

RESEARCH ARTICLE

Light level impacts locomotor biomechanics in a secondarily diurnal gecko, *Rhoptropus afer*

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ABSTRACT

Locomotion through complex habitats relies on the continuous feedback from a number of sensory systems, including vision. Animals face a visual trade-off between acuity and light sensitivity that depends on light levels, which will dramatically impact the ability to process information and move quickly through a habitat, making ambient illumination an incredibly important ecological factor. Despite this, there is a paucity of data examining ambient light in the context of locomotor dynamics. There have been several independent transitions from the nocturnal ancestor to a diurnal activity pattern among geckos. We examined how ambient light level impacted the locomotor performance and high-speed three-dimensional kinematics of a secondarily diurnal, and cursorial, gecko (*Rhoptropus afer*) from Namibia. This species is active under foggy and sunny conditions, indicating that a range of ambient light conditions is experienced naturally. Locomotor speed was lowest in the 'no-light' condition compared with all other light intensities, occurring via a combination of shorter stride length and lower stride frequency. Additionally, the centre of mass was significantly lower, and the geckos were more sprawled, in the no-light condition relative to all of the higher light intensities. Locomotor behaviour is clearly sub-optimal under lower light conditions, suggesting that ecological conditions, such as very dense fog, might preclude the ability to run quickly during predator–prey interactions. The impact of ambient light on fitness should be explored further, especially in those groups that exhibit multiple transitions between diel activity patterns.

KEY WORDS: Visual acuity, Locomotion, Performance, Kinematics, Vision, Gekkonidae, Desert, Fog, Stability, Lizard

INTRODUCTION

Vision plays many critical roles in animal survival, such as prey capture (e.g. Fouts and Nelson, 1999), predator avoidance (e.g. Webster and Webster, 1971), courtship (e.g. Murai and Backwell, 2006) and locomotion (e.g. Patla, 1997). Terrestrial animals, specifically, must continually integrate sensory information as they navigate through complex habitats, and this is often through the visual system. The ability to integrate sensory information flowing through the visual system is dependent on ambient light level (Cronin et al., 2014), such that animals moving in dim light require more time to integrate visual signals. The physiological properties of the visual system of vertebrates result in a trade-off between light

sensitivity and visual acuity. The former is critical in dim light conditions, whereas the latter is maximized in conditions of higher luminance. Indeed, the visual acuity of humans is greater than that of nocturnal vertebrates in bright light, but worse in dim light (Cronin et al., 2014). Categorizing a species as diurnal, nocturnal or crepuscular is not straightforward given that ambient light can vary dramatically across temporal and spatial scales. Given the importance of vision for movement, ambient light levels impact the ability of an animal to move quickly (Adams and Beaton, 2000), which will directly impact survival.

Much of what is known about vision and movement stems from research with humans. For example, humans actively steer towards a goal by visually identifying the path a few steps ahead (Field et al., 2007; Matthis and Fajen, 2013, 2014; Patla and Vickers, 2003; Wilkie et al., 2010), rather than focusing purely on the goal; this is probably because of the time required to take in visual feedback information and convert it into feedforward changes in locomotor strategy (Patla et al., 1991). Visual feedback information also alters locomotor strategies when moving in non-level environments. For example, the lower visual field adjusts movement and foot placements (Buckley et al., 2011; Marigold and Patla, 2008; Timmis et al., 2009; Timmis and Buckley, 2012), loss of visual information results in poorer upper body stability (Iosa et al., 2012; Logan et al., 2010) and reduction in visual field causes humans to use less efficient but safer strategies (Jansen et al., 2011). Although we are gaining a greater understanding of the integration of the two systems in humans, we still do not know whether these are applicable to other terrestrial animals that deal with far rougher terrain and the requirement for better capture or escape responses. Additionally, many groups of vertebrates, such as lizards, exhibit a range of diel activity patterns (DAPs), providing a range of natural conditions (Pianka and Vitt, 2003) that can strongly influence the visual system.

Geckos have a unique visual system, possessing highly sensitive colour night vision (Röll, 2001; Roth and Kelber, 2004) via unique photoreceptors for night vision—modified cones (Kojima et al., 1992; Pedler and Tilly, 1964; Röll, 2000). Because of this unique visual ability, geckos may rely heavily on their visual system to move around their natural environment. Geckos occupy a diverse range of habitats (Gamble et al., 2012; Johnson et al., 2005), and show a large amount of variance in their diurnal or nocturnal habits (Gamble et al., 2015). The light intensity in a gecko's habitat can severely affect their foraging activity (Seligmann et al., 2007) as well as the optimality of motion detection (Nava et al., 2009a,b), suggesting that locomotor adjustments may be required as light intensities change.

