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Movement-based signalling by four species of dragon lizard (family Agamidae) from the Kimberley region of Western Australia

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ABSTRACT

Communication signals underpin the social lives of animals, from species recognition to mate selection and territory defense. Animal signals are diverse in structure between and within species, with the diversity reflecting interacting factors of shared evolutionary history, constraints imposed on senders and receivers and the ecological context in which signalling takes place. The dragon lizards of Australia (family Agamidae) are known for their movement-based visual displays and are useful models for how ecology influences behaviour. However, we know little about the communication strategies of many species. Our aim here was to provide new knowledge on some of these species, focusing on the north-west of Western Australia. We filmed within-species pairwise interactions of *Diporiphora superba*, *D. bennetti*, *D. sobria* and *Ctenophorus isolepis isolepis*. We describe and quantify for the first time push-up displays by *D. superba* and *C. isolepis isolepis* and tail waving displays of *D. bennetti*. Only *D. sobria* did not generate movement-based visual signals. We have confirmed that more species engage in such behaviour than previously reported, but further work is required to document the full repertoire of these species. The implications of our work are discussed in the context of signal structure, function and environmental context.

Keywords: Agamidae, *Ctenophorus*, *Diporiphora*, display, dragon lizards, Kimberley, movement-based signal, 3D reconstruction.

Introduction

Communication is a fundamental component of the social behaviour of animals (Bradbury and Vehrencamp 2011). Animal signals provide information about species identity (Rodríguez *et al.* 2004), provide cues that facilitate opponent assessment (Stapley and Whiting 2006), help to attract (Pearl *et al.* 2000) and select mating partners (Guerra and Ron 2008), maintain social cohesion (Geerah *et al.* 2019) and warn off would-be predators (Hasson *et al.* 1989). The diversity in signal structure that we see today directly reflects multiple factors including phylogenetic history (Garcia *et al.* 2020), physical and physiological constraints on the sender that restrict what is possible (Hall *et al.* 2013), as well as the sensory systems of intended receivers (Witte *et al.* 2005). The ecological context in which signalling takes place can also influence signalling behaviour, either as a consequence of habitat structure (Hunter and Krebs 1979), the presence of heterospecific individuals (Greenfield 1988), or the potential for attracting the attention of predators (Cummings *et al.* 2003). Furthermore, environmental conditions at the time of signalling also influence signal structure and signalling behaviour (Peters *et al.* 2007), including anthropogenic influences (Slabbekoorn and den Boer-Visser 2006). Animal signals are therefore not only fundamental to the everyday lives of animals, they also provide valuable insight into the factors that affect animal behaviour.

Animal signals span many sensory modalities. Perhaps the most common is the use of acoustic signals, which are utilised across taxonomic groups from birds and mammals to frogs and insects (Seyfarth *et al.* 1980; Gerhardt and Huber 2002 ; Dalziell *et al.* 2021). Less well known is the use of chemical (Vane-Wright and Boppré 1993), electrical (Stoddard 1999) and vibratory (Elias *et al.* 2006) signals that are also spread across a diverse set of taxa. A final category are visual signals that rely on the perception of light. These include static visual signals defined by colour or appearance (Nicholson *et al.* 2007), as well as dynamic visual signals characterised by movement (Ramos and Peters 2016). Movement-based visual signals are not rare and are apparent in diverse taxonomic groups from invertebrates to vertebrates (Hebets *et al.* 2006; How *et al.* 2009; Dalziell *et al.* 2013). One group that is particularly well known for their dynamic visual displays are lizards (Ord *et al.* 2021). The movements generated by lizards range from simple head movements to complex movements of multiple parts of the body (Ramos and Peters 2016). Lizards use these displays in a variety of contexts including for resource defense (Peters *et al.* 2016) and other demonstrations of aggressive intent (Peters and Ord 2003), as well as in anti-predator (Cooper *et al.* 2004) and mating (Wu *et al.* 2018) contexts.

Movement-based visual displays are a common feature of the behaviour of Australian lizards, with much of the focus centred on the dragons (family Agamidae). Ramos and Peters (2016) surveyed the scientific literature, as well as technical reports, monographs and field guides to build a database of motion signalling by Australian dragons. At the time, there were 78 species in 14 genera and, of these, 34 species representing 12 genera were known to use motion-based signals. We described the signalling repertoire of the species and considered whether the occurrence of motion signals was influenced by broad ecological variables (arboreality, habitat type) and phylogeny. Broad ecological characteristics did not strongly influence the likelihood of signalling, but there was a strong influence of phylogeny on the type of signals utilised. One explanation offered for this was the relatively small proportion of reported signallers in a few genera, including *Diporiphora* and *Ctenophorus*, although it was suggested that much of the apparent lack of signallers may be due to a lack of knowledge of species' behaviour rather than a genuine lack of signallers.

