Roth et al. 2009), which should be helpful if a nocturnal gecko is forced to be active in bright light. The range of pupil dilation and constriction, along with the shape of the pupil, varies substantially across geckos (Fig. 2). It is unknown whether the various photic environments encountered by primarily diurnal geckos generate evolutionary changes of eye shape.

Retina structures corroborate the emerging pattern of improved visual light sensitivity in nocturnal geckos. Three major anatomical classes of modified cone photoreceptors have been documented in geckos so far (Underwood 1951; Tansley 1959, 1961, 1964; Dunn 1966a, 1966b, 1966c, 1969; Loew 1994), which we can corroborate with new data on the nocturnal leopard gecko (*Eublepharis macularius*; Figs 3, 4). Nocturnal geckos tend to have very large photoreceptor cells with wide and long outer



Fig. 2 Pupil size and shape across different species of nocturnal gecko. (a) *Sphaerodactylus roosevelti* in room light, (b) *E. macularius* in bright light, (c) *C. ciliatus* in dim light, (d) *C. ciliatus* in bright light, and (e) *Pachydactylus punctatus* in bright light.

segments (Röll 2000a), which represents one possible path toward better light sensitivity predicted by physiological optics. Diurnal gecko species have significantly smaller outer segments, yielding better spatial acuity. Similar to eye shape, it is unknown whether photic microhabitats influence the evolution of retina structures.

Color vision may be present in both diurnal and, surprisingly, nocturnal geckos, even though it is not clear whether locomotor performance benefits from the ability to differentiate light of different wavelengths. Three classes of visual pigments of geckos have been identified using microspectrophotometry (Loew 1994; Loew et al. 1996), with maximum

absorption in the “green” part of the spectrum (520–540nm), “blue” (445–470nm), and “UV” (364 nm). The presence of three different visual pigments in photoreceptors in combination with optical changes to increase light sensitivity theoretically allows geckos to differentiate colors even in dim light, as has been behaviorally confirmed in the helmet gecko (*Tarentola chazaliae*; Roth and Kelber 2004). Additional support for the importance of color vision in geckos stems from lens properties. Optical experiments have demonstrated that the refractive system of the nocturnal helmet gecko (*T. chazaliae*) is multifocal (Kröger et al. 1999; Roth et al. 2009), which means that different zones of the lens, from center to periphery, have different refractive properties. Such a multifocal system can mitigate the optical problem of chromatic aberration, that is, the acuity of color vision is improved. Meanwhile, the oil droplets found in the photoreceptors of some diurnal geckos are not considered to aid with color filtering as in other vertebrates, because they appear to be transparent (Röll 2000b).

The biochemical properties of the green cones of the nocturnal Tokay gecko (*Gekko gekko*) suggest that the speed of the visual cycle is intermediate compared to fast cones and slow rods of other vertebrates, which may be a functional adaptation to vision in low light (Kolesnikov et al. 2007). In turn, however, if slower visual cycles decrease the speed of recovery after photoreceptor bleaching (the rate of recovery of sensitivity is slower in rods than in cones; Fain et al. 2010), nocturnal geckos may have difficulties to see during the day. While seemingly rare, geckos can be forced to face photic environments different from what their eyes are evolutionarily adapted to (Geniez et al. 2004). Investigations of the dynamics of pupil constriction and dilation, as already hypothesized by Walls (1942), may provide a feasible mechanism to enable vision in bright light for nocturnal, very light sensitive geckos with slow recovery times. In addition, slow visual cycles may also link to lower temporal acuity, with current evidence suggesting that the flicker fusion frequencies of nocturnal geckos (*Gekko gekko*) is lower than that of diurnal geckos (*Phelsuma madagascariensis*) and other lizards such as *Iguana iguana* (Arden and Tansley 1962, Meneghini and Hamasaki 1967). Note, however, that Dodt and Jessen (1961) found relatively high flicker fusion frequencies in the nocturnal Mediterranean gecko (*Hemidactylus turcicus*).