Geckos move in a variety of complex habitats, and often do so by employing an adhesive apparatus located on the ventral surface of the toes (Birn-Jeffery and Higham, 2014, 2016; Russell, 2002; Russell and Higham, 2009; Russell and Oetelaar, 2015; Zhuang and Higham, 2016). The combination of visual and locomotor specializations makes geckos an ideal group for quantifying the

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relationship between the two. In addition, there are multiple transitions from nocturnality, the ancestral condition among geckos, to diurnality (Gamble et al., 2015). For example, the genus *Rhoptropus* is a secondarily diurnal genus of gecko found in southern Africa. They are within the *Pachydactylus* radiation, which includes a number of ancestrally nocturnal genera such as *Pachydactylus*, *Chondrodactylus* and *Colopus* (Bauer and Good, 1996). Within *Rhoptropus*, one species from Namibia, *R. afer*, has shifted to a cursorial lifestyle with a reduced adhesive system. In addition to running much faster than other species in the genus (Higham et al., 2015; Higham and Russell, 2010), it is also found on relatively level terrain (Collins et al., 2015). Given the high speeds and diurnal lifestyle, the ambient light conditions are likely to play a significant role in the escape behaviour of this species. Despite this, populations exist in a range of terrestrial habitats (Collins et al., 2015; Haacke and Odendaal, 1981) from the coast to many kilometres inland. Coastal Namibia experiences double the number of fog days annually of the inland areas (Eckardt et al., 2013; Lancaster et al., 1984; Olivier, 1995), and fog reduces the light intensity experienced by the geckos. The range in fog occurrence and density suggests that *R. afer* experiences a range of illumination over temporal and spatial scales.

We examined the effect of light intensity on the locomotion of *R. afer*. As ambient light was reduced, we expected animals to (1) move slower with their centre of mass closer to the ground and (2) use a wider stance width, to improve lateral stability, at non-favourable light intensities. These alterations increase body stability and prevent the likelihood of falling. Understanding the integration of vision and locomotion in such a diverse group as geckos could lead to a greater understanding of the plasticity of the visual system, its ecological effect and how climate change may further affect animals. It may also reveal control strategies that can lead to visual guidance control systems for robots.

MATERIALS AND METHODS

Animals

We collected seven adult individuals of *Rhoptropus afer* Peters 1869 in Namibia in 2013 around Swakopmund and Gobabeb (mass: 2.92 ± 0.43 g; intergirdle length: 2.59 ± 0.13 cm; means \pm s.e.m.). This sample size is based on previous experiments. Geckos were obtained from the range of ecological conditions experienced by *R. afer* (Lancaster et al., 1984; Olivier, 1995). Animals were caught by hand and transferred to the laboratory in Swakopmund in breathable cotton bags. All collections were approved by the Ministry of Environment and Tourism in Namibia (permit number 1706/2013 issued to T.E.H.) and by the IACUC at UC Riverside.

Experimental protocol

We modified the room light for each trial to four different light intensities: dark (no light), low light, medium light and high light. Light intensity was measured in lux before each trial using a Konica Minolta Illuminance Meter (T-10A) orientated vertically from the

trackway or angled towards the lateral camera (see below) in the same orientation as the animal's eyes at the start, middle and end of the trackway. Average light intensities across trials are recorded in Table 1, and were selected to reflect a range of measured light intensities in the natural habitat when animals were active. Light intensity was adjusted using desk lamps (60 W), room lights and a 600 W flood light. To enable recording in the dark and at low light intensities at a high frame rate, we also used five infrared lights (Phantom Lite Infrared Pro, Phantom Lite LLC). The room was otherwise isolated from outside light using blackout material over all windows and doors. Despite changes in light intensity, temperature was maintained at a constant across conditions.

All animals were run across a flat trackway, measuring approximately 1 m long and 0.1 m wide. Animals were gently tapped on the tail to induce escape locomotion. The trackway was covered in 60-grit sandpaper to mimic natural surfaces found in the habitats. Two high-speed video cameras (Phantom Miro M150, Vision Research Inc., NJ, USA) were used to record lateral and dorsal views of the trackway. The cameras were synchronized and recorded at 500 Hz, with the shutter speed at 1/600 s.

