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SHORT COMMUNICATION

Attention and distraction in the modular visual system of a jumping spider

Margaret Bruce[1], Daniel Daye[2], Skye M. Long[2], Alex M. Winsor[1], Gil Menda[3], Ronald R. Hoy[3] and Elizabeth M. Jakob[2],*

ABSTRACT

Animals must selectively attend to relevant stimuli and avoid being distracted by unimportant stimuli. Jumping spiders (Salticidae) do this by coordinating eyes with different capabilities. Objects are examined by a pair of high-acuity principal eyes, whose narrow field of view is compensated for by retinal movements. The principal eyes overlap in field of view with motion-sensitive anterior-lateral eyes (ALEs), which direct their gaze to new stimuli. Using a salticid-specific eyetracker, we monitored the gaze direction of the principal eyes as they examined a primary stimulus. We then presented a distractor stimulus visible only to the ALEs and observed whether the principal eyes reflexively shifted their gaze to it or whether this response was flexible. Whether spiders redirected their gaze to the distractor depended on properties of both the primary and distractor stimuli. This flexibility suggests that higher-order processing occurs in the management of the attention of the principal eyes.

KEY WORDS: Salticidae, Gaze direction, Principal eyes, Vision, Eye tracking

INTRODUCTION

Attention is the process of focusing on a selected aspect of a complex, multifaceted environment. In humans and other vertebrates, visual attention is often assessed by measuring gaze direction via eye or head movements (Corrigan et al., 2017; Land and Hayhoe, 2001; Tatler et al., 2010; Yorzinski et al., 2013, 2015, 2017). While processes analogous to selective visual attention have been demonstrated in invertebrates (e.g. Humphrey et al., 2018; Morawetz and Spaethe, 2012; Nityananda, 2016; Spaethe et al., 2006; van Swinderen and Greenspan, 2003; Wiederman and O'Carroll, 2013; Winsor et al., 2021), precise gaze direction is very difficult to monitor in most species (but see examples in Land, 1995). Where it is possible to measure gaze direction in invertebrates, we can take advantage of the rich psychological literature to design parallel experiments on visual attention (Winsor et al., 2021). Jumping spiders (Family Salticidae) are known for their visually guided behaviors, especially courtship and predation (Harland et al., 2012), and possess a visual system distinct from those of both vertebrates and insects. Jumping spiders have one pair of eyes with moveable retinas that make them particularly amenable to experimental assessment of

gaze direction. Here, we used a custom-built modified ophthalmoscope (Canavesi et al., 2011; Jakob et al., 2018) to record the gaze direction of the jumping spider *Phidippus audax* and tested how gaze direction is influenced by the sudden appearance of distractors detected by a separate set of eyes.

The jumping spider visual system consists of four pairs of eyes. Two pairs are forward facing: the moveable principal eyes possess the best spatial acuity known for a terrestrial invertebrate (Caves et al., 2018; Warrant and McIntyre, 1993), and overlap in their field of view with one pair of non-moving secondary eyes, the anterior lateral eyes (ALEs) (reviewed in Land and Nilsson, 2012). The ALEs are less spatially acute than the principal eyes but have a larger field of view and are excellent motion detectors (Fig. 1A,B) (reviewed in Morehouse et al., 2017). When the ALEs detect a moving object, the spider responds by orienting its body to direct its principal eyes toward it (Land, 1971; Zurek et al., 2010). In addition, when the spider's body is motionless, the ALEs direct the movement of the principal eyes to track moving objects and to locate objects that suddenly appear (Jakob et al., 2018). Thus, a spider can monitor a broad field of view with its secondary eyes, and then quickly direct its high-acuity principal eyes to examine objects of interest. Once the principal eyes are directed to an object, spiders exhibit an unusual behavior called scanning, in which the narrow, vertical, boomerang-shaped retinas of these eyes partially rotate while moving back and forth over the stimulus (Land, 1969a). These eye movements are thought to be integral to object identification.