The signal pathway from photoreceptors to retinal ganglion cells in geckos is virtually unknown. Available evidence suggests that, on average, there

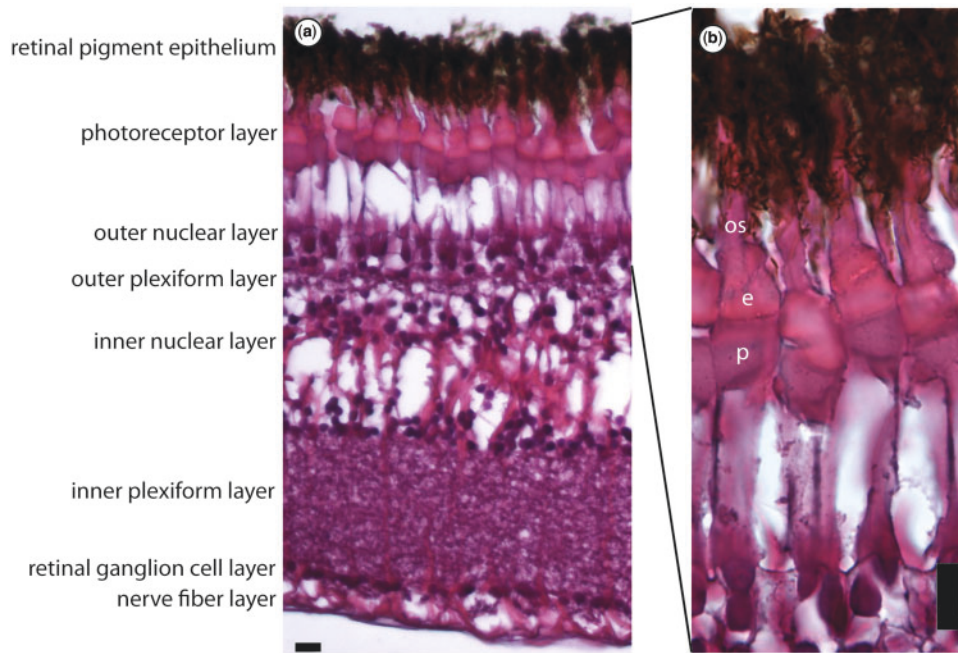


Fig. 3 Retina structure of the leopard gecko (*E. macularius*) (a) The cross section of the retina of the leopard gecko (*E. macularius*), stained with H&E, features the well-known layered retina structure seen across vertebrates. Incoming light travels through the nerve fiber and following layers until light is absorbed by photoreceptors. (b) Gecko photoreceptors are characterized by large paraboloids, ellipsoids, and outer segments. The outer segments, often formed as twins, are surrounded by retinal pigment epithelium. Scale bars equal 10 μm .

is very little retinal convergence of photoreceptors to retinal ganglion cells (Röll 2001), or possibly even a surplus of retinal ganglion cells (Pedler and Tilly 1964), which is good for acuity while unfavorable for light sensitivity. Cook and Noden (1998) described the mosaics formed by large ganglion cells of the retina of the common house gecko (*Hemidactylus frenatus*) and suggested a correlation between photoreceptor and ganglion cell mosaics. New data on the leopard gecko (*E. macularius*) corroborate low retinal convergence (Fig. 4), but more comprehensive studies are needed, both in terms of phylogenetic coverage as well as spatial analyses of the entire retinal area to detect possible regional specializations.

To summarize, the available evidence suggests that nocturnal geckos are evolutionarily adapted to vision in low light by virtue of the optics of their eyes and the biochemistry of their cones. Pupil, cornea, lens, and outer segments of the photoreceptors are all proportionately large, and the (modified) cones operate on a slower visual cycle than typical cones. Combined, such modifications are expected to substantially improve the light sensitivity of the eyes, while decreasing spatial and potentially also temporal resolution. The low retinal convergence observed in at least some gecko species is favorable for spatial visual acuity, which may help to mitigate the trade-off with sensitivity. Low temporal acuity may

be a limiting factor for interpretation of the optic flow field during locomotion. In contrast to nocturnal gecko species, diurnal geckos seem to have evolved proportionately smaller pupils and outer segments of the photoreceptors, all suggestive of maximizing high spatial acuity while sacrificing visual light sensitivity.

