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RESEARCH ARTICLE

Integrating evolutionary biology with digital arts to quantify ecological constraints on vision-based behaviour

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Abstract

- Motion vision is crucial in the life of animals, in controlling locomotion, in foraging, for predator evasion and in communication. However, information on the conditions for motion vision in natural environments is limited. Advancing knowledge of the ecological limitations that affect functional behaviour requires novel methodologies.
- 2. To explore motion ecology in more detail we describe an innovative method that integrates evolutionary biology with digital arts. A visualization tool that simulates three spatial dimensions plus movement through time, 3D animation is an innovative approach to understand dynamic environments. Animal signalling systems have provided useful insights into ecological limitations on behaviour, and we demonstrate the utility of our approach by examining motion displays of lizards surrounded by plant motion noise.
- 3. The effectiveness of signals in noise was considered under different circumstances, and in each case, we had complete control over the simulations. We used these scenarios to both validate our approach and to demonstrate its potential. The relevance to motion signalling of prevailing wind and resultant plant motion is now well established and we begin by replicating this effect and illustrate how we can explore this in quantitative detail. We further demonstrate its utility by providing novel insights into the benefits of signalling in the right place and at the right time, by manipulating immediate signalling backgrounds, variation in signaller-plant distances and light environments. Each of these simulations provide opportunities for investigation that would be impossible in nature.
- 4. Systematic measurements of motion ecology in detail are now achievable. In addition to insights into the evolution of motion signals, 3D environmental reconstruction will provide a test bed for other topics in the field of motion ecology, and a resource to enhance public engagement with science.

KEYWORDS

3D animation, motion signal, signal efficacy, signal evolution, visual saliency

1 | INTRODUCTION

To appreciate fully the forces that shape animal behaviour, it is necessary to understand the information-processing tasks under relevant conditions. Knowledge of the environment in which animals operate and the sensory processing demands that mediate behaviour are crucial. One important source of information for many animals comes from motion vision. Although much is known about the computational and neural principles of motion vision, information on the conditions for motion vision to function in natural environments is limited and requires innovative methods. In this paper, we demonstrate the utility of three-dimensional (3D) animation as a research tool. We focus on animal communication to showcase the possibilities, but subsequently emphasize its wider application.

Important insights into the sensory and ecological limitations that govern behaviour have been gained from studying animal signals. Signals have evolved to be effective in the environment in which they are emitted so the diversity we see in signal structure directly reflects ecological factors (Endler, 1992). The physical structure of microhabitats can affect signal transmission (Morton, 1975), which ultimately constrains the kinds of signals that are most effective (Hunter & Krebs, 1979). Environmental noise is also a major constraint on signalling because it competes with signals for limited sensory and cognitive processing abilities of receivers. To convey information effectively, animals are known to adjust their signalling strategies to remain salient against the ambient noise background (Ord & Stamps, 2008; Peters, Hemmi, & Zeil, 2007). Therefore, detailed descriptions of signal structure must go hand-in-hand with the careful analysis of the structure and dynamics of environmental noise in a manner applicable to the processing constraints facing receiver sensory systems. Research into acoustic signals has followed this philosophy (Henry & Lucas, 2008; Slabbekoorn & Smith, 2002), but complementary considerations of visual signals defined by movement are rare.

As visual motion is one of the most salient features in the world of animals, it is not surprising that the use of motion signals is widespread in the animal kingdom, from mammals (Rundus, Owings, Joshi, Chinn, & Giannini, 2007) to invertebrates (Elias, Land, Mason, & Hoy, 2006). However, motion signal efficacy is affected by the motion of wind-blown plants (Fleishman, 1986; Peters, 2008), which varies from moment to moment as environmental conditions change. Quantifying motion signals and noise in a meaningful way is not straightforward and requires a strategy that outlines the processing demands facing receivers (Peters, 2013). Physical measurements of plant movements will not be sufficient for quantifying motion noise, as they do not quantify plant motion in a manner that is relevant to the detection filters of receivers. A solution is needed that allows for simultaneous consideration of the physical movements of plants, variation in microhabitat structure, environmental variables and animal signals. The ability to systematically manipulate one or more of these components would also be beneficial. To achieve this in nature would be impractical. Even multiple synchronized cameras, filming at different times of the day throughout the year, would not sample the range of conditions required to characterize fully the image motion environment. Also, we would not achieve the level of control required to isolate key parameters, or to systematically manipulate one or more components.