In the present study, we sought to address the lack of information on the signalling behaviour of Australia's dragons. An obvious group upon which to focus was *Diporiphora*. Everything about their general appearance and behaviour suggests that movement-based signals are utilised, yet only two of 21 species in the genus had been reported to use such signals. Recent taxonomic revisions have seen the number of species in the genus increase by seven (Melville *et al.* 2019; Melville and Wilson 2019), but without adding new knowledge on their signalling behaviour. We examined the distribution of these species with the aim of choosing an area where multiple species could potentially be found and observed in a relatively short period. We chose the Kimberley region of north-west Western Australia and visited the region over a 2.5 week period in September 2018.

A number of agamid species can be found in the area but we report here on observations of four species (Fig. 1). *Diporiphora superba* is arguably the most distinctive of Australia's dragon lizards due its green colouration and long slender body, including an impressively long tail (Thompson and Withers 2005). This species has been characterised as slow moving and not suited to terrestrial locomotion, to the point of being clumsy on the ground (Melville and Wilson 2019). In contrast, *D. bennetti* is a small robust lizard that can be found on rock escarpments or in the shade of surrounding vegetation. Both species have a restricted distribution around the northern Kimberley (Melville and Wilson 2019). *Diporiphora sobria* is larger and more slender than *D. bennetti* and has undergone recent reclassification (Melville *et al.* 2019). It has a broad distribution from the southern Kimberley across the Northern Territory into western Queensland, preferring rocky habitats of savannah woodlands and grasslands. Movement-based signals have not been reported for any of these species. We also observed and filmed *Ctenophorus isolepis isolepis*. This

Fig. 1. Photographs depicting focal species and representative habitats from the present study. (*a*) *Diporiphora superba* and (*b*) *D. bennetti* and the rock platforms at Mitchell Plateau in which they were located. (*c*) *D. sobria* and grasslands near Halls Creek and (*d*) *Ctenophorus isolepis isolepis* in grasslands near to Wolfe Creek crater.

species has received some scientific attention, particularly with regard to thermal biology (Losos 1988; Melville and Schulte 2001) and microhabitat selection (Daly *et al.* 2007, 2008), and was reported in our earlier study to utilise backflips based on unpublished observations by one of us (JDJ). Our aim for the present work was to locate individuals of these species and to film within-species pairwise interactions. In the event that movement-based signals were produced, we would describe and quantify the movements.

Materials and methods

Study sites

We captured and filmed lizards at multiple sites in the Kimberley region of north-west Western Australia (Fig. 2) in September 2018. *Diporiphora superba* and *D. bennetti* are both restricted to areas in and around Mitchell Plateau. We filmed interactions of tethered individuals at the sites where we caught our first individual of each species at each site. For *D. superba* we filmed on a small rock platform above the creek line to the west of the camping ground (14°49′15″S, 125°42′53″E), whereas *D. bennetti* was filmed on rock outcrops to the south of the camping ground (14°49′23″S, 125°43′06″E). We captured and filmed *Ctenophorus isolepis isolepis* at Wolfe Creek Crater (19°10′22″S, 127°47′24″E) on sandy substrates among the compact shrubs. We filmed *D. sobria* at two sites, capturing different animals at each location. Our first site was just to the west of Halls Creek (17°29′09″S, 125°01′52″E), utilising rocks among small termite mounds and low lying shrubs. Our second final filming site was a pile of rocks located on the roadside between Tunnel Creek and Windjana Gorge (18°14′05″S, 127°39′26″E).