The question arises as to whether a spider examining an object with its principal eyes reflexively redirects them to a new stimulus detected by the ALEs, or whether this shift of attention is flexible. In some cases, it may be evolutionarily beneficial to suppress distraction from a primary task. For example, dragonflies can track the movements of a single individual in a swarm of flies without getting distracted by the movements of other flies (Wiederman and O'Carroll, 2013), whereas honeybees make incorrect decisions in a visual search task when distractors are present (Morawetz and Spaethe, 2012; Spaethe et al., 2006). In other cases, failing to attend to a new stimulus may be costly if it represents danger. Blue jays attending to a difficult foraging task are hindered in their ability to detect a target in the peripheral field of view, which could be a predator (Dukas and Kamil, 2000). Similarly, pilot tests suggested that salticids may suppress a redirection of their principal eyes to a new, potentially dangerous stimulus appearing in the field of view of their ALEs when they are visually 'locked on' to prey. *Freya pachomius* jumping spiders oriented to a video screen showing a video of a cricket were more likely to be captured by a vial approaching steadily from above and laterally compared with those oriented to a blank screen (M.B., unpublished data; methods following Hebets, 2005).

Here, we used a spider eyetracker to test the flexibility of the relationship between the principal and secondary eyes. Specifically, we tested whether the principal eyes were always redirected to a

[1]Graduate Program in Organismic and Evolutionary Biology, French Hall, University of Massachusetts Amherst, Amherst, MA 01003, USA. [2]Biology Department, 220 Morrill 3, University of Massachusetts Amherst, Amherst, MA 01003, USA. [3]Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA.

*Author for correspondence (ejakob@umass.edu)

E.M.J., 0000-0002-7796-8736
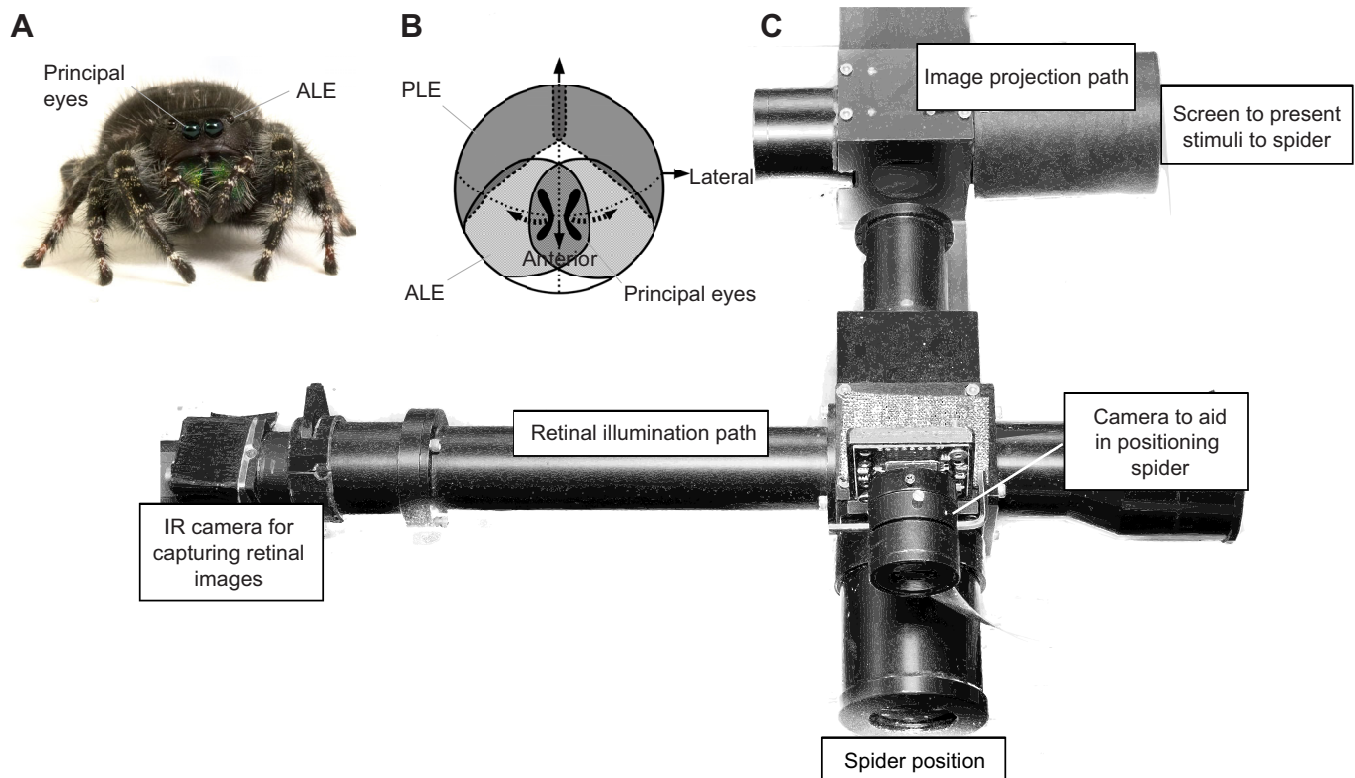
Fig. 1. Study animal and experimental setup. (A) The face of *Phidippus audax* showing the two forward-facing pairs of eyes: the principal eyes and the anterior-lateral eyes (ALEs). Photo credit: E.J. (B) The fields of view of the principal and the two larger pairs of secondary eyes, the ALEs and the posterior-lateral eyes (PLEs), in *Plexippus*, a spider with a similar eye size and arrangement to *P. audax*. The principal eye retinas are boomerang shaped and can be moved. Redrawn by S.M. Long, based on Foelix (2011) and Land (1985). (C) The design of the eyetracker, showing the path of the projected stimulus image as viewed by the spider, and the location of the infrared (IR) camera capturing the reflection from the spider's retinas. The retinas are illuminated with IR light shone directly through the spider's cephalothorax (not shown). Computer-generated rendering of photo taken by E.J.

