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Shaking things up: the unique feeding behaviour of western banded geckos when consuming scorpions

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Predators that feed on dangerous prey species must evolve mechanisms to reduce the likelihood of injury or death during a predation attempt. Scorpions are prime examples of dangerous prey items for insectivores, because they can inflict a venomous and potentially fatal sting when attacked. Despite this risk, the western banded gecko (*Coleonyx variegatus*), a generalist insectivore, occasionally preys on dune scorpions (*Smeringurus mesaensis*). We use high-speed videography to examine the modulation of prey capture biomechanics in relationship to prey type. The capture of undefended evasive (cricket) and non-evasive (worms) prey follows previous studies of lizard attack kinematics. However, we have discovered a unique shake-feeding behaviour used by western banded geckos when feeding on scorpions, whereby the gecko bites the scorpion, then performs very rapid side-to-side shaking with its head and body. Given the speed and violence of shake-feeding, we suggest that geckos shake the scorpion to cause mass trauma and subsequent immobility or, potentially, to break the stinger and render the scorpion harmless. This behaviour might be widespread among geckos that feed on these dangerous prey species.

ADDITIONAL KEYWORDS: arthropod – high speed – kinematics – lizard – performance – predator – prey.

INTRODUCTION

Prey capture in lizards has been documented across numerous species (reviewed by Schwenk, 2000; Bels & Whishaw, 2019; Montuelle & Kane, 2019). Lizards can use either jaw or lingual prehension when capturing prey, with very fast strike velocities in some species (e.g. 1 m s^{-1} in *Varanus* lizards; Montuelle *et al.*, 2012). However, most studies have focused on non-dangerous prey, such as grasshoppers, crickets, worms and others (e.g. Vollin & Higham, 2021). Some lizards will attack and consume dangerous prey (e.g. those producing venom), although the mechanisms underlying these attacks are, in general, poorly understood. However, past research has shown that lizards that use lingual feeding to eat venomous ants have evolved specialized feeding morphologies and behaviours to avoid stings (Meyers & Herrel, 2005; Sherbrooke & Schwenk, 2008).

Scorpions are among the earliest animals to invade terrestrial ecosystems (Rolfe, 1985), and they are still among the most successful. In many arid ecosystems, scorpion biomass is estimated to be greater than that of all vertebrates combined and greater than that of all other arthropods with the exception of ants and termites (Polis & Yamashita, 1991). These high densities make scorpions a valuable food source for predators that are able to subdue them. Consequently, a variety of predators have evolved mechanisms to circumvent the venomous stings of scorpions during predation attempts (Polis *et al.*, 1981).

Here, we tested experimentally the effect of prey type (scorpion vs. non-scorpion) on the subjugation behaviour used by the western banded gecko (*Coleonyx variegatus*), an abundant nocturnal eublepharid gecko endemic to arid regions of western North America. Western banded geckos are generalist insectivores,

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eating a variety of arthropods that are encountered opportunistically while actively foraging at night (Parker, 1972). Previous laboratory experiments found that banded geckos lunge at crickets by rapidly extending their hindlimbs and forelimbs, reaching velocities of almost 1 m s^{-1} (Vollin & Higham, 2021). However, that study was limited to crickets as prey. Dietary analysis has shown that banded geckos consume scorpions, at least occasionally, despite the risk of being stung (Parker & Pianka, 1974). Our study is the first to investigate quantitatively the unique shake-feeding behaviour that geckos use to subdue scorpions before ingestion.