Filming procedure

We followed previously established protocols to record displays of lizards (Peters *et al.* 2016). This involved the use of two video cameras recording simultaneously, and, at the conclusion of filming, placement of a calibration object in view of both cameras. The object featured 25 noncoplanar points with known distances in relation to

Fig. 2. Map of study sites in north-western Western Australia in which assessment of putative motion signalling was undertaken.

each other that is required for three-dimensional (3D) reconstruction of movements (see below). In the present study we used Sony RX10iii cameras filming at 100 frames per second. In previous work we have placed a tethered intruder in the territory of a resident (untethered) lizard. As our goal was to confirm the occurrence of movement-based signalling, we initiated and filmed a limited number of trials, tethered both individuals at a distance of 1 m and ensured both were in view of both cameras. Tethering of lizards around the torso is an established method that does not restrict movement when the line is loose. We filmed five interactions for *D. superba* and *D. bennetti*, four for *C. isolepis isolepis* and six for *D. sobria*. Our focus was on male–male interactions but we also filmed male–female (*C. isolepis isolepis*) and female–female (*D. superba*, *C. isolepis isolepis*) interactions (see Supplementary material Table S1).

Analysis

We describe in words the outcomes of our trials and, when a movement-based signal was recorded, we selected one to be processed. Using the method outlined by Hedrick (2008), we undertook 3D reconstruction of displays in Matlab (MathWorks Inc.) to characterise the movements in the display (see Peters *et al.* 2016 for application of this technique to the study of lizard displays). Points to be tracked varied between species so as to adequately represent the movement of the display of the given species. In each case, points were tracked frame-by-frame separately for each video. The set of *x*–*y* coordinate data from each camera view was then combined with calibration coefficients derived from a separate process, which involves locating the points of our calibration object from each camera view, to generate a single set of *x*–*y*–*z* coordinates of each point in each frame that represents a 3D reconstruction of these motor patterns. We computed speeds of movement separately for each point as the change in 3D position over time. Our approach to quantifying display movements provides representation of the temporal sequence of movements, but also accurate measurement of movement amplitudes that can be difficult from a single point of view (Ramos and Peters 2017*b*).

Results

Three of the four male–male trials involving *D. superba* resulted in the production of movement-based visual signals, whereas our single female–female trial did not yield a signal. The display action pattern (DAP) graph for the representative bout is presented in Fig. 3*a* and shows displacement over time for the eye and the elbow. This sequence featured both lizards on a rock substrate, with the display movement comprising a series of relatively slow push-ups generated by movement of the forelimbs. The bout lasted for 25 s and involved six push-ups of consistent amplitude to begin with (17, 15 and 16 mm), before reducing in the second part of the display (12, 13, and 11 mm). The fastest movements recorded were 6–7 cm/s. The forelimbs were used to generate the push-up movement, but as the amplitude of these limb movements is lower than that of the eye the lizard seemingly amplifies the limb movements by extending the head up and down at the neck. Subsequent bouts in this trial consisted of one or two push-ups of comparable amplitude and speed. The signals observed in other trials were consistent with the sequence we analysed, although these were performed by lizards in the foliage and movements were lower in amplitude.

Only one of the five male–male trials yielded a signal for *D. bennetti*. This pair was the closest match in size (1 mm) while the others were more disparate (7–10 mm: Table S1). The central part of this movement-based signal was tail movements. Tail movements in the first bout lasted 147 s followed by very rapid, low amplitude whole body movements before changing position. This was followed soon afterwards by a second, shorter bout of tail and body movements. The nature of the movements was otherwise the same in this second bout and we selected this bout for analysis. To characterise the movement of the tail, we tracked five points on the tail: the base (point 1) and tip (point 5) of the tail and then three intermediate points that divided the tail into roughly equal lengths. Most of the tail movement occurs at the distal end of the tail at points 3–5 (Fig. 4*a*). Displacement of these points over time is shown as DAP graphs in Fig. 4*b*. The DAP graphs reflect the rhythmic movement of the tail. The movements of each point are slightly out of synchrony with respect to time, which indicates that the intermediate point along the tail leads the next point, and then the tip, in an undulating side-to-side motion. Whole body movements follow the tail movements, and we tracked the eye and vent to characterise these movements (Fig. 5). After moving to a new position, the lizard performs three whole body jumps of decreasing amplitude.

None of the trials involving *D. sobria* resulted in a movement-based signal. Lizards in each pair were attentive toward the other and tracked any small movements they made, but dynamic signalling or any signs of posturing were not observed. Trials lasted 12–20 min and the appearance (colours and pattern contrast) of some individuals changed during the sequence, although this may have been a thermoregulatory response. We did not notice such changes in appearance in other species studied.

