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Familiar–unfamiliar discrimination based on visual cues in the Jacky dragon, *Amphibolurus muricatus*

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Territorial animals typically have the ability to discriminate between familiar and unfamiliar conspecifics. This enables residents to minimize the costs of resource defence by matching the intensity of their aggressive response to the level of threat posed by intruders. Although individual discrimination based upon chemical signals is well established in lizards, much less is known about the role of visual cues, despite the importance of this modality in social interactions. We conducted two series of video playback experiments, modelled on a habituation–dishabituation design, to test for visually mediated individual discrimination in an Australian agamid lizard. Captive males were shown a different digital video sequence of the same life-sized conspecific every day for 4 days. They were then tested in probe trials with either a novel sequence of the same male, or a matched sequence of a different male. One such series was conducted with footage of inactive basking lizards to evaluate the role of static morphological cues, while the other presented displaying males so that signal structure was also available. Lizards responded to a change in the identity of both static and displaying video males with increased substrate licking, a chemosensory behaviour that has consistently been reported in previous work with live opponents. The unfamiliar basking conspecific also evoked increased locomotor activity. These results show that Jacky dragons are capable of discriminating between familiar and unfamiliar intruders based upon static morphological cues alone.

Keywords: *Amphibolurus muricatus*; familiar–unfamiliar discrimination; individual recognition; Jacky dragon; opponent assessment; territoriality dear enemy effect; video playback; visual cues; visual displays

The ability to recognize different classes of conspecifics can be crucially important to species that engage in repeated social interactions. It is clear that individuals that tailor their behaviour to suit specific social situations are at a significant competitive advantage (Falls 1982). A well-studied example of this principle is the capacity of many territorial species to discriminate between neighbours and strangers. Neighbours share a border and have a stable agonistic relationship with the territory holder, whereas strangers do not. The hypothesized adaptive benefits of this cognitive capacity centre upon the relative threat posed by the two classes of opponent and the costs of escalated agonistic interactions. Since neighbours occupy a territory of their own, they are less likely than strangers to displace a resident. In addition, fighting entails numerous risks. These include injury, the loss of time and energy, and increased conspicuousness to predators (Marler & Moore 1988, 1989; Jakobsson et al. 1995; Brick 1998). The cost–benefit ratio associated with territory defence is hence likely to be substantially affected by the type of intruder (Jaeger 1981; Temeles 1994). This systematic variation favours individuals that can modify their response accordingly.

The typical behavioural expression of neighbour–stranger discrimination is the 'dear enemy' effect, in which territory holders respond less aggressively towards intrusions by neighbours across their shared territorial boundary (Fisher 1954). This phenomenon was first observed in songbirds, and the bulk of subsequent studies have continued to focus upon avian systems (reviewed in Falls 1982; Ydenberg et al. 1988; Temeles 1994; Stoddard 1996). Researchers have generally used acoustic

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playback to simulate territorial intrusions in the field and to explore the mechanisms underlying neighbour–stranger recognition (Stoddard 1996). This highly successful approach has been extended to include other vocally mediated territorial systems, such as those of anuran amphibians (Owen & Perrill 1998; Bee & Gerhardt 2001; Lesbarreres & Lode 2002; Bee 2003).

When neighbour–stranger discrimination is mediated by other sensory modalities, such as vision or olfaction, 'playback' is much less straightforward. Analyses have hence depended largely upon measuring responses to live stimuli, in either spontaneous or staged experimental encounters. This has been a valuable method for studying territorial behaviour and comparing the 'dear enemy' effect between sexes and species (Gromov et al. 2001; Jaeger & Peterson 2002; Leiser 2003; Frostman & Sherman 2004). However, options for manipulating characteristics of the opponent are relatively constrained, which complicates the task of identifying the cues and signals involved in neighbour–stranger recognition.