However, these goals are achievable in simulated environments created with sophisticated 3D animations. The use of realistic 3D models of signalling animals and habitats offers great potential for exploring the evolutionary constraints on movement-based signals. Animations have been used to manipulate visual signals for playback experiments in multiple systems including spiders (Harland & Jackson, 2002), birds (Watanabe & Troje, 2006), snakes (Nelson, Garnett, & Evans, 2010), lizards (Peters & Evans, 2003) and in fish (Zbinden, 2004). However, while past studies have created 3D environments for virtual reality experiments (Dolins, Klimowicz, Kelley, & Menzel, 2014), the full power of 3D animation has not been harnessed to simulate signalling environments, and certainly not as a computational platform for quantifying the role of planted environments in dictating signal evolution.

In this paper, we describe the construction of virtual environments to explore the interaction of motion signal and motion noise. We first outline the steps involved in reconstructing a signalling animal. This is followed by descriptions of the tasks required to reconstruct microhabitats, including the dynamic properties of wind-blown plants and the light environment. Finally, we discuss how simulations are filmed and exported for analysis, as well as the quantitative strategies for comparing simulations. To demonstrate the utility of this approach, we set up four scenarios utilizing the same signal to explore ecological parameters that are predicted to affect signal efficacy. Our goal was to demonstrate the level of control we can achieve within the animated environment and its ability to explore phenomena of interest in detail.

2 | MATERIALS AND METHODS

We do not provide a detailed manual for animation, but a demonstration of the key components in developing 3D models and building animations. We used Maya 2015 (AUTODESK Inc.) software to create a virtual environment, but other options are available (see Table S1). Although the number of commands available to the user can be overwhelming, free tutorials and a comprehensive knowledge network are available online (see also Supplementary Methods for tips to avoid common mistakes).

2.1 | Creating and animating the 3D model

A territorial display of a Jacky dragon (*Amphibolurus muricatus*) was elicited in the field using a tethered animal introduced to the focal lizard and filmed using a dual camera system. To reconstruct the signalling motion, we digitized the position of multiple body parts throughout the sequence, and subsequently combined the data from two camera views to reconstruct the signalling motion in 3D and quantify real physical amplitudes. The digitizing process utilized a free Matlab application for camera calibration, digitizing features of interest and 3D reconstruction of movement information (Hedrick, 2008); see Peters, Ramos, Hernandez, Wu, and Qi (2016) and Bian, Elgar, and Peters (2016) for applications of this technique.

We used subdivision-modelling techniques to create our 3D models. This refers to the process of sculpturing polygons and surfaces and later subdividing the polygon mesh to produce smooth organic forms. In computer animation, the 3D model is represented in two parts: a surface representation used to draw the morphology of the character (referred to as *skin* or *mesh*) and a hierarchical set of interconnected bones (called the *skeleton* or *rig*) used to animate (*pose* and *keyframe*) the mesh. To start building the mesh, we broke down the morphology of the animal into several main parts to determine the overall geometry. The head and body of the lizard were modelled from a basic cube. By manipulating the vertex position on the cube, we gradually built up the details to correspond with the physical form. We used realistic images of the animal to superimpose surfaces of polygons into the correct morphology, and then pull out the limbs and tail from the body through the same shaping process (Figure 1a). Since the animal is bilaterally symmetrical, we only needed to model one side of the body and instructed the software to mirror the geometry offset along its axis. This helped to minimize errors in creating uneven structures on both sides of the body. After completing the shaping process, we used average values from a database of morphological measurements of the Jacky dragon to



FIGURE 1 Maya screenshots of the (a) lizard model, (b) texture map (left) and model with the texture wrapped around the surface (right), (c) wireframe mesh and skeleton and (d) joint controllers as a colour gradient

make minor adjustments to the model. Finally, a digital photograph of lizard skin was wrapped on to the model surface (Figure 1b) in a process referred to as *UV Mapping*. The model is now ready for animation.