MATERIAL AND METHODS

We conducted a series of standardized feeding experiments using animals captured from sand dune ecosystems in the lower Sonoran Desert of south-western Arizona, USA. The study methodology was approved by the San Diego State University institutional animal care and use committee (protocol 19-08-009C). Banded geckos were collected under an Arizona State Scientific Collecting Permit (SP506470). Geckos were housed temporarily in plastic terraria (30 cm × 20 cm × 15 cm) lined with sand collected from their habitat and maintained for 2–3 weeks in captivity on a diet of laboratory-bred crickets and mealworms. Given that geckos are exclusively nocturnal, feeding trials were conducted between 18:00 and 06:00 h at ambient night-time temperatures (20–25 °C). At the onset of a trial, the lid of the terrarium was carefully removed in order that the trial could be recorded with a high-speed camera (Edgertronic SC1) at either 498 Hz (two trials) or 1288 Hz (29 trials). Trials were recorded in darkness, but infrared spotlights were positioned above the terrarium to provide light that could be seen by the camera, but not by the animals. The camera was always positioned directly above the terrarium to provide a dorsal view of the feeding behaviour.

An arthropod collected from the same habitat as the gecko was then placed in the terrarium and allowed to move freely. Arthropods used as food included dune scorpions (*Smeringurus mesaensis*) or one of three non-venomous arthropods caught opportunistically: an antlion lacewing (*Paranthaclisis* sp.), field cricket (*Gryllus* sp.) or sand roach (*Arenivaga* sp.). All wild-caught arthropods were approximately the same size as the 15–20 mm crickets and mealworms used to maintain geckos in captivity; that is, all were small enough to be readily consumable. For all geckos, the snout–vent length was measured immediately after feeding trials in order that it could be used to calibrate distances in digitized video frames. We used each of nine individual geckos up to one time in trials with non-venomous arthropods (N = 8) and up to three times in trials with dune scorpions (N = 21).

To quantify the characteristics of feeding behaviours, we examined digitized video frames using a combination of IMAGEJ (v.1.53), DLTDATAVIEWER v.5 (Hedrick, 2008) in MATLAB (R2016b) and RSTUDIO (Rv.4.0.3). Prey contact was scored as the frame in which the gecko contacted the arthropod with its open mouth. When geckos exhibited shake-feeding, we counted the total number of shake cycles, with each shake cycle defined as a full head movement from one side of the midline to the other and back to the starting position. To determine the duration of a typical cycle of head shaking, we averaged the first five full cycles of the first trial for each individual gecko. We determined whether geckos were stung during any part of the feeding episode by visual documentation of contact between the scorpion stinger and the gecko, and we determined that scorpions were still mobile after bouts of shake-feeding if they exhibited any leg, tail or pincher movements during ingestion. For a subset of videos, and when video quality was sufficient, we estimated several kinematic variables.

To extract kinematic data, we first used IMAGEJ to trace the midline of the gecko from snout to vent in the frame immediately before the gecko beginning to lunge towards the prey, then used the measured snout–vent length to set the length of the tracing and calibrate the frame. We then measured both the straight-line distance between the left eye and the centre of the pelvic girdle (which was later used to calibrate videos for analysis using two discrete points) and the distance between the tip of the snout and the closest part of the prey. In MATLAB, we then digitized five points within each video: centre of the pelvic girdle; centre of the pectoral girdle; left eye; tip of the snout; and, on the scorpion, the posterior of the abdomen. The x–y files were imported into RSTUDIO (R v.4.0.3), and the x–y points were then calibrated by setting the distance between the left eye and cloaca equal to the straight-line distance measured in IMAGEJ. We then applied a 50 Hz low-pass Butterworth filter to the point–point displacement values for the snout. Lunge velocity and acceleration were then calculated from the filtered data, and we used generalized linear models to compare lunge velocity and acceleration between different prey types (scorpion or other).