newly appearing distractor stimulus, or whether this response is flexible. We showed spiders pairs of video stimuli. First, a primary stimulus appeared. While the spider scanned the primary stimulus with its principal eyes, a distractor stimulus appeared in the field of view of only the ALEs. We recorded whether the gaze of the principal eyes shifted to the distractor stimulus or continued to scan the primary stimulus. Using this protocol, we conducted two experiments. In the first, we varied the complexity and ecological significance of the primary stimulus to test whether spiders were less likely to shift their gaze away from images that were particularly relevant. In the second, we varied qualities of the distractor stimulus to test whether its shape or motion influenced its ability to attract the gaze of the principal eyes.

MATERIALS AND METHODS
Experimental subjects
We tested 51 adult female *Phidippus audax* (Hentz 1845) jumping spiders, captured using sweep nets and by hand with vials from fields and structures in Hampshire Country, MA, USA. Spiders were housed in a lab kept at 25°C with a 16 h:8 h light: dark cycle. They were kept in individual plastic boxes (18×13×10 cm), and provided with a stick, a hollow black tube and plastic foliage for habitat enrichment. Spiders were fed crickets (*Acheta domesticus*) once weekly and provided with water *ad libitum*. Unpublished data (M.B.) from another experiment suggested that hunger state did not affect spider response, even when spiders were food deprived for several weeks. Animals were not harmed in this study.

Use of the specialized eyetracker
We used a customized salticid-specific eyetracker (Fig. 1C) (Canavesi et al., 2011; Jakob et al., 2018) to map the changing position of the spider's principal eye retinas as they viewed stimuli. The eyetracker is a modified ophthalmoscope, inspired by the work of Land (Land, 1969a,b; Land and Nilsson, 2012).

Spiders viewed video images projected through the eyetracker while we recorded the position of their retinas with an infrared (IR) video camera, as described in Jakob et al. (2018). We illuminated the retinas through the spider's carapace with an 850 nm infrared light directed with a dual branch light guide equipped with a focusing lens (Thorlabs Inc., Newton, NJ, USA). We observed the stimulus presentation and the retinal position simultaneously in separate windows in real time on a computer monitor. After the experiment, video of retinal movement was superimposed on and aligned with stimulus videos for scoring (Jakob et al., 2018).

Trial protocol
For each trial, individual spiders were tethered with a plastic dental disposable microbrush (Easyinsmile, Passaic, NJ, USA) attached to the cephalothorax using a 1:1 mixture of gum rosin (Acros Organics, Fairlawn, NJ, USA) and beeswax (Stackich Inc., Troy, MI, USA). To eliminate glare from the IR light, the waxed microbrush was painted black (DecoArt Americana Chalkboard Paint, Stanford, KY, USA, in the first experiment and Stuart Semple Black Paint, CultureHustle, Dorset, UK, in the second experiment). We secured the tethered spider in front of the eyetracker and ensured that it was properly aligned and could see stimuli in all areas

of the visual field using a calibration routine described in Jakob et al. (2018). Using a program created in Processing (v2.2), we presented a primary stimulus at the center of a spider's visual field. In real time, we watched the spiders' principal eye retinas on the computer monitor. When the retinas were positioned over the primary stimulus and actively scanning it with back-and-forth and twisting motions, we used a keystroke to trigger the presentation of a distractor stimulus in an area of the screen visible only to the ALEs (Fig. 2A). The distractor location was under the control of the experimenter and differed from trial to trial depending on the location of the principal eye retinas.