Both male–male trials for *C. isolepis isolepis* yielded a signal, whereas the male–female and female–female trials did not. This movement-based signal is represented in Fig. 6*a*. The lizard begins by raising the body off the substrate, most notably by elevating the vent, before leaning forward while maintaining the feet in the original position. Eventually, the lizard leans forward too much and the limbs move to stabilise the body off the ground. The lizard then lowers the upper body toward the substrate and raises it up again. The

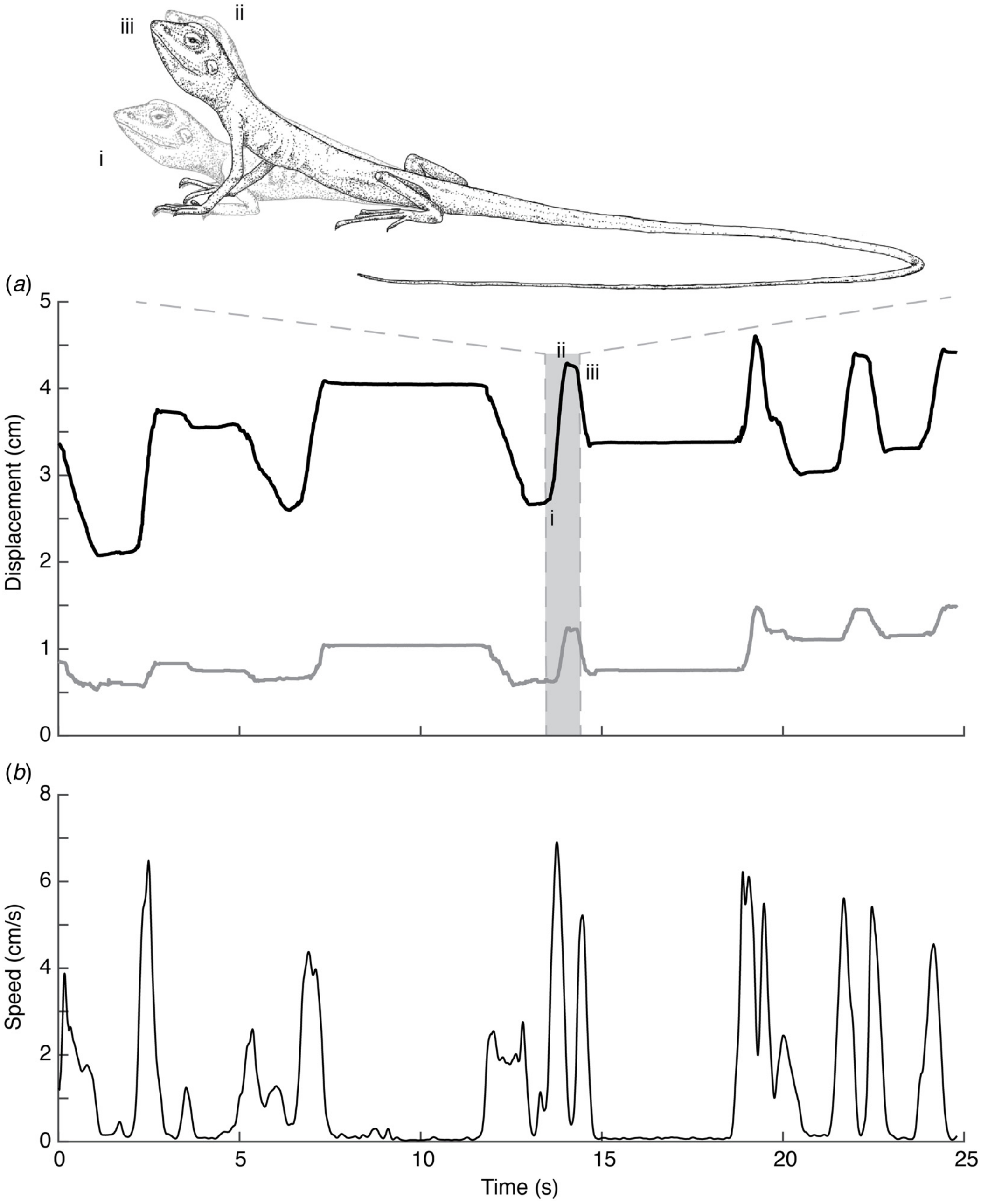

Fig. 3. (*a*) Display action pattern (DAP) graph of *D. superba* showing the change in position of the eye (black line) and forelimb joint (elbow; gray line) over time. (*b*) Speed of movement of the eye over time. The peak speed occurs around the 13 s mark which is attributed to a high amplitude push-up depicted by the shaded region of (*a*). Roman numerals labelled on the DAP profile correspond with drawings of the lizard's movement.

push-up by *C. isolepis isolepis* is rapid (Fig. 6*b*), and in other sequences was repeated one or two more times in quick succession after changing position.