Iguanian lizards rely primarily on vision for locating food, avoiding predators and communication. As a general rule, members of this lineage show resource defence polygyny: males establish territories that overlap the home ranges of several females (Carpenter 1965; Carpenter & Ferguson 1977; Jenssen 1977; Stamps 1977, 1983). There is some evidence to suggest that males are capable of neighbour–stranger discrimination, forming 'dear enemy' relationships with neighbours. Several researchers have staged interactions in the field by tethering intruders at territorial boundaries, an approach that takes advantage of naturally occurring spatial relationships (Fox & Baird 1992; Husak & Fox 2003; Husak 2004). These studies have reported increased aggression to unfamiliar individuals and to displaced neighbours. However, a potential drawback of the tethering method is abnormal behaviour by the intruder as a consequence of capture, handling and restraint (Stamps 1978).

An alternative approach involves removing lizards from their natural territories and staging contests in a neutral arena (Glinski & Krekorian 1985; Husak & Fox 2003). This method has the benefit of testing for the role of familiarity in the absence of environmental cues. On the other hand, Fox & Baird (1992) have urged caution when generalizing from neutral arena studies, as the costs and benefits associated with the 'dear enemy' effect are derived directly from the control of territorial resources, without which there is presumably less motivation to defend against intruders of any type.

Another common captive protocol involves manipulating the degree of familiarity between individuals with no previous interaction history. In most cases, a resident–neighbour relationship is established with a single prolonged exposure. Testing then occurs either in a neutral arena (Trigosso-Venario et al. 2002) or in the subject's home enclosure (Qualls & Jaeger 1991). Housing lizards together for long periods in small enclosures is an effective method for creating a dominant–subordinate relationship and can be useful in testing the effects of familiarity in nonterritorial species (Font & Desfilis 2002). It is, however, unlikely to recreate the type of social structure observed among territory residents in nature (Carpenter 1965; Prieto & Ryan 1978; Deslippe et al. 1990).

All of the neighbour–stranger discrimination experiments referred to above used live lizards as stimuli. This approach can be limiting because both morphological and behavioural features, such as size, shape, colour patterns, posture and movements, could reveal the identity of an intruder. The specific cues mediating a differential response have typically not been identified. Territory holders can potentially recognize an intruder as belonging to a particular species, sex, population or class, or even as being a specific individual. Recognition processes thus form a hierarchically arranged nested series, in which each step demands a more extensive system of categorization. Successful performance at one level need not imply a corresponding ability at others. A useful approach for evaluating the potential for discrimination is to assess patterns of variation in signal structure.

The most extensively studied element of Iguanian territorial behaviour is the push-up display, in which the head is moved vertically by the coordinated action of neck and leg muscles. Dynamic displays are often accompanied by modifying elements such as colour changes, lateral compression, tail-flicks and dewlap extension (Carpenter 1965; Carpenter & Ferguson 1977). Several studies have investigated the potential of these movements to signal identity by quantifying display characteristics within individuals, populations, sexes and species (Carpenter & Ferguson 1977; Jenssen 1978; Jenssen & Gladson 1984; Martins 1991; Lovern et al. 1999; Orrell & Jenssen 2003). For example, a display element that is relatively stereotyped within individuals, but highly variable between them, has the potential to mediate individual recognition (Jenssen 1978). Similarly, differences in display structure between the sexes could serve a sex recognition function (Martins 1991).

These findings do not demonstrate recognition based on push-up displays, but show that it is in principle possible. Experimental manipulation of potential cues is required to confirm that the observed pattern of variation is functionally important. Methods such as painting and dyeing have been used to isolate the visual attributes used by lizards for both species recognition (Losos 1985) and sex recognition (Cooper & Burns 1987; Cooper 1988; Cuadrado 2000), but there has been no unambiguous demonstration of familiar–unfamiliar discrimination based solely upon visual cues.