To estimate the angular velocity and acceleration achieved during head shaking, we calculated the angle of the head of the gecko as the angle between the pelvic girdle, pectoral girdle (vertex) and the snout for a subset of trials (Fig. 1). Given that the scorpion is often elongated while being swung around, we also estimated the angular velocity, angular acceleration, torque and centripetal force experienced by the scorpion as it rotates around the y-axis of the head

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of the gecko. We then calculated the angular velocity and acceleration for two angles: the angle created by the pelvic girdle, pectoral girdle and the snout (i.e. angle of the head of the gecko), and the angle created by the pectoral girdle, snout and the scorpion (Fig. 1). To examine whether there was the potential for a whiplash-like effect when the gecko rapidly changed direction, we conducted a cross-correlation analysis between the two angles. All angular velocity and acceleration values were calculated from filtered (50 Hz low-pass Butterworth filter) frame-to-frame changes in the angles. To calculate torque (T), we first modelled the scorpion as a rod with a length (L) of 1 cm and mass (M) of 2 g, which allowed us to make a rough estimate of rotational inertia (I; eqn. 1) as follows:

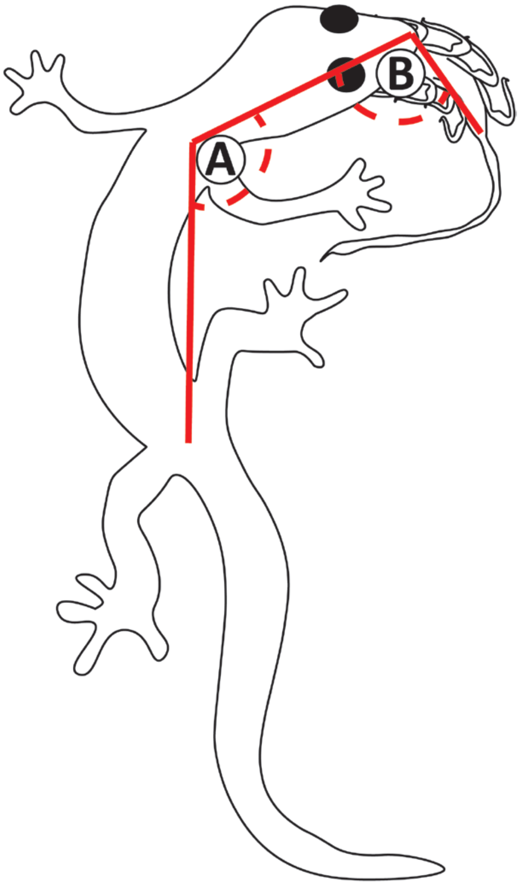

Figure 1. An illustration of the methods used to calculate the angle of the head of the gecko (A) and the scorpion (B).

$$I = \frac{1}{3} M \times L^2 \tag{1}$$

We then multiplied the rotational inertia by the maximum angular acceleration of the scorpion rotating around the gecko to calculate torque. We then estimated centripetal force (F_c) by isolating the x–y coordinates of the scorpion for half of a shake cycle (from the left-most point to the right-most point) and used the R package 'conicfit' to fit a circle to the points and calculate a radius (r). We then used the maximum velocity of the scorpion (V), a mass of 2 g and the calculated radius to estimate centripetal force (eqn. 2) as follows:

$$F_c = \left(M \times V^2\right)/r \tag{2}$$

We extracted kinematic data for the scorpion only if it was clearly visible in the video, was not wrapped around the head of gecko and did not contact the sides of the enclosure. Unless stated otherwise, values are given as the mean ± SD.

RESULTS

PREDATORY BEHAVIOUR TOWARD NON-VENOMOUS ARTHROPODS

Geckos exhibited typical predatory behaviour toward all non-venomous arthropods (Dial, 1978; Bels *et al.*, 2019). This consisted of carefully approaching moving arthropods with slow stalking movements. Once they were within a few centimetres, they struck at the prey by pushing forwards with their hindlimbs and rapidly straightening their spine, launching their head towards the prey (Vollin & Higham, 2021). When attacking non-venomous prey, geckos on average reached a mean maximum velocity of 0.57 m s^{-1} and a maximum acceleration of 30.03 m s^{-2} (Table 1). Prey was seized in the mouth upon contact, occasionally shaken once or twice, and consumed within 10–20 s (Video 1).