Discussion

In this short field-based study we sought to determine whether movement-based displays are part of the social behaviour of a small group of species, about which little dedicated behavioural work had been previously undertaken. We recorded movement-based signals by three of the four focal species. *Diporiphora superba* and *D. bennetti* were not previously known to produce signals of this kind so our recordings and descriptions are the first for these species. We also recorded descriptions of previously undescribed signalling behaviour in *C. isolepis isolepis*. Signals are an integral part of the social behaviour of lizards and directly

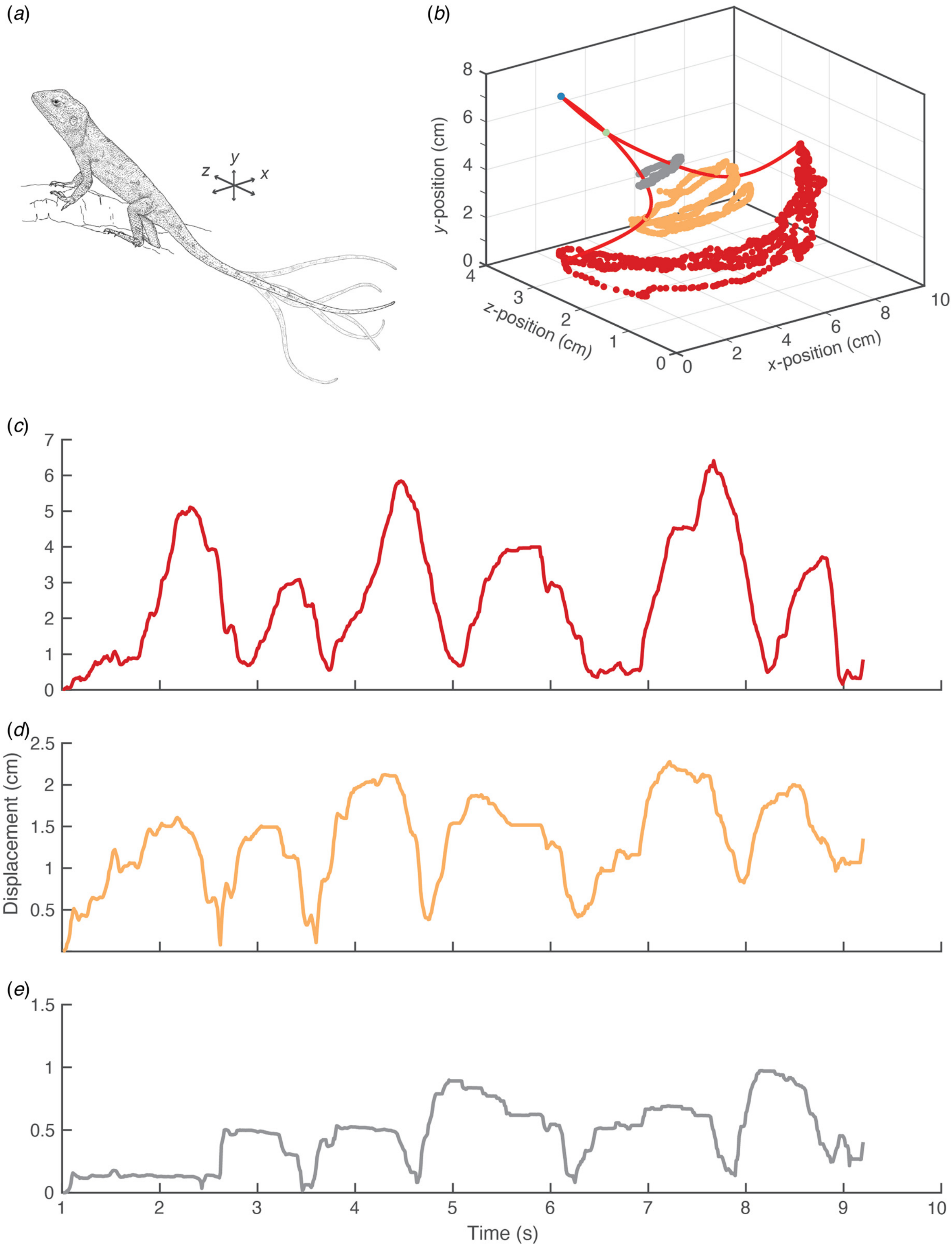

Fig. 4. (*a*) The display of *D. bennetti* is dominated by tail movements. (*b*) The positions of five parts of the tail over the course of the display reveal that the movement is constrained to the distal part of the tail (blue points at the base of the tail through red points at the tail tip). Display action pattern (DAP) graph showing the change in position of the (*c*) tail tip and the (*d*, *e*) next two points of the tail (colours correspond with those depicted in (*b*)).