Before each trial, each individual was held for 30 s in the light condition of that trial to allow their eyes to adjust to the new light intensity before being motivated to run across the trackway. Changes in eye dilation between light conditions in *R. afer* were also recorded and took at most a few seconds. Three steady and straight strides for both forelimb and hindlimb were obtained per individual and condition. Each individual was marked using white nail polish and these points were placed on the mid-pectoral/pelvic girdle as well as in between the two girdles. On the right side of the body, markers were also placed on joints: shoulder/hip, elbow/knee, wrist/ankle and metacarpophalangeal (MCP)/metatarsophalangeal (MTP) joint. The order of treatments was randomized among individuals.

Data analysis

Markers were digitized using DLT_dv5 (Hedrick, 2008) custom-written software for Matlab. Digit III tips on the forelimb and hindlimb were also digitized. These landmarks provided 3D coordinates for each marker with x , y , z directions being fore–aft, medio-lateral and vertical, respectively. A centre of mass (CoM) proxy was calculated using the dorsal markers along the mid-line of the body, and was used to calculate CoM fluctuations, speed and acceleration. Stride details were based from foot contact to the subsequent foot contact of the same foot, and only measured along the fore–aft axis. Step length and time were calculated from foot contact until foot contact of the ipsilateral foot. Step width was the medio-lateral distance between the CoM and digit III. Although this is not the actual step width between the foot and its contralateral foot contact, it is representative of approximately half that distance and provides details on how sprawled a posture was used. Duty factor was the proportion of foot contact with the ground compared with the stride time.

A virtual leg was calculated in the sagittal plane as the distance between the CoM and the MCP/MTP. This allowed leg retraction

Table 1. Average light intensities recorded during experimental data collection

Light condition	Start of runway		Mid-runway		End of runway	
	Vertical	Angled	Vertical	Angled	Vertical	Angled
No	0.04±0.01	0.07±0.02	0.163±0.11	0.25±0.15	0.04±0.02	0.08±0.04
Low	370.37±31.43	348.16±39.31	419.37±6.31	408.53±11.80	432.32±6.91	402.42±16.31
Medium	6400±703.62	3914.21±190.77	7603.68±174.14	4833.68±661.35	6826.84±116.38	4349.47±347.68
High	13,862±495.81	16,381±400.79	18,446±330.38	21,662.1±277.79	19,894.5±177.72	24,590.5±357.92

Light intensity (lx) was measured by an illuminance meter, either orientated vertically or angled towards the lateral camera.

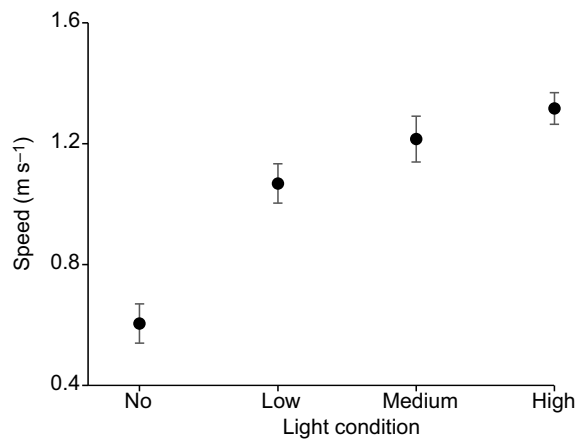


Fig. 1. Changes in speed with increasing ambient light intensity. Speed was significantly different between the differing light intensity trials (ANOVA: $F_{3,6}=17.91$, $P<0.005$). Speed in the ‘no-light’ condition was significantly slower than that in all other conditions (Dunn–Sidak *post hoc*: $P<0.005$); *R. afer* also ran slower in the low light condition compared with the medium and high light conditions (Dunn–Sidak *post hoc*: $P=0.03$ and $P<0.005$, respectively). Sample size was seven individuals, with three trials averaged per individual; values are means \pm s.e.m.

velocity to be calculated; this is the backwards movement of the leg during the second half of swing phase. The leg retraction velocity is associated with leg control and determines foot contact angle, which is linked to successful stance phases and reductions in leg loading (Blum et al., 2011; Daley and Usherwood, 2010). Leg retraction velocity is modified in non-level conditions to counteract perturbations and allow successful negotiation of non-level terrain (Birn-Jeffery and Daley, 2012; Blum et al., 2014).