PREDATORY BEHAVIOUR TOWARD SCORPIONS

When tested with scorpions similar in size to other arthropods, geckos on average reached a mean

Table 1. Descriptive statistics for the kinematics of geckos lungeing towards scorpion and non-scorpion prey

Prey	Mean velocity (m s^{-1})	Maximum velocity (m s^{-1})	Maximum acceleration (m s^{-2})
Non-scorpion	0.41 (0.27–0.79)	0.57 (0.24–1.00)	30.03 (13.63–58.21)
Scorpion	0.47 (0.21–0.64)	0.76 (0.53–1.10)	36.86 (14.36–61.12)

Values are the mean (minimum–maximum).

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maximum velocity of 0.76 m s^{-1} and a maximum acceleration of 36.86 m s^{-2} (Table 1). When compared with the kinematics of geckos lungeing at non-scorpion arthropods, the maximum acceleration obtained by geckos was similar (estimate = 6.83, SE = 4.82, d.f. = 28, $P = 0.17$); however, geckos attacking scorpions did reach higher maximum velocities (estimate = 0.20, SE = 0.07, d.f. = 28, $P = 0.006$). The increase in maximum strike velocity when attacking scorpions is likely to be driven by the positive correlation between attack distance and maximum strike velocity ($r = 0.47$, $P = 0.009$), and geckos tending to attack scorpions (mean = 21.2 mm) from greater distances than they do other prey types (mean 14.6 mm).

Despite similarities in lunge kinematics, upon contact, geckos violently and repeatedly shook scorpions immediately after seizing them in their jaws. Although this shaking movement was too rapid to analyse using standard video (Video 2), when filmed at ~1200 frames s^{-1} it was clear that geckos conducted shake-feeding by rapidly swinging side to side and rotating their head and body for several seconds (Video 2). This behaviour resulted in scorpions being torqued and thrashed against the substrate, after which they often (but not always) appeared dead or immobile when being consumed. Shake-feeding was exhibited exclusively in relationship to scorpions, and almost all scorpions were shaken repeatedly before being consumed. Summary data on feeding trials are presented in Table 2.

CHARACTERISTICS OF SHAKE-FEEDING BEHAVIOUR

Given that we recorded feeding behaviours dorsally with a single camera, we could characterize shake-feeding in only two (x,y) dimensions. However, it was apparent that, although the majority of motion was in the x–y plane, scorpions were also moved in the z dimension (i.e. dorsoventrally) as geckos flung them from side to side (Video 2). Future trials will combine multiple camera angles to reconstruct three-dimensional movements.

Scorpion shaking consisted of very rapid side-to-side oscillations of the head accomplished by combining rotations of the cervical vertebrae with back-and-forth movement of the spine and pectoral girdle relative to the pelvic girdle. In a full cycle of the movement, the head accelerated from ~90–110° to the side, through the midline (0°) to −90 to −110°, and then back in the other direction to the starting position (Fig. 2). On average, the geckos in our study shook scorpions at a frequency of 13.06 ± 2.0 Hz. During the first five shake cycles, geckos on average reached a maximum angular velocity of 127.9 rad s^{-1} and a maximum angular acceleration of 16 512.4 rad s^{-2}. Kinematic information for each of the first five shake cycles is presented in Table 3. We were able to extract kinematic information for the scorpion during eight shake cycles recorded from three geckos (one to five cycles per gecko). We found that the average angular velocity of scorpions being shaken was 202.15 (range 149.71–267.31) rad s^{-1} and average angular acceleration was 28 328.65 (range 20 245.33–40 031.86) rad s^{-2}. The cross-correlation analysis determined that on average the angle of the scorpion lagged the angle of the head of the gecko by 13.5 ms (17.4 frames), with a mean correlation coefficient of 0.65 (Fig. 3). While being shaken by the gecko, we found that scorpions experienced a mean torque of 0.002 ± 0.0004 N m and a centripetal force of 0.339 ± 0.15 N.