Optomotor responses of three related taxa of fan-fingered geckos (*Ptyodactylus* spp.) with different activity patterns appear to confirm differences in visual performance (Frankenberg 1981). While the most diurnal gecko's ability to detect a moving stimulus increased with light intensity, the most nocturnal gecko's ability to detect such a target was independent of light intensity. Similarly, populations of the primarily diurnal big-scale dwarf gecko *S. macrolepis* differ in their visual performance depending on their primary photic environment (Nava et al. 2009). Geckos collected from shaded forests have optimal motion detection in dim light, whereas geckos collected in more brightly-lit environments have optimal motion detection at higher light intensity.

Vision as a key for motor-driven behaviors

For animals that move through their environment, optic flow is critical for providing information regarding movement direction and magnitude. Birds

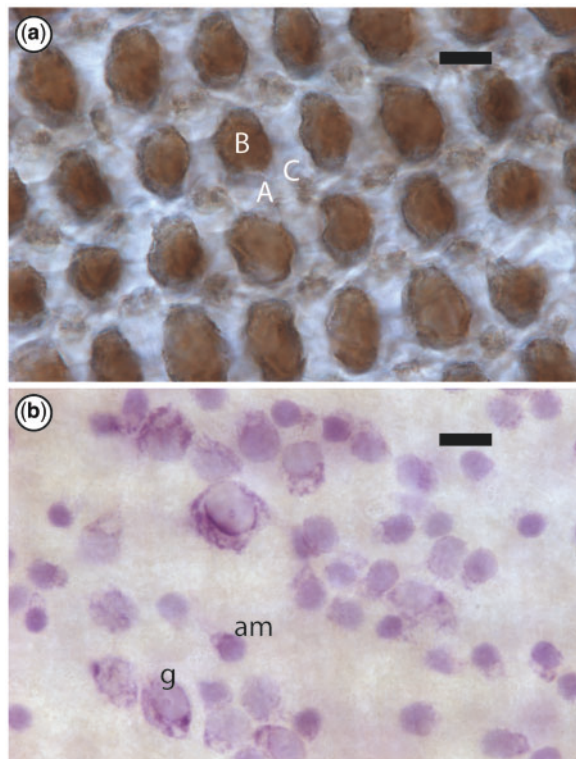


Fig. 4 Images of a retinal flatmount of the leopard gecko (*E. macularius*) stained with cresylviolet, taken at the same location with identical magnification. (a) The photoreceptor layer is characterized by a very regular mosaic pattern. The image shows the photoreceptors at the level of the ellipsoid bodies, imaged as a flatmount with the retinal ganglion cell layer facing up. Following Underwood's (1951) nomenclature, type B twin photoreceptors feature a single, large ellipsoid, while types A and C are substantially smaller. A (single) and C (twins) can be distinguished in this image by identifying small pairs of ellipsoids, but the distinction is often difficult. (b) The retinal ganglion cell layer shows a variety of different ganglion cells (g) and displaced amacrine cells (am). Based on cell counts, the convergence from photoreceptors to retinal ganglion cells is low (ca. 1–2 depending on location). Scale bars equal 10 μm .

and flying insects will utilize the movement of the environment relative to the eyes as feedback to control locomotor speed and trajectory (e.g. Bhagavatula et al. 2011; Ros and Biewener 2016). For example, a recent study created an internally rotating environment using a large vertical cylinder with a rotating visual pattern (Ros and Biewener 2016). The hummingbirds in the study accurately matched the imposed rotational speed and flew with the rotating cylinder. This occurred even when the spatial and temporal frequencies were varied based on the birds' positions within the cylinder when presented with the rotating visual stimulus. In addition to flying animals, a number of invertebrates have been shown to rely heavily on visual information to guide their locomotor speed and direction, such as in the crab

(Tomsic 2016). Given that the use of optic flow for locomotor control covers a large swath of the phylogeny of animals, it is likely that fast-moving terrestrial animals, such as geckos, will also use optic flow to control their locomotor speed and kinematics. The inextricable link between vision and locomotion in moving animals calls for an integration of the fields when considering how an animal moves in its environment.