Statistical analyses

All statistical analyses were performed in custom-written scripts in Matlab. As speed was expected to play an important role in the strategy *R. afer* used at different light intensities, speed needed to be removed from all other variables; therefore, all variables of interest were regressed against speed. If the regression was significant ($P<0.05$), and if enough data were explained by this trend ($r^2>0.15$), then the residuals were used for further analysis. To compare between light intensities, the data were run through an ANOVA (assumptions were met), using light intensity as the fixed factor and individual as a random factor. F -values were adjusted for the interaction term (light intensity \times individual), with the mean squares of the interaction term being used as the denominator for calculating

the F -statistic for the main fixed effect. This method is set according to procedures by Zar (1996).

RESULTS

Speed was significantly different between the differing light intensity trials (Fig. 1; $F_{3,6}=17.91$, $P<0.005$). Speed in the ‘no-light’ condition was significantly slower than that in all other conditions (Dunn–Sidak *post hoc*: $P<0.005$), whilst *R. afer* also ran slower in the low light condition compared with the medium and high light conditions (Dunn–Sidak *post hoc*: $P=0.03$ and $P<0.005$, respectively).

As expected, many of the spatio-temporal variables generally associated with speed changes were highly correlated with speed (Table 2). Factors such as duty factor decreased with light intensity, whilst stride length and stride frequency increased with light intensity (Fig. 2). Once these variables were speed regressed and residuals used for further analyses, these effects were not significant (e.g. forelimb duty factor: $F_{3,6}=0.35$, $P=0.79$; hindlimb stride length: $F_{3,6}=0.58$, $P=0.64$). Interestingly, duty factor was above 0.5, denoting a vaulting gait, in the no-light condition in the forelimb, but shifted to a bouncing gait (<0.5) at all other light intensities.

Some variables were not affected by speed, such as step width and step length (Table 2). Step width was significantly wider in both forelimb and hindlimb in the no-light condition compared with all other conditions (Fig. 2; forelimb: $F_{3,6}=5.00$, $P=0.01$; hindlimb: $F_{3,6}=3.54$, $P=0.04$). In contrast, step length – the distance the CoM moves whilst the foot is in contact with the ground – was maintained across all light conditions (Fig. 2; forelimb: $F_{3,6}=0.85$, $P=0.48$; hindlimb: $F_{3,6}=1.60$, $P=0.22$). This indicates that the changes seen in stride length (Fig. 2) are achieved through greater movements of the CoM during the swing phase of the leg.

As often seen in gait variables, changes in footfall timing were significantly associated with speed (Table 2), but once speed was taken into account, differences between light intensities were no longer statistically significant (e.g. forelimb stride time: $F_{3,6}=0.07$, $P=0.97$; hindlimb stance time: $F_{3,6}=0.14$, $P=0.94$). In the forelimb in the no-light condition, stance phase was longer than swing phase, but under all other conditions, this was reversed (Fig. 3), indicating the change in duty factor mentioned above. In contrast, in the hindlimb, it is only in the no-light condition that stance and swing phase can be statistically separated (hindlimb swing time: $F_{3,6}=4.04$, $P=0.02$); under all other light conditions they were of similar duration (Fig. 3). Stride time in both forelimb and hindlimb was similar across low to high light conditions, but during the no-light condition, stride time was significantly longer (e.g. forelimb Dunn–Sidak, no-light against all other conditions $P<0.005$).

Table 2. Speed regression results

Variable	Forelimb				Hindlimb			
	Slope	Intercept	P -value	r^2	Slope	Intercept	P -value	r^2
Duty factor	-0.25	0.66	<0.005*	0.72*	-0.17	0.71	<0.005*	0.59*
Step width	-0.003	0.01	<0.005*	0.1	-0.001	0.02	0.06	0.04
Step length	-0.003	0.03	0.04*	0.05	0.006	0.03	0.006*	0.08
Stride length	0.04	0.04	<0.005*	0.69*	0.04	0.04	<0.005*	0.61*
Stride frequency	7.82	4.9	<0.005*	0.69*	7.75	5.07	<0.005*	0.64*
Stance time	-0.06	0.11	<0.005*	0.54*	-0.06	0.11	<0.005*	0.48*
Swing time	-0.01	0.06	<0.005*	0.22*	-0.01	0.05	<0.005*	0.27*
Stride time	-0.07	0.17	<0.005*	0.56*	-0.07	0.16	<0.005*	0.49*
$\Delta\text{CoM}_{\text{stance}}$	-0.0002	0.0004	0.52	0.005	-0.00009	0.0005	0.83	0.0005
Leg retraction velocity	882.62	511.6	<0.005*	0.29*	4001.8	-140.32	0.002*	0.13

$\Delta\text{CoM}_{\text{stance}}$, centre of mass at stance.