The animating process begins by creating a virtual skeleton made up of bones that are connected at *joints* (Figure 1c). Skeletons do not imitate real anatomy or physical processes. Rather, they are control objects at appropriate locations (joints) to control the deformation of the model. We first created a chain of joints along the limbs and body of the model, and then implemented individual controller objects for each set of joints to gain precise control of the geometry as well as global displacement and local movements of the model. After building the joints, we integrated and bound the skeleton to the model through a process known as skinning. In Maya, smooth skinning allows each vertex to follow a limited number of joints with the amount of influence affected by each joint represented as a numerical scale [0,1]. This scale can be modified from a spreadsheet or virtually painted directly onto the model with the values represented as colour gradients through a process often named weight painting (Figure 1d). After the 3D model is correctly connected to the skeleton, we started the animation process. The joint controllers became useful here, because rather than manipulating every joint to achieve a signal pose, the controllers act like the strings that a puppeteer uses to animate a puppet, and a vast range of movement could be achieved by a small set of control bars. We used position data from our frame-by-frame analysis of the display to set the coordinates for each controller and for all frames throughout the sequence. We finish with a display sequence to match our model species that comprises four distinct components including tail flicking, limb waving, push-ups and whole-body movements.

2.2 | Creating the virtual habitat

Jacky dragons inhabit woodlands and coastal heath of southeast Australia, and are often seen perched on fallen timber. We created a virtual habitat that contains relevant features rather than a specific habitat. A base plane was created first, using inbuilt geometric tools to sculpt an undulating landscape that reflects the local terrain (Figure 2a). We added realistic 3D models of trees, smaller plants and logs, created using the same sculpting method as the lizard. These plants were placed in the scene using the position of the lizard as the centre point. We integrated plant models with a script that guides plant movements. Within Maya, the scripts of any physical movements are built on physically accurate equations, which can be precisely manipulated using a slider bar, in order to generate realistic plant movements under different wind conditions (Akagi & Kitajima, 2006). Realistic plant models also can be purchased from third-party providers that are fully rendered with textures, lighting and windmotion animation specifications. These models are easy to manipulate and can be tailored to specific requirements. After deploying the major plant species in the environment, the next stage of crafting the environment was to paint in smaller grasses using Maya's Paint Effects brush system (Figure 2b). The grass has an integrated wind controller that allows for easy animation in the final stages of the process. The

grass clumps can be linked according to location within the habitat, as location will affect how plants react to wind.

With the ground landscape completed, lighting and shadows were added to the scene. The simulation of light environments are based on physically accurate lighting coefficients (lones, Krupkin, Sbert, & Zhukov, 2003). A single directional light was added to simulate the sun and thereby create naturally over-casting shadows from rocks, logs and plants. Smaller area lights were also added to illuminate the main character in the scene (the lizard), but were for the purposes of these demonstrations only and should be excluded for greater realism (Figure 2c). The position and scale of lights can be controlled using transformation tools within Maya.

2.3 | Filming within a virtual environment

Virtual cameras are placed in the scene and manoeuvred into position using simple translocation functions within Maya. Each virtual camera is invisible to other cameras and so cannot obscure the scene from any other viewpoints. Once a specific camera is selected, the software will display the scene as if we are looking through a real camera (Figure 2d). Attributes such as viewing angle, depth of field, focal points and zoom/scale can be easily adjusted. For this paper, we disabled depth of field functionality, as we want all objects within the scene to be clear and focused. Finally, the Maya scenes were rendered as complete audio video interleave files at 25 frames-per-second.