As noted above, much of the research focusing on the role of vision in motor-driven behaviors has involved human locomotion. Manipulation of the visual field, through the use of goggles, has proved a valuable tool for understanding how humans utilize visual information to navigate obstacles (Jansen et al. 2011). A small visual field ($40^\circ \times 20^\circ$) resulted in both a reduction in speed and the selection of wider paths around obstacles. The authors concluded that balancing problems associated with a restricted visual field caused increased energy expenditure through the adoption of a wider step (Jansen et al. 2011).

Although few studies have altered light levels in human locomotion studies, they are powerful for generating hypotheses for comparative studies. A recent study examined the role of dim light in gait speed, footfall patterns, and trunk parameters during level walking in older people (Helbostad et al. 2009). Locomotion was assessed using an electronic gait mat and triaxial piezoresistant accelerometers. Reducing light level did not have a strong influence on gait parameters, although further visual manipulations under dim light strongly influenced locomotor speed and variability (Helbostad et al. 2009). Another recent study manipulated lighting condition and assessed three-dimensional kinematic gait data (Huang et al. 2017). The authors found that, as light level decreased, stride width increased and stride length, stride time, and double support time all decreased. Gait variability increased, measured as the coefficient of variation in stride length, stance time, and double support time (Huang et al. 2017). Increased variability under low light conditions has been observed in other studies (Figueiro et al. 2011). Overall, we expect that diurnal animals will experience increased variability and a more cautious gait as light levels decrease.

There is a dearth of studies examining the role of light in the locomotion of non-human terrestrial vertebrates. One study observed the activity and locomotor behavior of 16 species of carnivores in different light conditions (Kavanau and Ramos 1975). These observations were in both indoor and outdoor enclosures.

For the nocturnal carnivores, such as the long-tailed weasels and striped skunk, nighttime running was much faster, and activity was much higher. The species exhibiting the fastest running speeds (coyote and red wolf) were both diurnal. Interestingly, the authors found large differences in individual responses to illuminance conditions, whereas other individuals exhibited stereotyped responses to changing light (Kavanau and Ramos 1975).

Gecko locomotion and vision

Gecko locomotion has been studied extensively, especially in relation to the acquisition or secondary simplification of the adhesive apparatus (Zaaf et al. 2001; Vanhooydonck et al. 2005; Autumn et al. 2006; Russell and Higham 2009; Higham and Russell 2010; Birn-Jeffery and Higham 2014, 2016a; Higham et al. 2015, 2017; Zhuang and Higham 2016; Collins and Higham 2017; Naylor and Higham 2019). Geckos that bear a fully-developed adhesive system (with toepads) undergo a complex series of movements during inclined locomotion (Russell and Higham 2009). This involves digital hyperextension that precedes the end of stance, and the unfurling of digits after foot contact at the beginning of stance. This rearrangement has resulted in slower locomotion given that it takes time to apply and release the adhesive system with each footfall. Given that geckos are visual predators, and some can run very fast (Higham and Russell 2010), the photic environment is likely to have a strong influence on locomotor performance. Incorporating light level has been absent from the literature, apart from a single study that examined the impact of changes in light condition on the locomotion of the diurnal gecko *Rhoptropus afer* (Birn-Jeffery and Higham 2016b). They found that locomotor speed was the lowest in the “no-light” condition, and this occurred via a reduction in stride length and stride frequency. The center of mass was also lowered in the “no-light” condition, along with the adoption of a more sprawled posture. Why would a diurnal gecko reduce locomotor speed and lower the center of mass when light is restricted? If one goal is to maintain optic flow, then a reduction in speed is necessary to incorporate sensory information from the environment. This could be defined by both the temporal acuity and the light intensity in the environment.