In the first experiment, we used multiple primary stimuli but kept the distractor stimulus constant. Primary stimuli were a black cricket silhouette, a black oval with the same number of pixels, or a treatment with no primary stimulus but simply a blank screen. The distractor stimulus was always a black oval. Both primary and distractor stimuli appeared suddenly and then remained motionless. We chose these stimuli because in pilot tests we found that while spiders looked at both the cricket and oval stimuli, they explored the cricket stimulus more actively than the oval stimulus, with a higher rate of torsion and scanning back and forth. Each spider received each treatment in random order (determined by a random number generator) with a 3 min break in between presentations.

In the second experiment, we tested whether the type of distractor stimulus influenced a shift in gaze direction by the principal eyes. Spiders always began these trials by examining a cricket silhouette as the primary stimulus. Distractor stimuli were presented in random order and consisted of a black cross, a cricket silhouette, a rapidly expanding ('looming') black circle, and a rapidly shrinking ('receding') black circle. The looming and receding stimuli changed size in approximately 1 s and then were motionless. *Phidippus audax* do not react behaviorally to receding stimuli but back away from looming stimuli, a response mediated by the secondary eyes (Spano et al., 2012). Pilot data suggested that spiders in the eyetracker spend some time scanning images of crosses, which bear some resemblance to cricket antennae and spider legs, but not as much time as they spend on cricket silhouettes. Each

spider received each treatment in random order with a 3 min break between each presentation.

For both experiments, we scored from video whether or not a spider shifted its gaze from the primary stimulus to the distractor stimulus immediately upon its presentation. We analyzed the data in R version 3.6.2 (http://www.R-project.org/) with a mixed-effect logistic regression model using the function 'glmer' from the package lme4 version 1.1-21 (Bates et al., 2015). We classified spider identification number as a random effect to account for multiple tests with the same individual (Harrison et al., 2018). Stimulus type and trial order were fixed effects. In the first experiment, we compared the response of spiders when they were viewing a blank screen with no stimulus present, which we planned as the null treatment, with their response to each of the stimuli. In the second experiment, there was no logical null treatment, so we applied a *post hoc* Tukey test with the function ghlt from the package multcomp to assess differences between all pairings.