*Significant result; bold indicates a significant regression from which residuals were used for all further analysis.

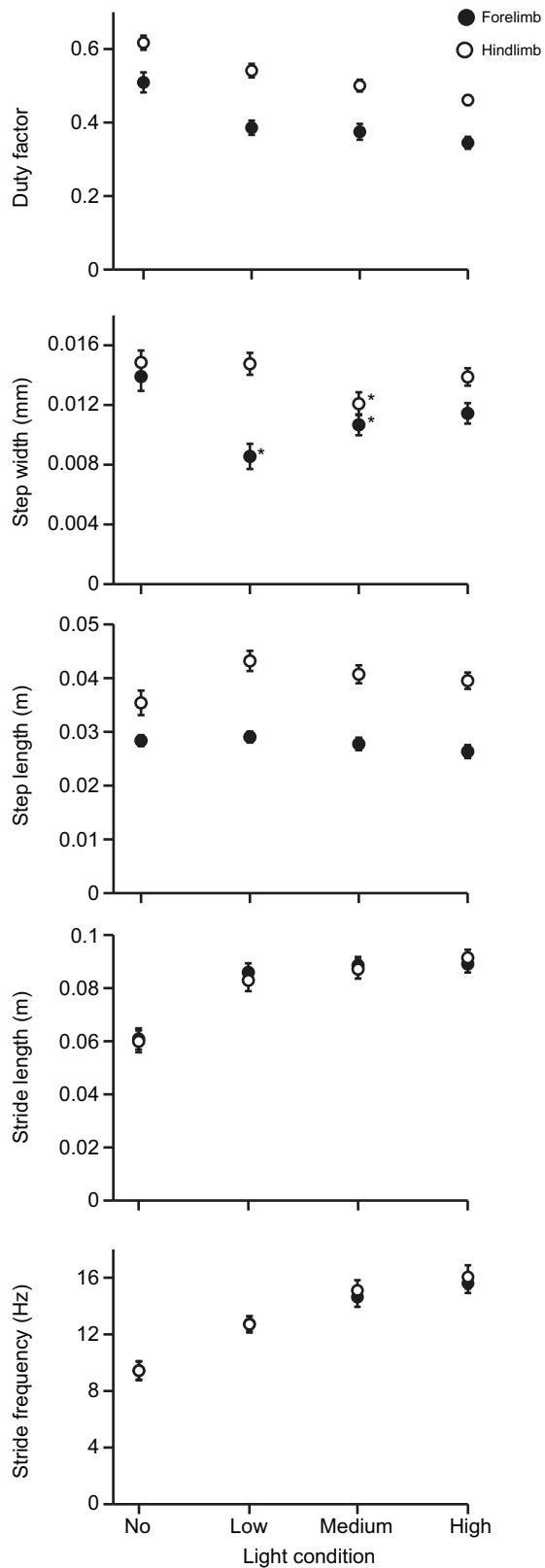


Fig. 2. Spatio-temporal changes with ambient light intensity in forelimb and hindlimb. As light intensity increased, speed was increased via increases in stride length and stride frequency in the forelimb and hindlimb. Step width was reduced with increasing light intensity, suggesting an alteration in posture. Duty factor was above 0.5, denoting a vaulting gait, in the no-light condition in the forelimb, but shifted to a bouncing gait (<0.5) at all other light intensities. Values are means \pm s.e.m.

The changes in the movement of the CoM were not correlated with speed (Table 2). The vertical height of the CoM was significantly lower at footfall (CoM_{ipos}) in the no-light condition in both the forelimb ($F_{3,6}=5.79$, $P=0.005$; Dunn–Sidak *post hoc* tests, all $P<0.05$) and the hindlimb ($F_{3,6}=3.25$, $P=0.05$; Dunn–Sidak *post hoc* tests, all $P<0.05$) compared with that at all other light intensities (Fig. 4). However, the change in CoM during the stance phase ($\Delta\text{CoM}_{\text{stance}}$) did not significantly differ in either the forelimb or the hindlimb across all conditions (forelimb: $F_{3,6}=0.71$, $P=0.56$; hindlimb: $F_{3,6}=0.91$, $P=0.46$). In general, the only deviations in the CoM occurred in the no-light condition (Fig. 4); at all other light intensities, the movements of the CoM were similar.