Another issue with studying the role of ambient light on gecko locomotion is that many geckos are categorized as nocturnal or diurnal with very limited (or no) field data. One option would be to examine activity patterns in semi-natural laboratory

conditions. Using 14 species of gecko from Israel, Frankenberg (1978) quantified the laboratory activity with an actograph, a plastic box mounted on a triple beam balance, carrying a pen that marked the movements on a thermograph drum. Interestingly, activity was more diurnal in the winter than in the summer in all taxa except *Ptyodactylus hasselquistii* (Frankenberg 1978). Additionally, geckos that live in arid regions appear more nocturnal than those living in more humid areas or those with wider distributions. Many of the species examined exhibited diurno-nocturnality, being active during the day and night, although this again shifted with seasons in many species (Frankenberg 1978). This reinforces the idea that, although we generally categorize geckos as nocturnal, crepuscular, or diurnal, many have the ability to be active across different light conditions. Therefore, much more work is needed to characterize variation in activity patterns among and within gecko species in nature.

Locomotor performance: new data

In our experiments, nocturnal geckos were significantly slower than the diurnal species in the bright condition, and they did not exhibit a significant drop in performance with changes in light conditions (Fig. 5). In contrast, the diurnal species (*R. afer*) exhibited a significant drop in performance in the dark condition, and one species of nocturnal gecko (*C. variegatus*) was significantly faster than *R. afer* in the dark condition (Fig. 5). We should note that our sample sizes are relatively small, and future work that includes multiple transitions to diurnality should be included. However, shifts to diurnality are accompanied by a reduction in photoreceptor (Röll 2000a) and overall eye size (Schmitz and Higham 2018), so the increased locomotor sensitivity to changes in light conditions is not necessarily surprising. Overall, it appears that diurnal geckos are effective at seeing in bright conditions, but at the cost of poor running performance under dim light conditions. Nocturnal geckos, in contrast, maintain the ability to move effectively in bright conditions.

What might explain the lack of performance response to bright light levels among nocturnal geckos? It seems feasible that the enormous pupil constriction described above reduces influx of light to an extent that avoids excessive photoreceptor bleaching. Although the pupil of a nocturnal gecko is typically fully constricted in bright light, it is common to maintain four pinholes running along the center vertical axis of the eye (Murphy and Howland 1986;