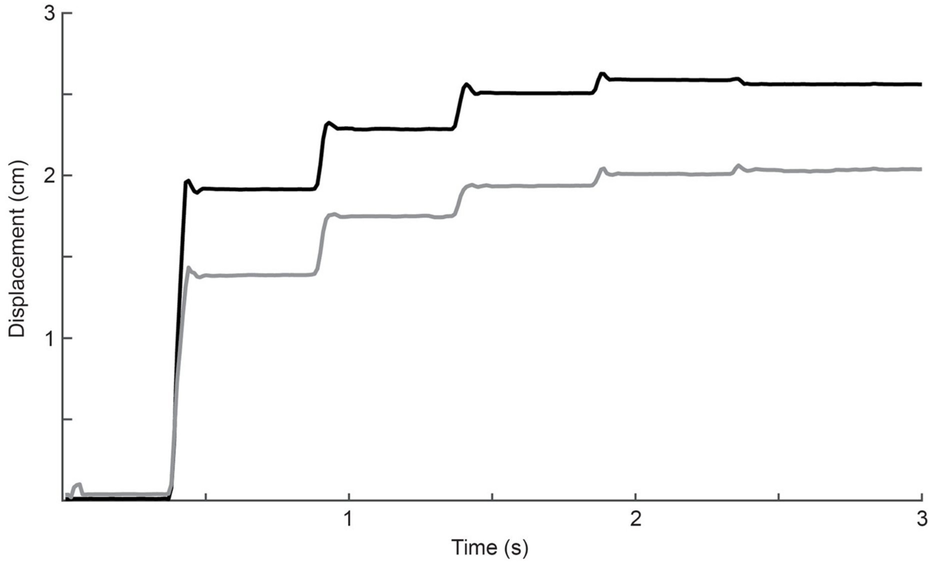

Fig. 5. Following sustained tail movements, *D. bennetti* performs a few brief whole body movements, which are captured here by tracking the eye (black line) and vent (gray line). An initial large amplitude movement is followed by a number of much smaller movements.

reflect the ecological circumstances in which these species operate. As such, documenting in detail the behaviour of species is important.

Diporiphora superba is unique among Australia's dragon lizards in both appearance and behaviour. We confirm anecdotal reports that the species can be hard to locate in vegetation during the day but is more readily found at night. However, the first two individuals we found were observed in the mid-afternoon as they moved across a rock platform, and the species were not as clumsy and slow moving as has been previously reported (Melville and Wilson 2019). Indeed, we observed multiple individuals move swiftly across the rock substrate, including, on one occasion, the use of bipedal running (Fig. S1). Although their general behaviour was in contrast to our expectations, their signalling behaviour does match previous accounts of their slow locomotor behaviour. Push-up movements were among the slowest we have recorded for Australian agamids, peaking at just over 6 cm/s in the display we quantified. This is in stark contrast with the push-up generated by *C. isolepis isolepis* in the present study, which peaked at just over 35 cm/s. It is also substantially slower than that of other Australian dragon lizards whose displays were quantified in the same manner, including *Gowidon longirostris*, *Ctenophorus caudicinctus* and *C. pictus*, which all have peaks well above 25 cm/s (Ramos and Peters 2017*a*). Interestingly, the speeds are very similar to that of *C. fordi* (Ramos and Peters 2017*b*), which is not territorial and signals only when close to other lizards. It is possible that rapid movement has not been selected for in both species.