The backwards movement of the leg during the second half of the swing phase differed to a greater extent in the hindlimb than in the forelimb (Fig. 5); the hindlimb also exhibited much faster leg retraction velocities in the lighter conditions. The forelimb leg retraction velocity was significantly affected by speed, whilst the hindlimb leg retraction was not (Table 2); therefore, only forelimb leg retraction velocity was adjusted to account for speed (see Materials and methods). There was a distinctive trend of increasing leg retraction velocity with increasing light intensity in both the forelimb and the hindlimb (Fig. 5). In the forelimb, leg retraction velocity was significantly lower in the no-light condition compared with that in all other conditions ($F_{3,6}=13.05$, $P<0.005$; Dunn–Sidak *post hoc* tests, all $P<0.005$). In contrast, the hindlimb showed no significant differences between the leg retraction velocities in each condition; this is probably due to the large variance seen in these values (Fig. 5).

DISCUSSION

Linking animal locomotion to diel activity patterns is important for understanding the co-evolution of vision and locomotion. We found that a diurnal gecko, *R. afer*, adjusts its locomotion on level terrain under differing light intensities. These geckos significantly reduce their speed, and associated spatio-temporal characteristics, when moving in reduced light conditions. Other factors, such as changes in CoM position, stance width and leg retraction, which are not associated with changes in speed, are also altered, suggesting an adjustment in the neuromechanical control of locomotion when visual input is reduced.

Changes in speed with varying light conditions

Rhoptropus afer are able to sprint at up to 2.5 m s^{-1} in their natural habitat (Higham and Russell, 2010) and are considered cursorial animals that use sprinting as an escape strategy (Bauer et al., 1996; Collins et al., 2015; Haacke, 1976; Johnson and Russell, 2009; Lamb and Bauer, 2006; Odendaal, 1979; Werner, 1977). Therefore, sprinting fast is likely to be very important for the survival of this species. However, the geckos in our study were unable to maintain the same sprint speed in conditions of no or low light, as sprint speed was significantly reduced. This agrees with previous studies involving adjustments to visual information that also resulted in humans decreasing their speed (François et al., 2011; Halleman et al., 2010; Jansen et al., 2011; Marigold and Patla, 2008; Matthis and Fajen, 2013, 2014). This suggests that, in sub-optimal light conditions, the ability to evade predators may be significantly reduced. So, why is locomotor speed reduced when visual acuity is depressed? Reducing running speed in reduced light conditions provides a greater time frame in which to receive any visual information to differentiate between objects in the environment. It also allows greater time to use other systems for feedback information, which cannot be obtained prior to the step landing, such as proprioceptive feedback, which has a delay of around

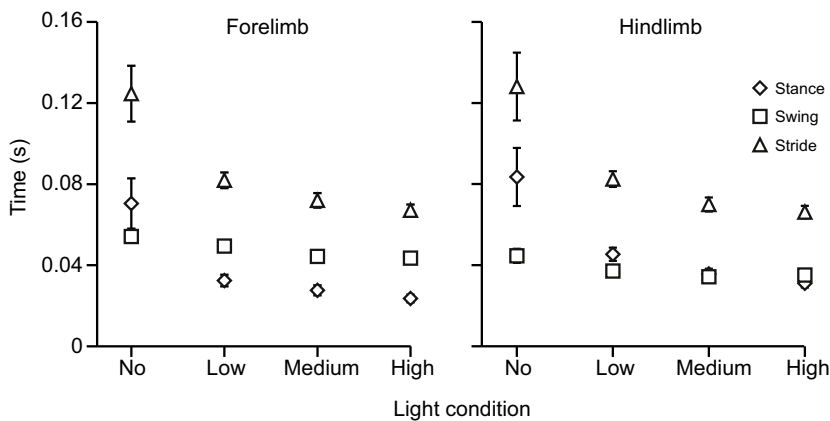


Fig. 3. Effects of ambient light intensity on footfall timings. In the hindlimb, it is only in the no-light condition that stance and swing phase can be statistically separated (hindlimb swing time: ANOVA: $F_{3,6}=4.04$, $P=0.02$); under all other light conditions, they were of similar duration. Stride time in both the forelimb and hindlimb was similar across low to high light conditions, but during the no-light condition, stride time was significantly longer (e.g. forelimb Dunn–Sidak *post hoc* test, no-light against all other conditions: $P<0.005$). Values are means \pm s.e.m.