DISCUSSION

Our research documented a previously little-known, high-performance predatory behaviour used by lizards to subdue venomous arthropods. The high-speed shake-feeding used by banded geckos is similar superficially to behaviours reported in other predators, including other lizard species. Whiptail lizards (*Aspidoscelis gularis*) also violently shake scorpion prey, but not crickets or other harmless arthropods (O'Connell & Formanowicz, 1998); mammalian carnivores often use shake-feeding to kill or dismember prey before consumption

Table 2. Summary of all arthropod feeding trials with banded geckos

N	Prey type	Gecko stung	Prey shaken	Shake cycles	Shake duration (s)	Prey immobilized after shaking
Eight geckos, ten trials	Non-scorpion	Not applicable	30% (3 of 10)	5 ± 1	0.3 ± 0.1	33% (1 of 3)
Nine geckos, 21 trials	Dune scorpion	90% (19 of 21)	100% (21 of 21)	31 ± 7	1.4 ± 0.5	62% (13 of 21)

Values are the mean ± SE. No individual gecko was tested more than three times for each treatment. See Table S1 for full dataset of gekco behavior and lunges, and Table S2 for angular data.

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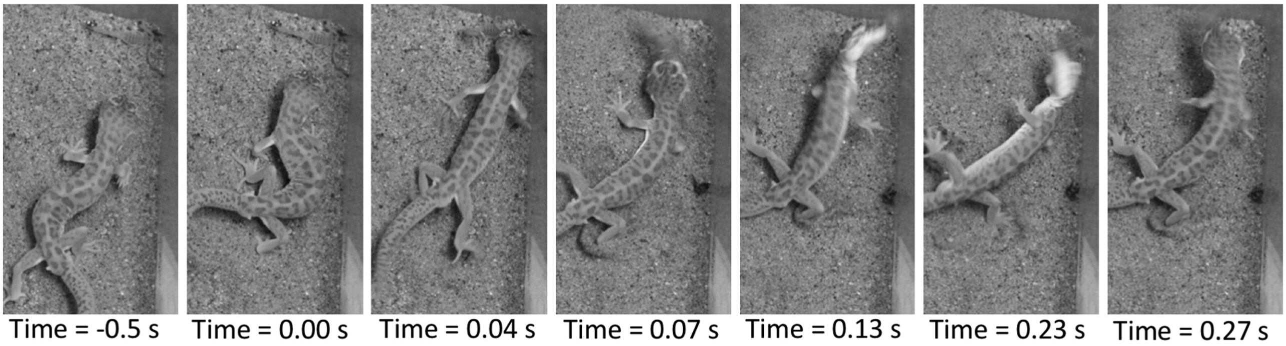

Figure 2. Still-picture frames from a single shake cycle from a typical scorpion predation trial. At time −0.5 s, the gecko is approaching the scorpion. Time 0.0 s is the frame immediately before the start of the lunge towards the scorpion. At 0.04 s, the gecko has grasped the scorpion in its jaws. At 0.07 s, the gecko begins the first shake cycle, beginning with a rightward head movement. At 0.13 s, the gecko has reached the apex of the rightward movement and begins the leftward head movement. At 0.23 s, the gecko has reached the apex of the leftward head movement and begins moving the head rightward again. At 0.27 s, the head of the gecko has returned to the midline, completing one full shake cycle.

Table 3. Descriptive statistics for the first five shake cycles during attacks from geckos on scorpions

Parameter	First cycle (N = 7)	Second cycle (N = 7)	Third cycle (N = 6)	Fourth cycle (N = 6)	Fifth cycle (N = 4)
Maximum angular velocity (rad s^{-1})	133.6 (86.6–202.5)	120.4 (56.6–188.0)	147.5 (116.5–184.8)	115.9 (81.2–173.5)	119.2 (101.6–128.6)
Maxium angular acceleration (rad s^{-1})	15 963.7 (10 290.9–26 558.7)	15 880.7 (10 945.0–20 579.0)	20 932.1 (10 739.9–35 912.1)	15 069.8 (11 104.4–22 758.9)	14 112.2 (9642.5–17 501.2)

Values are the mean (minimum–maximum).