2.4 | Demonstrations within a virtual environment

To demonstrate the utility of our approach, we selected four scenarios in which the detection of motion signals is predicted to be affected by habitat structure and environmental conditions:

- Prevailing wind conditions—the movement of wind-blown plants plays an important role in signalling behaviour (Ord & Stamps, 2008; Peters & Evans, 2007). To explore this, we used the same scene, viewed from the same angle and featuring the same signal. The only difference between the sequences was the wind level and resultant plant movements. We created three animation sequences featuring no wind, moderate wind and strong wind conditions.
- 2. Local backgrounds—Motion vision is strongly influenced by local backgrounds (Peters, Hemmi, & Zeil, 2008), therefore we created two animation sequences that were identical, except for the object immediately behind the displaying lizard. We used a large rock in one sequence, and a plant (Lomandra sp.) in the second sequence (Figure 3a), with strong wind conditions in each. These sequences allow us to consider whether the immediate background in a noisy environment can improve signal efficacy in a manner similar to birds that create stages to ensure strong chromatic contrast of colourful ornaments (Endler & Thery, 1996).
- **3.** Signaller-plant distances—The position of the signaller relative to surrounding plants will affect perceived motion amplitudes, which







FIGURE 2 Modelling the microhabitat starts with (a) an undulating base plan with sand texture before (b) the inclusion of major objects—trees, rocks, logs and grasses. (c) A static spherical photograph is applied to the background and directional lights (orange lines) for the scene. (d) Final scene from one camera view

might be important for determining signal effectiveness (Peters, 2010). We created two sequences to examine this prediction, with the difference between sequences being the position of the lizard relative to the dominant grass: at the same distance from the receiver as the plant, or positioned closer to the receiver than the plant (Figure 3b).

4. Different light environments—The light environment is crucial for static visual signalling systems (Endler, 1992). As motion vision mechanisms are known to be highly dependent on brightness and contrast, it is possible that the distracting effects of shadows and variation in the light environment alters the relative effectiveness of motion signals. We created a spotlight integrated with motion patterns of over-casting tree branch shadows. The light was oriented in the same direction directly facing our lizard model in each of the sequences, but we changed the lighting intensities by manipulating the luminosity of the spotlight scale from zero to ten, and as light intensity increases so does the over-casting shadow. We developed two sequences with constant wind level but different light intensities: natural lighting and intense shadows (Figure 3c). These sequences (a)



FIGURE 3 Representative frames from animations to examine the effect of (a) different backgrounds, (b) signaller-plant distances and (c) different light environments

enabled us to explore the interaction between actual plant movements, shadows generated by plant movements and variation in light intensity.

All animation sequences were 176 frames duration (c. 7 s at 25 fps) and exported at HD resolution $(1,920 \times 1,080 \text{ pixels})$ for analysis (see Movie S1).

2.5 | Scene analysis

Videos generated in the virtual environment (Figure 4a) can be analysed in the same way as videos filmed in nature. Visual motion is computed from correlated changes in brightness in neighbouring photoreceptors and a computational implementation of this is the correlation-type elementary motion detector (EMD). Multiple EMDs

FIGURE 4 (a) Rendered frames from two sequences featuring exactly the same signal but in wind-still (left) and windy conditions (right). Animation sequences were analysed in three ways with output from each analytical approach shown for the same frame in wind-still and windy sequences. (b) Visual motion computed by correlation-type elementary motion detectors in which colour indicates the direction of movement and saturation reflects relative speed. (c) Gradient detector models showing angular speeds irrespective of movement direction. (d) Saliency analysis using motion information alone predicts focal points for attention