30–40 ms (Duysens et al., 2000; Zill, 1985). Speed is affected greatly by light conditions, and this effect is likely to increase when the environment becomes less uniform. Reductions in speed may help to prevent falling, alongside increasing time for feedback information from other sense systems. An alternative explanation for the decreased speed under conditions of decreased illumination may be that it decreases the likelihood of being detected by predators. Future investigation of predators, including their visual capabilities, will be important for teasing this apart.

Vision and stability

Stability may be a significant problem during times when visual input is sub-optimal. Here, *R. afer* altered neuromechanical control of body position by using a significantly more sprawled posture (wider step width; Fig. 2) as well as maintaining the CoM closer to the ground in no-light conditions (Fig. 4). These particular variables were not altered purely because of speed changes and therefore are suggestive of a different neuromechanical control strategy during times of reduced visual input. Alongside these two postural adjustments, the increase in duty factor indicates a vaulting gait was used in no-light conditions, whilst at other times a bouncing gait was used. A vaulting gait would probably allow the animal to use static stability (Ting et al., 1994), which combined with the more sprawled posture would also increase the stability of the animal (Full and Koditschek, 1999). Stability, particularly in the upper body in bipeds, is an issue in visually impaired situations (Iosa et al., 2012)

and more cautious control strategies are used instead (Hallemans et al., 2010; Jansen et al., 2011). Thus, it appears that there are commonalities among a wide range of vertebrate groups.

Leg retraction can affect the stability of the locomotor system (Blum et al., 2011, 2010; Seyfarth et al., 2003), the size of the disturbances a system can reject (Karszen et al., 2011) and the leg loading during a stance phase (Blum et al., 2014; Vejdani et al., 2013). Adjusting leg retraction velocity alters the landing posture, adjusting a trade-off between achieved successful stance phase versus reducing leg loading (Daley and Usherwood, 2010). Active changes in leg retraction velocity are seen in perturbation experiments (Birn-Jeffery and Daley, 2012; Blum et al., 2014), and here *R. afer* appears to actively slow down the retraction velocity in no-light conditions (Fig. 5). According to the theoretical work of Daley and Usherwood (2010), this would result in landing with a shallow leg angle (if the ground is in the same position vertically), leading to higher leg forces. As *R. afer* has restricted vision in no-light conditions, reducing retraction velocity provides the animal with a greater time ‘safety’ margin to accommodate changes in ground level to the previous foot contact. This gives more time for the foot to retract backwards without exceeding the point where no ground contact is made and a fall may occur. Knowledge of the height of ground contact is an important input for locomotor control, which is often provided via visual feedback information. When visual information regarding ground contact is not available, adjustments to ground clearance are made to increase the ‘safety