(Kruuk, 1976; Vincent & Bekoff, 1978; Taylor, 1987; Hocking *et al.*, 2015); roadrunners shake and beat prey against the substrate before consumption (Beal & Gillam, 1979); crocodiles dismember prey by shaking (Johnson, 1973); and a recent study of loggerhead shrikes showed that they immobilize or kill larger vertebrate prey via rotational acceleration imparted by high-speed head shakes (Sustaita *et al.*, 2018).

Although detailed kinematic data from many of these taxa are lacking, our analyses indicate that banded geckos perform in a similar manner to endotherm predators. Sustaita *et al.* (2018) found that loggerhead shrikes kill small rodents by shaking them at a frequency of 11 ± 3 Hz, slightly slower than geckos shaking scorpions in our study. However, the angular velocities and accelerations of the body of mice shaken by shrikes (~39 rad s^{-1} and 2700 rad s^{-2}, respectively) were much lower than our estimates of scorpions being shaken by geckos (~202 rad s^{-1} and 28 000 rad s^{-2}, respectively). Geckos are likely to achieve these velocities through their much greater relative body size in comparison to scorpions, allowing them to move the entire scorpion body in large back-and-forth arcs on either side of the head (Video 2). Our video recordings also showed that, although scorpions were almost always shaken violently before consumption using the same basic side-to-side head and body movements, this was far from a stereotyped behaviour. Geckos exhibited variability in the duration of shake cycles, the degree to which they moved their forequarters while shaking, and other aspects of the behaviour. This variation could reflect individual differences in experience or temperament, or situational responses to the scorpion itself.

Although prey-shaking kinematics have apparently not been documented in mammalian carnivores (despite the consistent use of shake-feeding by canids and pinnipeds), Dickerson *et al.* (2012) examined the kinematics of shake-drying in a number of species of mammals across a range of sizes. In order to dry their pelage, small rodents, such as mice, can shake their bodies at ~30 Hz, whereas large carnivores shake at 4–6 Hz. At 14 Hz, the shake-feeding behaviour of our geckos was similar to shake-drying speeds of rats and guinea pigs. These findings are all the more remarkable given that we are comparing the kinematics of a

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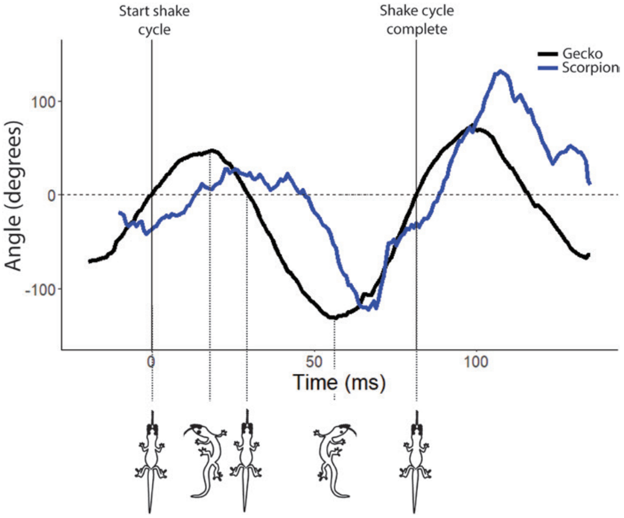

Figure 3. The angle of the head of a gecko (black) and the scorpion (blue) during ~1.5 shake cycles.

nocturnal ectotherm filmed at ambient temperatures of ~22–25 °C with active endotherms (birds and mammals) well known for high-speed pursuit and attack of prey. Future research could examine more closely the physiological constraints overcome by geckos in maintaining this level of performance over repeated bouts of shaking (some lasting for > 10 s, or > 140 body oscillations).