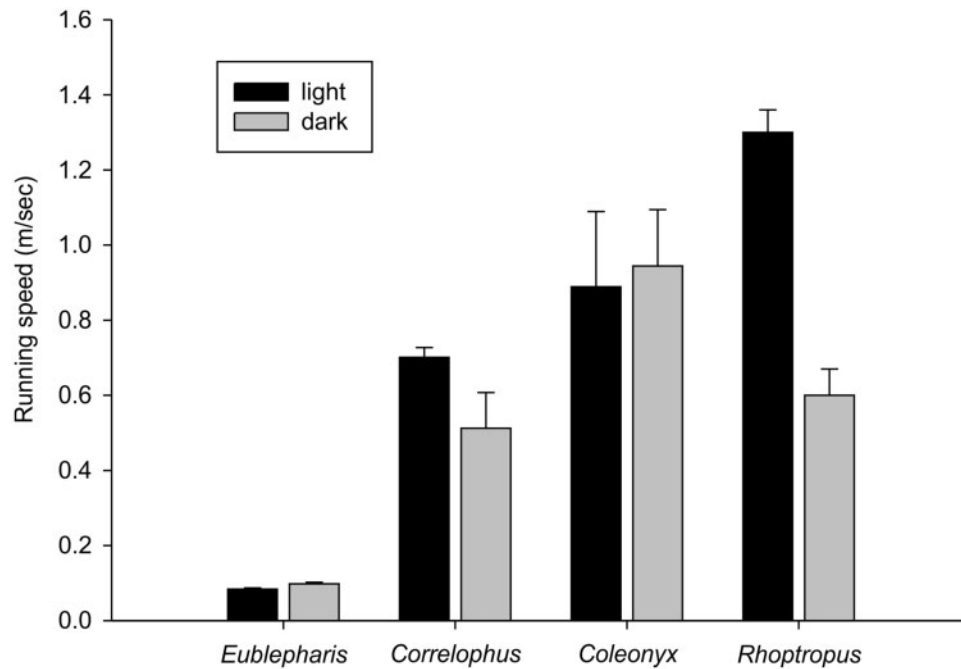


Fig. 5 Maximum sprint performance under different light conditions in four species of gecko. The light condition was approximately 12,000 lx, and the dark condition was under 1 lx. The four species on the left are nocturnal, whereas *R. afer* is diurnal.

Roth et al. 2009). The function of these pinholes has been discussed, and they are likely helpful to maintain the ability to judge distances by means of Scheiner's disc (Murphy and Howland 1986). When fully dilated, the large pupil size results in a small depth of field which is useful for estimating the distance to objects in the visual scene. Depth of field is inversely correlated with pupil size (Green et al. 1980), hence a single very small pinhole would have a very large depth of focus, virtually eliminating focus blur as a distance measure. The presence of multiple pinhole pupil may eliminate that problem. Therefore, through active changes in the barrier to light, nocturnal geckos likely maintain comparable visual capabilities across a range of conditions.

However, if nocturnal geckos can maintain comparable visual abilities across dim and bright photic environments, what explains their slower running speeds compared to diurnal geckos? We hypothesize here that the running speed of nocturnal geckos may be limited by their reduced spatial and temporal visual acuity, which they evolutionary traded for better light sensitivity. A reduction of spatial and temporal acuity may alter optic flow to an extent that requires speed reduction.

Future directions for gecko vision and locomotion

Geckos exhibit remarkable diversity in their diel activity patterns, with numerous shifts from an

ancestrally nocturnal condition to a diurnal activity pattern. In addition, there is a considerable range of activity within single species and/or groups. Thus, variation exists at both evolutionary scales and short temporal and spatial scales. Locomotion depends on the photic environment by providing the optic flow information needed to guide an animal through its complex environment (Fig. 1), which means an integrative framework is necessary for understanding how geckos survive and reproduce. In addition to the incorporation of both visual and locomotor traits, both the photic and physical environment must be examined. Below are some specific directions for the field as a possible roadmap for more integrative projects.

- (1) Finer resolution regarding ecological conditions is critical for understanding shifts in visual system and locomotion. We often characterize geckos as being nocturnal or diurnal, but it is clear that geckos frequently occupy a range of conditions. If the patterns observed in our preliminary data reflect geckos in general, then perhaps nocturnal geckos would be more likely to exhibit variation in their diel activity pattern (due to lack of locomotor cost), whereas diurnal geckos should rarely be active at night due to the locomotor cost. Furthermore, few attempts have been made to quantify habitat clutter or how arboreal and terrestrial geckos might see their environment differently.

- (2) Is locomotion directly linked to photic environment? Our preliminary results suggest that diurnal species will move faster, but will also suffer the most when light is restricted. Is this true across the multiple transitions to diurnality? It is critical to collect more data regarding the role of photic environment on gecko locomotion in order to employ modern phylogenetic comparative methods. The repeated shifts to a diurnal activity pattern provide a perfect situation for investigating convergence and many-to-one mapping of form to function.
- (3) How might other ecological factors, such as habitat structure, interact with light intensity to impact locomotion? If additional habitat complexities (increased clutter, branching, obstacles, etc.) exacerbate the negative impacts of dim light on diurnal species, then we expect a narrow range of activity patterns. However, those populations or species moving on relatively simple terrain might have more flexibility in their activity patterns. In other words, these diurnal individuals/species might be more likely to move under dim light conditions. These questions could be asked from an intraspecific or interspecific perspective, providing multiple avenues of study.
- (4) The knowledge of the visual system of geckos, from opsins to pupils, is largely known from a few representative case studies. These case studies have provided important insights about how gecko eyes might function across different photic environments, but one should be cautious to generalize findings from a few model species to an entire clade comprised of more than 1000 species. Geckos provide a unique opportunity to study evolutionary adaptations to photic environments, because there are many independent transitions. It is feasible that evolution has found different optical solutions to the challenges of transitions between photic environments. For example, pupil dynamics are likely to play a major role in the ability of a gecko to rapidly modulate the amount of light hitting the retina (Frankenberg 1979). There are situations, such as when a predator in the middle of the day exposes a nocturnal gecko, that rapid pupil constriction could mean life or death. Given that geckos can experience pupil area changes of up to 350 times (Denton 1956), it is imperative to maintain the ability to rapidly constrict.
- (5) Finally, behavioral and modeling studies are lacking. Comparative behavioral experiments