In contrast, the role of olfactory cues in lizard social interactions is well understood. Lizards typically use their tongue to obtain chemical information about conspecifics (reviewed in Mason 1992; Cooper 1994), so discrimination can be tested by presenting isolated odours and measuring the rate of tongue extensions. This method has been used to demonstrate discrimination based on sex (Cooper & Vitt 1984), reproductive state (Cooper & Perez-Mellado 2002), relatedness (Main & Bull 1996) and familiarity (Alberts & Werner 1993; O'Connor & Shine 2006). The relative importance of chemical and static visual cues in social interactions has also been studied in one species (*Podarcis hispanica*) by altering the colour and odour of a live stimulus lizard (Lopez & Martin

2001b; Lopez et al. 2002). Olfactory cues were found to override visual ones at close range.

This asymmetry in current knowledge is partly due to the inherent difficulty of manipulating visual characteristics, particularly movements. Recent advances in video playback techniques provide a potential solution to the problem of reproducing dynamic visual stimuli (Rosenthal 1999), at least for those systems in which playbacks can be shown to evoke natural responses (Evans & Marler 1991; Clark & Uetz 1992; Kodric-Brown & Nicoletto 1997). A growing number of studies have demonstrated the effectiveness of video stimuli in eliciting natural social behaviour in lizards (Macedonia & Stamps 1994; Macedonia et al. 1994; Clark et al. 1997; Ord & Evans 2002, 2003; Ord et al. 2002).

Jacky dragons are Australian agamids. Although agamids and iguanids are closely related groups within the infraorder Iguania, and share many behavioural traits (Stamps 1977; Frost et al. 2001), comparatively little is known about the structure and function of agamid visual signals. We used video playback to assess the role of visual cues in opponent recognition. This approach allowed uniquely precise tests of sensitivity to variation in morphology and movement, while controlling for correlates such as individual olfactory characteristics and spatial location. Lizards were shown two series of video sequences: one depicted an inactive basking male conspecific, while the second included push-up displays. At the end of each series, we conducted ‘probe’ trials, in which subjects saw either the same individual or a different male. Based upon previous studies, we predicted that lizards would be able to discriminate between video clips of familiar and unfamiliar conspecifics, and that they would hence respond faster, more aggressively, and with more exploratory behaviour when confronted with an unfamiliar male.

METHODS

Subjects

We used 20 adult male Jacky dragons caught between 1999 and 2004 in National Parks around Sydney, Australia (Botany Bay National Park and Royal National Park). They ranged in size from 17.0 g and 76 mm snout–vent length (SVL) to 41.0 g, 110 mm SVL. We caught them by noosing and transported them in calico bags to indoor housing facilities at Macquarie University. Housing consisted of individual pens (64 × 75 cm and 120 cm high) with opaque plastic sheeting on three sides to prevent visual contact with neighbouring conspecifics and clear Perspex on the remaining side for the presentation of visual stimuli and recording of behaviour. The pens had a sand substrate and contained branches and native vegetation to facilitate climbing, basking and hiding. Environmental systems in the rooms were adjusted to mimic summer conditions with a 14:10 h light:dark cycle and a temperature of approximately 26°C. A heat lamp (125 W, 240 V Philips Spotone) was suspended over each pen to enable behavioural thermoregulation and UV lamps (300 W Osram Ultra-Vitalux) were provided to prevent vitamin deficiency. The lizards were fed twice weekly with live crickets dusted with vitamin supplements (RepCal) and had access to water ad libitum. The pens were sprayed with water on a daily basis to ensure constant humidity levels. The lizards participated in other behavioural experiments and remained healthy throughout this period, before being released at the site of capture. Our housing and experimental procedures, including capture and release techniques were approved by the Macquarie University Animal Care and Ethics Committee and the NSW National Parks and Wildlife Service.

Video Stimuli

Recording

Video sequences of lizards basking and performing the push-up/body-rock display were recorded according to the procedure developed by Ord et al. (2002). We modified the pens by covering the floor with a thick layer of foliage and adding a wooden perch directly beneath the heat lamp. The room temperature was then reduced to 18–20°C, exaggerating the thermal gradient within the pens and encouraging the lizards to bask. A light-blue cardboard backdrop was placed behind the perch to standardize the contrast between lizard and background. The lizards were allowed a week to acclimate to these new conditions before filming commenced.