Our limited comparative data indicate that geckos use shake-feeding exclusively when attacking scorpions, but the function of the behaviour is still not entirely clear. It is likely to be used to immobilize or kill scorpions before ingestion, but 40% of shaken scorpions were still somewhat mobile when ingested; hence, the behaviour might be effective only occasionally in this regard. Our estimates of the torque and centripetal force imparted to scorpions during shake-feeding did not indicate that debilitating forces were involved, but these estimates may not be completely accurate. Given that we filmed with only one camera, we were able to model movements in only a single plane, and the resolution of our cameras meant that we had to make simplifying assumptions concerning scorpion anatomy. Future work should quantify motions in three dimensions and use more detailed videos to calculate forces imparted on scorpions.

However, although geckos are still frequently stung while eating scorpions, shake-feeding could greatly limit the amount of venom that scorpions are able to inject in comparison to non-shake-feeding. Another possibility is that geckos are disabling or breaking the stinger of the scorpion by beating it against the substrate, as is done by bee-eater birds to disable the stings of honeybees (Fry, 1969), but we could not determine whether the stingers were damaged in our videos. An analysis of the mechanical properties of scorpion stingers indicated that they are robust to in-plane stress applied during sting penetration, but subject to fracture from forces applied from lateral directions (Zhao *et al.*, 2016), as might occur during violent shaking. The aculeus of the telson (the narrow, tapering end of the stinger) is the most delicate portion, and scorpions in nature are occasionally found with damaged or missing aculei (van der Meijden & Kleinteich, 2017), indicating that the stinger may be somewhat prone to breakage. Future research could examine mechanical damage to stingers after bouts of shaking to assess this hypothesis. Additionally, the rapid side-to-side motion of shake-feeding coupled with the angle of the scorpion lagging behind that of the gecko could result in a whiplash-like effect when the gecko rapidly pulls the scorpion in the opposite direction at the far left or right apex of the movement.

Scorpions are very widespread and successful arthropod taxa, and many larger predators have evolved adaptations for counteracting their venomous stings. These include not only the physical mechanisms we report here, but also physiological resistance to venom. Other lizard species (Zlotkin *et al.*, 2003), grasshopper mice (Rowe *et al.*, 2013) and, perhaps, some bats (Holderied *et al.*, 2011) are resistant to effects of scorpion venom. It is even possible that banded geckos themselves have some physiological resistance to the effects of scorpion venom, and shake-feeding is a complementary adaptation for counteracting venomous stings. Similar to the anti-scorpion adaptations evolved by grasshopper mice (Rowe *et al.*, 2013) or the anti-newt defences evolved by garter snakes (Brodie *et al.* 2002), this system is also ripe for comparative evolutionary analyses. Different populations or species of geckos could exhibit local adaptation for exploiting scorpions as a food source. Given the numerical dominance of scorpions in desert ecosystems, it is likely that other desert insectivores have also evolved mechanisms to circumvent defensive stinging, perhaps involving equally impressive physical performances. Future comparative investigations in desert squamates might be fruitful in documenting the form and function of such behaviours.

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Charles Cummings and two anonymous reviewers for suggestions that greatly improved the final version of this manuscript. M.D.W., G.A.F. and R.W.C. designed the research and collected the data; M.D.W. performed statistical analyses; all authors contributed to the writing of the original manuscript and revisions, approved the final version of the manuscript and agree to be held accountable for the content therein. The authors declare no conflicts of interest.

DATA AVAILABILITY

All summary data are provided as online Supporting Information. Original video recordings analysed for this paper are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Gecko behaviour and lunge data.
Table S2. Gecko angular data.
Video 1. Western banded gecko feeding on non-scorpion prey (public URL https://youtu.be/fwZdWSan6Rw).
Video 2. Western banded gecko employing shake-feeding on dune scorpion prey (public URL https://youtu.be/WNVHg4XnHiM).

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