interconnected in a grid can be used to model motion in 2D scenes captured on video (Zanker, Hofmann, & Zeil, 1997; Figure 4b). This approach allows for biologically plausible scene analysis by incorporating knowledge of the visual capabilities of our study animals, such as spatial resolution and temporal integration times. The gradient detector model for motion analysis is an alternative that does not seek to replicate biological visual systems (Figure 4c). The choice between these two might depend on the nature of the motion as EMDs are suggested to perform best in low signal-to-noise ratios, whereas gradient detectors are more suited to high signal-to-noise situations (Potters & Bialek, 1994). An alternative option is to use saliency analysis, which seeks to identify the regions of the scene that attract the most attention. Itti, Koch, and Niebur (1998) described a computational model for saliency-driven bottom-up selective attention to objects, which involved scanning a saliency map computed from local feature contrasts, including motion. In Figure 4d we used graph-based visual saliency, which uses local computations, as well as global information, to obtain a saliency map predicting salient areas of the scene (Harel, Koch, & Perona, 2006).

To quantify differences between sequences within each scenario, we used sequences featuring lizard displays in the absence of plant movement to identify where motion occurred (baseline) and to generate a binary mask representing areas of known lizard movement for each frame of the animation (see Figure S1). By multiplying the saliency data with the binary mask, we obtained estimates for the relative salience of the lizard movement for each frame (Figure 5a). The no wind sequence was used as a baseline for the changing wind conditions and different light environments. A new baseline sequence was created for the comparison of different backgrounds, while separate baseline sequences were created for the near and far signaller-plant distance sequences.

3 | RESULTS

We created multiple animation sequences to explore the role of prevailing wind, background objects, signaller-plant distances and different light environments, and quantified the relative change in saliency of lizard displays. We obtained saliency measures frame by frame for each sequence, as shown in Figure 5a (bottom panel) for varying wind conditions. Saliency scores range [0,1], but the threshold for detection by a receiver would need to be empirically determined. Here, we selected 0.8 as a conservative threshold for reliable detection, and represented detectability as raster plots (Figure 5a, top panel). The number of frames in which a given sequence exceeds this threshold was then summed (Figure 5b). As shown, the proportion of the no wind (or baseline) sequence is less than one because the lizard is not moving in every frame. We then determined the relative percentage change in effectiveness from the baseline for the other two sequences (Figure 5b inset). Consideration of the data need not be limited to a single threshold value and so we computed the relative change in efficacy from the baseline for the full range of saliency values (Figure 5c), and use this approach to consider each of our signalling scenarios.

As expected, the predicted effectiveness of lizard displays declines with prevailing wind (Figure 5c). Manipulating the immediate background, from a noisy plant to a static rock, resulted in only a modest improvement in effectiveness at higher threshold values (Figure 6a). However, the manipulation we imposed retained the same components in each scene, just in different positions, so the improvement represents the change in figure-ground segmentation in local regions of the scene. Manipulating signaller position relative to plants, while keeping all other components the same, resulted in a modest efficacy advantage for signals separated from plants (Figure 6b), as suggested elsewhere (Peters, 2010). Results for manipulation of the light environment were somewhat unexpected. Under both moderate and strong wind conditions, increasing shadows and areas of intense light served to enhance the signal (Figure 6c).

4 | DISCUSSION

An interdisciplinary approach that unites biology with the creative digital arts is proposed as an innovative way to quantify the relationship between animal behaviour and environmental characteristics. We presented a quick road map to demonstrate the research applicability of 3D animation as a laboratory tool by focussing on motion signalling of lizards under a range of circumstances. This was carefully chosen to provide a broad overview of the capabilities afforded by this simulation tool. However, we emphasize below that the foundations we lay here could be extended and applied to other topics. We not only anticipate theoretical advancements in sensory ecology and behaviour, but also foresee derived benefits for education and community engagement in ecology.