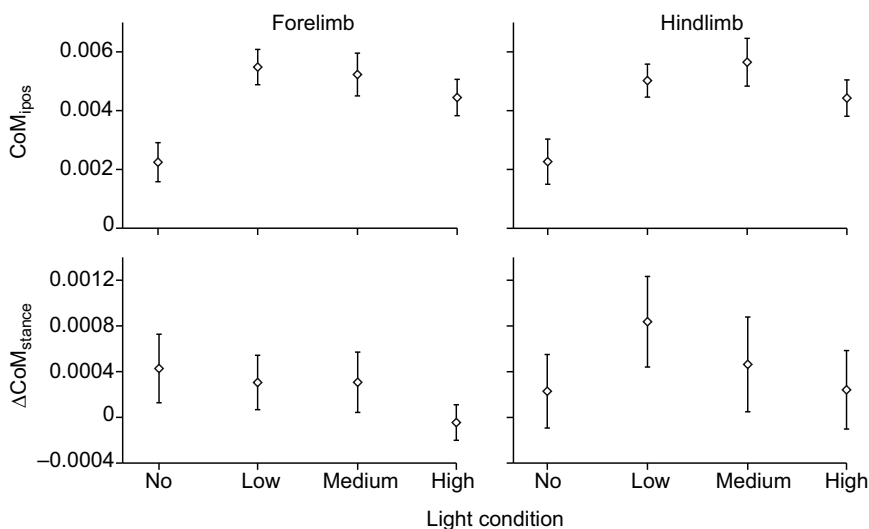


Fig. 4. Postural centre of mass (CoM) changes with ambient light intensity. The vertical height of the CoM at footfall (CoM_{ipos}) was significantly lower at footfall under the no-light condition in both the forelimb (ANOVA: $F_{3,6}=5.79$, $P=0.005$; Dunn–Sidak *post hoc* tests, all $P<0.05$) and the hindlimb (ANOVA: $F_{3,6}=3.25$, $P=0.05$; Dunn–Sidak *post hoc* tests, all $P<0.05$) compared with that at all other light intensities. However, the change in CoM during the stance phase (ΔCoM_{stance}) did not significantly differ in either the forelimb or the hindlimb across all conditions (forelimb: ANOVA: $F_{3,6}=0.71$, $P=0.56$; hindlimb: $F_{3,6}=0.91$, $P=0.46$). Values are means \pm s.e.m.

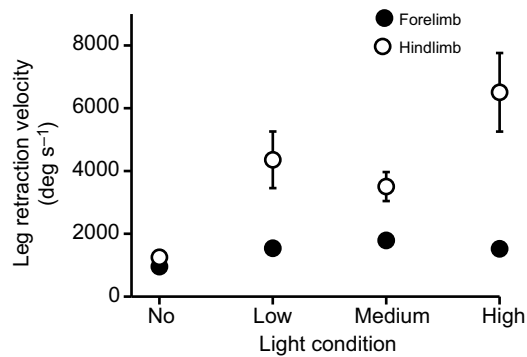


Fig. 5. Leg retraction velocity changes with ambient light intensity. There were no significant differences in the hindlimb retraction velocity. In the forelimb, leg retraction velocity was significantly lower in the no-light condition compared with that in all other conditions (ANOVA: $F_{3,6}=13.05$, $P<0.005$; Dunn–Sidak *post hoc* tests, all $P<0.005$). Values are means \pm s.e.m.

factor' (Matthis and Fajen, 2014; Timmis and Buckley, 2012), although there is a minimum level of visual information below which falls are highly likely (Matthis and Fajen, 2013).

Moving in foggy habitats

Daytime ambient light levels can vary dramatically among habitats via a number of factors, such as canopy cover in a forest (Nava et al., 2009b; Pringle et al., 2003), cloud cover and fog level. 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 light as a result of the presence of the droplets (Cronin et al., 2014; Gultepe et al., 2007; Houghton, 1931). Of these, light scattering has the greatest impact on visibility in fog (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. This overall reduction in light penetration has the potential to alter the effective light level for animals on the ground. Thus, locomotion in foggy conditions is likely to represent locomotion under low light conditions. Given that *R. afer* is observed moving in its natural habitat under foggy conditions, moving under low light conditions is a relevant and important ecological factor for this species.

One question is whether *R. afer*, which evolved from a nocturnal ancestor, may have been pre-adapted to moving in low light conditions. Our study indicates that the transition to diurnality has precluded the ability to see effectively in darkness, as evidenced by the reduction in performance and postural shifts to enhance stability. Although *R. afer* is observed moving under foggy conditions, it is possible that the window of activity or the type of behaviour employed might be altered when the level of fog is high. If this is the case, foraging time may be severely limited during certain times (Lancaster et al., 1984; Olivier, 1995). Alternatively, many different ecological factors may accompany the coastal fog, potentially reducing predation on *R. afer* in this habitat. This would then lead to a decreased selection pressure on sprint speed. Future work that addresses this and other factors, such as the retinal modifications of *R. afer* relative to other nocturnal members of the *Pachydactylus* radiation, will provide considerable insight into the evolution of diurnality.

Conclusions and future directions

Compared with its behaviour under high levels of ambient light, *R. afer*, a secondarily diurnal gecko, reduces its speed, adopts a

sprawled posture and reduces its hindlimb retraction velocity when ambient light is reduced. These biomechanical alterations need to be linked with the morphology and physiology of the visual system of *R. afer*, but also compared with the biomechanics and visual system of other diurnal and nocturnal species within the *Pachydactylus* radiation of southern Africa. The plasticity of eye morphology and physiology is also unexplored among geckos. The coastal populations of *R. afer* may also have developed differential eye morphology to accommodate the decreased light levels, such as enhanced light sensitivity. Detailed examination of the retinal ganglion cell layer in order to determine ganglion cell densities, coupled with focal length estimates, will provide measures of visual acuity across geckos that vary in their diel activity pattern.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Both authors developed and discussed the project. Both authors also contributed to collecting the specimens and data. A.V.B.-J. analysed the data. Both authors wrote the manuscript.

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