that incorporate optomotor response experiments would provide important information regarding how geckos respond to their environment. This, coupled with investigations of the flicker fusion frequency via electroretinography, is needed to understand how optic flow is utilized by geckos during movements. Optical modeling can be added to explore what geckos can see, from what distance they can see, and how light conditions impact vision.

Methods

Histology

As part of a larger comparative study that is beyond the scope of this contribution, we studied the eye histology of the nocturnal leopard gecko. Animals were euthanized following IACUC protocol (UCR AUP 20170039), and eyes were removed within approximately 20 min postmortem. Eyes were fixed in 4% paraformaldehyde solution in phosphate buffered saline (PBS) for a total of 2 h, with a small incision near the sulcus during the first 15 min, and a completely cut away cornea and extracted lens for the remainder of the fixation. After fixation, the eyes were transferred to PBS for long-term storage and kept at 4°C. Histological cross sections were obtained from paraffin-embedded eyes. Before embedding, eye cups were carefully cleaned of all adherent muscular and connective tissues, and the vitreous body was removed as much as possible without damaging the retina. The paraffin blocks containing the embedded eyes were sliced with a microtome at a thickness of 5–10 μ . Mounted tissue slices were stained with hematoxylin and eosin following standard protocols. Flatmounts yielded information about the size, spacing, and density of retinal ganglion cells and photoreceptors. As for the paraffin sections, the first step included the careful removal of ocular muscle and connective tissue. Next, the sclera, the external layer of the eye cup, was cut away. The choroid was more firmly attached to the sclera than to the retina and largely came off during the sclera removal but some pigment remained. The isolated retina was flattened onto a gelatinized microscope slide by making a series of straight incisions, and subsequently stained with cresylviolet following standard protocols. All resulting sections and wholemounts were imaged with an Olympus BX61 brightfield microscope at various magnifications.

Locomotor performance

Using three species of nocturnal gecko (*E. macularius*, *Correlophus ciliatus*, and *Coleonyx variegatus*)

and one species of diurnal gecko (*R. afer*), we examined the role of ambient light on locomotor performance. The data for *R. afer* is from [Birn-Jeffery and Higham \(2016b\)](#). We used both a dark and a bright light condition, and light intensity was measured using a Konica Minolta Illuminance Meter (T-10A) angled toward the laterally-placed camera (see below). The light intensities for the bright and dark conditions (at the midway point of the trackway) were 21,662 lx and 0.25 lx, respectively. As in [Birn-Jeffery and Higham \(2016b\)](#), five infrared lights (Phantom Lite Infrared Pro, Phantom Lite LLC) were used in order to view the geckos without visible light. Blackout material prevented any light from entering the filming room. Temperature was maintained throughout the experiments.

A single high-speed camera (Phantom Miro M110, Vision Research Inc., NJ, USA), operating at 250 Hz, was used to capture a lateral view of the geckos running down a 1 m long trackway that was covered in 60-grit sandpaper. Prior to running, the geckos were held in the light condition for at least 30 s, enough time for the pupil to dilate or constrict. The tip of the snout was digitized in Matlab ([Hedrick 2008](#)), and this was used to quantify maximum running speed. We then compared maximum performance across species and photic environment ([Fig. 5](#)).

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