4.1 | One habitat—Multiple opportunities

4.1.1 | Controlling environmental context during motion signalling: From simulation to replication

We explored several environmental constraints on motion signal efficacy in a virtual environment. Wind-induced plant motion as a major source of motion noise is well known but rarely quantified in detail (but see, Fleishman, 1986; Peters, 2008). We have simulated three wind conditions and shown how increasing wind intensity affects motion signal efficacy. With the ability to systematically increase wind speed within our animation environment, we will obtain a more complete picture of how wind-induced plant motion affects signal efficacy, and predict changes to signal structure required if they are to remain salient in different wind environments. We have also quantified the effect of immediate local background and signaller-plant distances, as well as variation in light intensity and over-casting shadows. These have not been explored previously in the context of motion signalling. Importantly, all our simulations provide us with complete control of the signalling context, which is unparalleled in studies of motion signalling and not achievable in nature.



FIGURE 5 An illustration of how changing wind conditions influence the efficacy of the lizard signal. (a) *Bottom panel*: Maximum saliency score over time in regions of the image frame that are known to feature lizard display movement (determined from analysis of the no wind sequence). Lines are shown for the three animation sequences: no wind (black), moderate wind (grey) and strong wind (red). *Top panel*: Raster plot for the three sequences depicting frames in which maximum saliency scores exceed 0.8. (b) The number of frames in each of the three animation sequences that exceeded the 0.8 threshold value. *Inset*: Percentage difference in efficacy from no wind sequence for the lizard display in moderate and strong wind. (c) Relative change in efficacy as a function of saliency threshold value for moderate (grey) and strong (red) wind conditions

Here we relied on the dynamic power of the software to faithfully simulate plant species and their specific movements. Underlying these tools are in-depth studies to determine physical equations of motion that achieve realistic animations of wind-induced vegetation movements (Akagi & Kitajima, 2006; Zhang et al., 2007). In fact, deformation of any type of object in an animated environment, such as hair movements or clothes dynamics, are achieved using physicsbased dynamic simulation systems (Stam, 2009). We can thus be relatively confident that our simulated plant movements are realistic. However, it is possible to recreate actual habitats using information on the local terrain, topography and spatial distribution of plants. This includes creating plant models that match plant shape, branching structure and stem/leaf characteristics. It is also possible to replicate the dynamic properties of a given plant in nature. To achieve this, a marker-less motion capture technique could be employed to recreate the geometric structure of actual plants, as well as the dynamic properties of their interaction with wind from 2D footage of real plants (Diener, Reveret, & Fiume, 2006). Briefly, the technique utilizes velocity information obtained from optic flow analysis and uses statistical clustering methods to organize features into a hierarchical structure. This is subsequently refined according to geometrical structure, and the final 3D hierarchical structure is then used as a motion controller



FIGURE 6 Change in efficacy for sequences examining the effect of (a) immediate background, (b) signaller-plant distances and (c) light environments as a function of changing saliency threshold

for animating plant models. Individual researchers are therefore able to determine whether simulation or replication of plant movements is appropriate for their objectives. The simulation of real-world lighting conditions is also achievable. In Mental Ray[®], a rendering plug-in for Maya, a high-dynamic range photometric lighting system (*Sun & Sky*) allows users to select lighting conditions according to the exact date, time and location. Rendering engines of this kind use physically based computational algorithms when rendering (Kniss, Premoze, Hansen, Shirley, & McPherson, 2003). This means the simulations are accurate and predictable as they are designed to follow physical laws (Moeck & Selkowitz, 1996).

The creation of simulated environments provides opportunities to predict the consequences of habitat modification in the context of motion signal efficacy. Motion noise environments will be altered following events that change the plant environment. Natural events like fire and storm (wind and rain) damage might have important consequences for inhabitants because it changes the noise environment in important ways. Storms often modify the environment by relocating the position of plants, which might change the spatial distribution of noise. In the case of low-severity fire events, many plants will be impacted by the removal of leaves and higher order branches, which are a dominant part of the noise environment (Peters, 2013), and motion noise might be reduced dramatically. The signals of species like the Jacky dragon might become highly conspicuous. The costs of highly conspicuous signals include wasted energy and increasing the likelihood of detection by predators. Under conditions of increased predation risk, signallers are expected to modify their signalling behaviour accordingly (Steinberg et al., 2014). Simulated environments can be used to replicate these events and enable us to quantify before and after effects as it relates to motion signalling, and to predict changes in signalling.