RESULTS AND DISCUSSION

In our first experiment, trial order was not significant, and we dropped it from the model. Spiders looked at the distractor stimulus significantly less frequently when they were examining a cricket primary stimulus compared with trials where they were looking at a blank screen. In contrast, the spiders' propensity to look at a distractor did not differ between trials in which they were initially looking at an oval versus a blank screen (Fig. 2B, left; $\beta_{intercept(blank)}=3.45\pm1.61$ s.e.m.; $\beta_{oval}=-0.80\pm1.38$, $z=-0.58$, $P=0.566$; $\beta_{cricket}=-4.61\pm2.03$, $z=-2.27$, $P=0.023$; see Movie 1). In the second experiment, trial order was nearly significant ($P=0.06$), and we analyzed the data with both the reduced model without trial order, and the full model. In the reduced model, spiders were more likely to shift their gaze to the looming video, but no other comparisons were significant (Fig. 2B, right; loom–cricket: $z=3.09$, $P=0.011$; loom–cross: $z=2.78$, $P=0.027$; loom–shrink: $z=-3.17$, $P=0.008$; cross–cricket: $z=0.38$, $P=0.981$; shrink–cricket: $z=-0.11$, $P=0.999$; shrink–cross: $z=-0.49$, $P=0.962$; see Movie 2 for examples). The same patterns were seen in the full
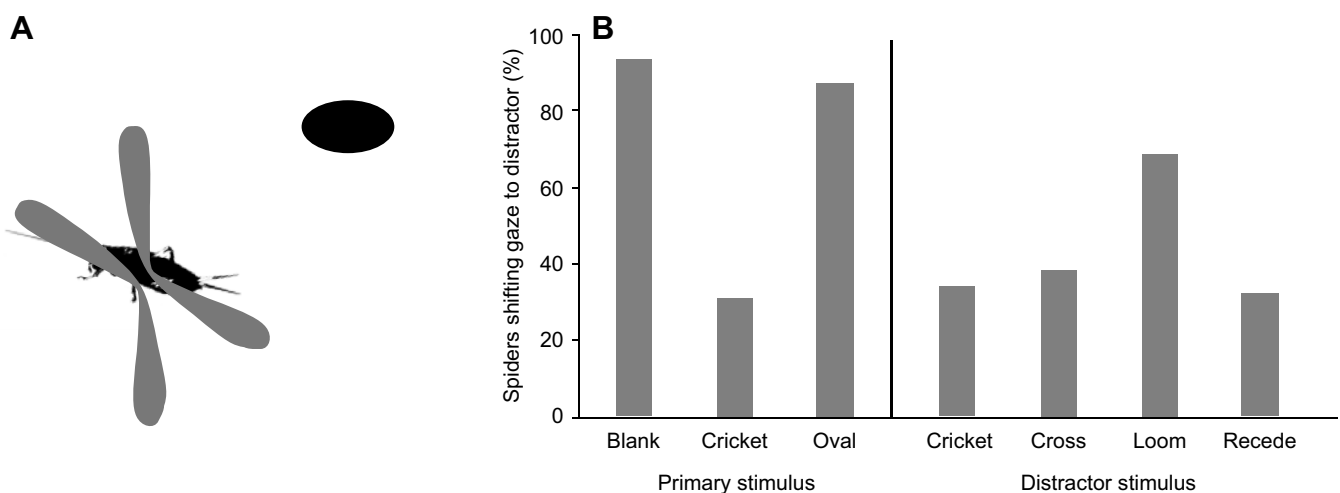
Fig. 2. Experimental design and results. (A) The experimental design: as the spider viewed a primary stimulus (here, a cricket), a distractor stimulus (here, an oval) was presented in the field of view of the ALE, and we monitored whether the principal eyes moved to the distractor. Drawing by M.B. (B) Left: response to a distractor stimulus based on the type of primary stimulus. Spiders shifted their gaze to the distractor stimulus significantly less often when the primary stimulus was a cricket versus a blank screen, but there was no difference between blank screen and oval treatments. We tested 16 spiders. One test with a blank screen was not scorable because of poor video quality. Right: response to a distractor stimulus based on the type of distractor stimulus. Looming stimuli (disks growing in size) were more likely to attract the gaze of the principal eyes than were either non-moving stimuli (cross and cricket) or receding stimuli (disks shrinking in size). We tested 35 spiders with each stimulus. One video each from the 'cross' and 'shrink' groups was not scorable because of poor video quality.

model, with the exception that the loom-cross comparison was no longer significant (z=2.26, P=0.107). Although salticids have some independent control of their principal eyes, in both experiments, when spiders looked at the distractor, they did so with both eyes. The exception was one spider in the second experiment, which shifted only one eye to the cross while keeping the other eye on the primary stimulus. There were negligible differences between our analyses regardless of whether we classified that spider's behavior as 'did not shift gaze' (as we did for Fig. 2B) or 'shifted gaze'.

We previously showed that the principal eyes of jumping spiders require input from the motion-detecting ALEs to locate and track objects (Jakob et al., 2018). Here, we show that the redirection of the gaze direction of the principal eyes from a primary stimulus to a new distractor stimulus detected by the ALEs is flexible, and depends on characteristics of both the primary and distractor stimuli (Fig. 2).

These results are relevant to the important function of 'distractibility' in a complex environment where an animal must forage and avoid predators simultaneously. Our first experiment shows that spiders are less likely to shift their gaze to a distracting stimulus, a black oval, when they are examining a salient object, a cricket. This result is in line with studies of the limits of attention across many taxa. For example, blue jays perform more poorly on foraging tasks that require them to divide their attention between possible targets (Dukas and Kamil, 2000), marmots engaged in social play are slower to respond to alarm calls (Blumstein, 1998), and guppies exhibiting a nose-down foraging posture are less likely to flee from a predator model than those not engaged in foraging (Krause and Godin, 1996). In other jumping spiders, vigilance decreases as visual tasks increase in difficulty (Humphrey et al., 2018). Humans also pay less attention to distracting moving stimuli when performing a difficult central task (Rees et al., 1997). An even more direct comparison with our results comes from eyetracking experiments in humans. The control of eye movements in humans results, in part, from an interplay between the foveal areas of high spatial acuity and the peripheral region of lower spatial acuity, analogous to the principal and secondary eyes of spiders. Humans attending to a visual task with their foveas are less able to detect a distractor in their peripheral field when the foveal task has a higher cognitive load, even when the experimenters controlled for visual complexity of the task (Savage et al., 2019). In future experiments, it would be interesting to disentangle whether the cricket image evoked a different response from the other images because of its structural complexity or because of its salience as prey, which might indicate an increased cognitive load.