We have confirmed that movement-based signals are used by *D. superba* but have not established the function or context of these displays. Are slow moving push-ups a necessary adaptation brought about by interacting physical and ecological factors? *Diporiphora superba* is a slender species with a body size in the mid-range for Australian agamids (~75 mm SVL), but with tails 3.8 times the length of the body (as measured in the present study) that are among the longest for the genus (Thompson and Withers 2005). Their limbs are also notably spindly and in contrast to the robust limbs of other members of the family. Such morphological adaptations are ideal for occupying small shrubs (Herrel *et al.* 2001) where they spend a large part of the day and may constrain the kinds of movements they can reliably generate. Furthermore, as they do spend considerable time in vegetation, we speculate that generating fast, powerful push-up displays might compromise their stability within the plants. An alternative explanation is that the displays we observed serve a non-aggressive function, similar to the use of displays by *C. fordi*. The movement also resembles slow 'head bow' movements of *A. muricatus* (RAP, pers. obs.), although the function of such movements is unclear for this species, which also utilises rapid movement-based displays in aggressive contests between males (Peters and Ord 2003). Further work will be needed to determine the function of displays by *D. superba* and to consider factors that influence this behaviour.

From our observations, it would appear that the core component of the movement-based displays of *D. bennetti* are tail movements. Our earlier review identified 10 species that performed tail movements, of which seven were classified as tail flicking on the basis of side-to-side movements of the tail. None of the descriptions of tail flicking displays cited in our review have quantified the movement in the

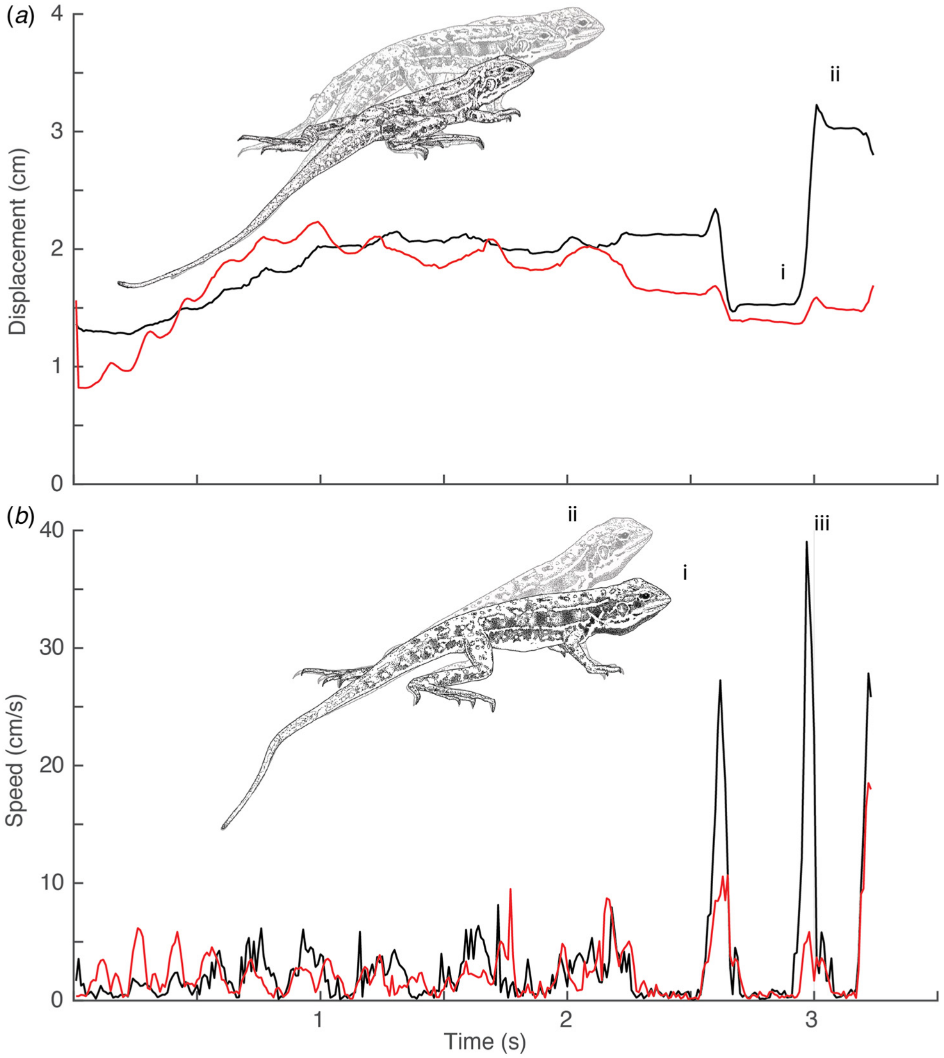

Fig. 6. (*a*) Display action pattern (DAP) graph measured at the eye and (*b*) speed profile for displays by *C. isolepis isolepis*. The display begins with the lizard raising its body from the substrate and slowly leaning forward, as shown in the illustration at (*a*). The display ends with a push-up movement in which the lizard first lowers its head. Roman numerals at (*a*) depict the movement of the push-up and correspond with the illustration at (*b*). Movements are generally slow until the final push-up movement, which is quite rapid (iii).