4.1.2 | Extension: Dynamic scenes in the context of colour vision

As recent research supports a role for chromatic input to motion processing (Cropper & Wuerger, 2005), it is worthwhile to consider dynamic scenes also in the context of colour vision. An important assumption in our simulations is that the RGB colour space we use is relevant to the receiver. However, our rendered scenes are optimized for human colour vision systems, which comprise short (blue), medium (green) and long (red) wavelength cones. We can convert rendered scenes from standard RGB to a colour space that represents the relative response of the three types of cones, known as the LMS colour space. Scene analysis, such as the saliency approach adopted here, could then consider animations separately for each cone. Furthermore, rendered animations could be post-processed to model how colour vision deficiencies affect the information available for motion vision to operate. Human observers with normal colour vision see scenes differently to others that lack medium (deuteranopia) or short (tritanopia) wavelength cones (Figure 7). Interestingly, our simulations of colour vision deficiencies suggested that the salience of lizard displays is reduced, particularly for deuteranopia, despite being identical



FIGURE 7 Post-processing of an animation sequence to simulate normal human colour vision (top row) and colour vision deficiencies: deuteranopia (middle row) and tritanopia (bottom row). For each, the functioning cones are shown (left column) along with a representation of the scene utilizing the functioning cones (centre column), and a salience map for a single frame (right column). Conversion of images to deuteranopia and tritanopia undertaken according to (Machado, Oliveira, & Fernandes, 2009)

movements of both animal and plants. The RGB conversions we used to generate these colour-deficient sequences could be modified to represent a variety of species with cone sensitivities similar to our own. Furthermore, colour conversions of textures can be undertaken at the time of model creation, and Tedore and Johnsen (2016) provide an excellent description of how to replicate colour vision capabilities of animals with very different spectral sensitivities.

4.2 | Further applications in motion ecology

As motion is a fundamental source of information for many animals, replicating natural environments in sophisticated detail within a virtual environment can provide a test bed for exploring motion ecology more broadly. Through systematic manipulation of environmental features and animal movements, we can understand more clearly the image motion computation requirements for a variety of functional behaviours. For example, movement is a key requirement for the identification of prey and predators (Figure 8a). In the case of adult Jacky dragons, movement breaks the camouflage of an otherwise cryptic lizard and might be detected by a nearby avian predator, such as laughing kookaburras (*Dacelo novaeguineae*) that perch

on elevated vantage points and scan the environment for potential prey (Figure 8b). However, the image motion generated by a looming kookaburra might in turn be detected by lizards (Figure 8c) and evasive action taken. Animations provide a powerful way to understand these interactions in greater detail (Nelson et al., 2010), including a novel implementation of the use of animal-borne cameras to quantify changing visual motion cues as animals move (Kane & Zamani, 2014). Following on from this, as animals move through their environment they generate optic flow that is used for navigation (Srinivasan, Zhang, Lehrer, & Collett, 1996). Our virtual simulations could allow for controlled, repeatable investigations of the consequences for optic flow under a variety of environmental circumstances by utilizing animal-borne cameras in a virtual environment.