Our second experiment, using looming and shrinking distractors, shows that spiders are more likely to shift their gaze if the distracting stimulus is growing in size compared with still images that simply appear or an image that shrinks in size. Looming stimuli are likely to be particularly relevant to the spider. Spider predators include birds, other spiders, mantids and wasps (reviewed in Foelix, 2011). Wasps and birds, in particular, move quickly and may descend from above or approach laterally. Previously, Spano et al. (2012) found that spiders backed away from looming stimuli and that this response is mediated by the ALEs. It is not just movement, but looming movement, that triggers a response: in Spano et al. (2012), spiders did not back away from shrinking stimuli, and in our data, shrinking stimuli were no more likely to cause spiders to shift their gaze than were non-moving stimuli appearing in the field of view of the secondary eyes.

Allocating attentional resources requires the prioritizing of sensory information from diverse sources. Our data suggest that sometimes suddenly appearing input from secondary eyes is prioritized over that from the principal eyes, and sometimes not. In jumping spiders, visual information from the principal and secondary eyes is first processed separately, and then these streams of information are combined in the protocerebrum (Strausfeld, 2012). We hypothesize that the close integration between the principal and secondary eyes, demonstrated here and in Jakob et al. (2018), is permitted by their direct connection in the protocerebrum via large neural tracks that allows rapid communication (Long, 2021; Steinhoff et al., 2020).

Comparative studies will shed light on how this close integration between the eyes has evolved. While most true spiders have eight eyes, their arrangement, size, field of view and acuity vary across families. Moveable principal eyes are found in other spider families, but their muscular control is presumably less precise. Besides salticids, we know most about the vision of *Cupiennius salei* (Family Ctenidae), a night-hunting sit-and-wait predator (Kaps and Schmid, 1996; Neuhofer et al., 2009; Schmid, 1998). Their principal eyes are also mobile, but in contrast to salticids, their eyes are controlled by four rather than six muscles and can be moved only laterally. The field of view of their principal eyes is wider than that of salticids, and is shared not with the ALEs but with the posterior medial eyes (PMEs; reviewed in Barth, 2002). The wide field of view of the *Cupiennius* principal eyes suggests that the precise targeting required by salticid principal eyes may be unnecessary, but there appears to be some control by the PMEs of the principal eyes: telemetry demonstrates that muscles of the principal eyes are activated when objects move in the visual field of the secondary eyes, even when the principal eyes are masked (Neuhofer et al., 2009). The anatomy of other spiders suggests the possibility of similar mechanisms for coordination between pairs of eyes. In the sit-and-wait crab spiders (Thomisidae), the principal eyes are controlled by four muscles as in *Cupiennius*, overlap the field of view of the ALEs as in salticids, but have a wider field of view than in salticids (Insausti et al., 2012). In the wolf spider *Lycosa leuckartii*, the field of view of the principal eyes is shared with those of both the PMEs and ALEs (Clemente et al., 2010). The visual processing areas of the brains of other spider families are both smaller and often less internally organized than in jumping spiders, and there appears to be no direct communication between the optic neuropils of the principal and secondary eyes (Long, 2016, 2021). Behavioral and neurobiological studies in the Araneae offer an opportunity to understand how attentional shifts are mediated in animals with multiple eyes.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.B., R.R.H., E.J.; Methodology: M.B., D.D., S.M.L., E.J.; Software: M.B., D.D., S.M.L.; Validation: D.D., A.M.W., E.J.; Formal analysis: M.B., D.D., A.M.W.; Investigation: M.B., D.D.; Resources: E.J.; Data curation: D.D., E.J.; Writing - original draft: M.B., E.J.; Writing - review & editing: M.B., D.D., S.M.L., A.M.W., G.M., R.R.H., E.J.; Visualization: E.J.; Supervision: E.J.; Project administration: E.J.; Funding acquisition: E.J., R.R.H., S.M.L., G.M.

Data availability
Data are available from the Dryad digital repository (Bruce et al., 2021): dryad.
v15dv41vz

Supplementary information
Supplementary information available online at
https://jeb.biologists.org/lookup/doi/10.1242/jeb.231035.supplemental

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