same way that we have here for *D. bennetti*, but most can be characterised by rapid movements in seemingly random directions, rather than the rhythmical tail movements described here for *D. bennetti*. Once again we have confirmed the use of movement-based signals in this species, but do not know what else is in their repertoire. If this does turn out to be the core display of the species, then it will be quite unique for Australian agamids. *Amphibolurus muricatus* uses tail flicking at the start of its display (Peters and Ord 2003), and the duration of this movement is related to environmental conditions (Peters *et al.* 2007). This is also true of other Australian agamid species, though the tail movements do not seem to be as reliably performed. In all of these species, however, the tail movements are followed by other motor patterns that represent the core of the display. The body movements following tail waving by *D. bennetti* were not substantial, comprising whole body jumps off the substrate of approximately 5 mm and repeated a few times before changing position and tail waving is resumed. It is difficult to know the role that these movements play in signalling exchanges. It is intriguing to consider the possibility that tail-movements represent the core component of the display of *D. bennetti*, as this is rare for Australian agamids studied to date. Such signalling behaviour is well known for agamids overseas (e.g. *Phrynocephalus* sp.: Peters *et al.* 2016), as well as for non-dragon species in Australia such as the rainbow skinks (*Carlia* sp.: Langkilde *et al.* 2005) from the family Scincidae.

Our original review did indicate that *C. isolepis isolepis* utilised movement-based visual displays (Ramos and Peters 2016). This reflected unpublished accounts of backflips being used in the context of male–female interactions, which might facilitate the presentation of ventral colours during the mating season. However, the descriptions we provide herein for this species are entirely new. The display we describe here is relatively simple. Prior to generating a rapid push-up movement, the lizard slowly raises the body from the substrate and leans forward. The slow movement that starts the display is quite different to its general locomotor behaviour of rapidly moving across the substrate around clumps of vegetation (Losos 1988; Daly *et al.* 2007, 2008). Indeed the species' association with more compact substrates might even be due to its penchant for rapid locomotor behaviour (Downey and Dickman 1993). Transitioning from slow deliberate movements to a rapid push-up may serve to accentuate the speed of the push-up. *Ctenophorus isolepis isolepis* has proven amenable to field-based research and has proven useful for understanding thermal behaviour and habitat partitioning in arid environments, and we encourage further research into its social behaviour.

We made multiple attempts to elicit movement-based displays from *D. sobria*. Despite following the same procedures as with other species examined herein, which is also consistent with our other work, we did not observe movement-based signals in this species. This certainly sets the species apart from the others, but we are not willing to rule out visual signalling entirely. First, it is too soon to suggest that dynamic displays are absent as we may have inadvertently chosen pairs poorly or conducted trials at the wrong time of year. Secondly, visual signalling might take on a different form in this species and we recommend that future efforts also consider the possibility of changes in visual appearance – colour and pattern – over the course of pairwise interactions, particularly around the hindlimbs. We were not able to formally assess this as a potential signal or cue from our observations, and it is hard to distinguish it from potential correlates of responses to the thermal environment. Recent work on another Australian dragon, *Pogona vitticeps*, suggests that colour change can serve both thermoregulatory and signalling functions simultaneously (Smith *et al.* 2016).

In summary, we have been able to confirm an earlier assumption that insufficient knowledge was limiting our understanding of the extent of movement-based visual signalling by Australian dragons, with two new species now identified and new knowledge provided about another. We have no doubt that there will be more species added to the list as we and others take time to look at their behaviour more closely. Although we confirm the use of movement-based signals, we do not claim to have documented the full repertoire of behaviour. Also, little is known about the social behaviour of our focal species and we need to understand the context in which these signals are used and how the species deal with other ecological and environmental factors that are known to be relevant to other species. Signals are central to the behaviour of animals and documenting these behaviours in detail helps us to understand better their ecological circumstances.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study are available in La Trobe University's research repository OPAL, powered by FigShare at doi:10.26181/18665726.

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