4.3 | Multiple habitats—A world of possibilities

4.3.1 | Translocations in a simulated environment

Environments feature a variety of plant species and multiple exemplars of the same species, yet each plant will move differently in response to wind due to differences in plant structure and geometry



FIGURE 8 (a) 3D reconstruction of a laughing kookaburra (*Dacelo novaeguineae*) approaching a basking lizard. Respective viewpoints of the (b) approaching avian predator and (c) lizard prey

(Peters, 2013). In addition to plant geometry, wind-induced plant movements are determined by habitat location and topography affecting relative exposure to wind (Hannah, Palutikof, & Quine, 1995), and the presence of other plants in the environment that affect the characteristics of wind (De Langre, 2008). Therefore, different micro-habitats represent distinct image motion environments (Peters, 2008), and this variation must be a crucial determinant of motion signal structure. It has been informative to broadcast acoustic signals in different environments to explain the relationship between environment and behaviour (Slabbekoorn & Smith, 2002), but analogous options for motion signals are not available and translocating species across

different habitats is restricted by government regulations in most circumstances. However, detailed reconstructions of multiple signalling environments provide an exciting opportunity to consider how the signals of one species would "perform" in other environments. Translocating species between habitats in a simulated environment is an exciting extension to the work herein (Figures 9 and S2). The Jacky dragon (Figure 9a) is common in coastal heath of south-eastern Australia, while the long-nosed dragon (*Gowidon longirostris*; Figure 9b) can be found in rocky gorges of central and western Australia. Both species generate complex motion signals, but the motion noise environments are very different. Using 3D animation as a sophisticated

FIGURE 9 Recreating different microhabitats in 3D animations enables consideration of motion signal efficacy of "translocated" species. (a) Jacky dragon (*Amphibolurus muricatus*) habitat and close-up view of a (b) Jacky dragon and (c) long-nosed dragon (*Gowidon longirostris*) in this coastal environment. (d) Long-nosed dragon habitat and close up view of (e) long-nosed and (f) Jacky dragons in this rocky gorge



simulation tool we can quantify the effectiveness of signals in each of these habitat types and predict the extent to which simple plasticity in signalling will mediate different environmental conditions.

4.3.2 | Whole new worlds

Our objective is to demonstrate that virtual technologies can be used to examine important questions in animal ecology. The simulations we present herein, and which we believe showcases the utility of 3D animation, focuses on motion signalling in terrestrial environments at a scale of metres. This represents our core focus, but the method is not so limited. We see these tools being applicable to understanding how animals interact with their environment from the perspective of a viewer located anywhere in the environment. Virtual environment reconstruction encourages a fresh look at the physical world and we encourage others to consider very different types of environments (Figure 10a), and vastly different scales—from hundreds of metres to macro-level analysis (Figure 10b-d).

5 | CONCLUSION

Our method is an extension in the use of 3D technology and represents a powerful tool for motion ecology owing to its ability to faithfully simulate lighting, shadows, geometry, motion and time-based transitions. The control we are afforded would be impossible to achieve in nature. While it is necessary to ground-truth simulations using data from real environments (Chouinard-Thuly et al., 2017),



FIGURE 10 (a) Frame sequence of an underwater scene featuring a shortfinned eel (*Anguilla australis*). Rendered frames showing 3D environments for consideration at (b) landscape, (c) habitat and (d) macro-spatial scales we can now address recalcitrant topics in animal behaviour and sensory ecology that concerns the relevance of environmental motion. Importantly, animation is not only an innovative tool for biology, it is an exciting opportunity to engage public attention, and as a teaching tool for students. With modest additional work, the simulated microhabitats could be repurposed as interactive applications for tablets, touch screen devices and exhibition displays in museums and schools that provide for better user experiences and enhance opportunities for self-guided learning. The connections we build between science and the general public will be necessary for preserving valuable natural resources for future generations.

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AUTHORS' CONTRIBUTIONS

The project was designed by R.P., T.C. and X.B. Animation work was undertaken by X.B., W.L. and A.P. Manuscript was prepared by X.B. and R.P. with input from all authors.

DATA ACCESSIBILITY

The Maya scene file used in this work is available at https://doi. org/10.4225/22/59b76544ed52e (Bian, Chandler, Laird, Pinilla, & Peters, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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