The recording equipment was mounted on a trolley, which could be wheeled in front of each pen. Illumination was provided by 800-W photographic P2/11 tungsten–halogen lamps, which were angled to place the perch shadow out of camera frame. We used a digital video camcorder (Canon XL1; optical resolution 625 lines; shutter speed 1/250 s; aperture F8) and mini-DV tape (Sony DVM60EX and DVM60PRO). To avoid variation in image characteristics, we used the type of monitor on which stimuli were later played back (Sony Trinitron Colour PVM-14M2A) as a viewfinder during filming. We adjusted focal length and camera alignment by using a template fixed to the front face of the monitor, so that there was no variation in perch position on the screen and the lizard was life sized.

We made all of our recordings between 0800 and 1400 hours, which correspond to the period of peak activity in our indoor population (Ord 2001). A small terrarium (30 × 20 cm and 20 cm high) containing a male lizard was placed on the trolley immediately below the camera and concealed with a black cloth. The trolley was then positioned in front of a pen, camera and lights were adjusted as necessary, and the cloth removed. The presentation of the male in the terrarium was designed to stimulate display behaviour in the lizard being filmed. We continued filming until the subject lizard leapt off the perch.

Editing

We used video footage of four male lizards in the playback experiment (Table 1). These ranged in mass from 24.5 to 45.0 g and in size from 88 to 108 mm SVL. Two lizards were recorded between August and September 1999 and two during May 2004. Footage was digitally transferred using a Sony DSR-25 DVCAM video deck

Table 1. Characteristics of the stimulus lizard and video sequences

				Morphology sequences		Display sequences	
Pair (year filmed)	Stimulus identity	Weight (g)	SVL (mm)	Push-ups per sequence	Bouts of locomotion, average per sequence	Push-ups per sequence	Bouts of locomotion, average per sequence
1 (1999)	A	45.0	108	0	0	20	10.0
	B	24.5	90	0	0	20	9.4
2 (2004)	C	38.0	94	0	0	20	7.6
	D	27.0	88	0	0	20	5.8

SVL: snout–vent length.

connected via an IEEE 1394 ‘firewire’ interface to a Macintosh G4 running iMovie 3.0 (Apple Computer). Clips were then imported into Final Cut Pro 3.0 (Apple Computer) and assembled into sequences.

We created 10 sequences for each stimulus male (40 in total). These consisted of a 2-min baseline period, during which an unoccupied perch was shown, followed by 8 min in which the lizard was present on the perch, either basking or displaying aggressively with occasional locomotion (Fig. 1, Table 1). Presentation duration was designed to approximate that typical of agonistic interactions in a large outdoor enclosure (D.A. Van Dyk, personal observation). To facilitate subsequent scoring, we added a brief marker tone (inaudible to the subject) at the moment when the lizard appeared.

We generated five sequences of each stimulus male (20 in total) during which he was inactive on the perch. These were constructed by selecting a clip in which the lizard was stationary and repeating it as necessary. We used a 1-s cross-fade transition to avoid apparent movement between successive clips and selected a different clip for each sequence, so that no two showed the lizard in the same position.

The other five sequences of each stimulus male (20 in total) depicted aggressive push-up/body-rock displays on the perch (Fig. 1). Since we wished to assess individual distinctiveness in signal structure, rather than overall rate, we standardized the total number of push-up/body-rocks per sequence at 20. The push-up/body-rock motor pattern can be repeated multiple times within a single display and displays commonly occur in bouts. Although push-up/body-rock totals were matched for all 20 sequences of this type, each sequence preserved the variation in temporal pattern characteristic of natural displays and bouts, with between one and four push-up/body-rocks per display and at least one display/min (Table 1). The resulting average display rate (1.3 displays/min) falls somewhat below the population estimate of 4.05 displays/min obtained by Ord & Evans (2003). We chose this value to minimize the occurrence of extreme submissive behaviour such as hiding or fleeing.

Completed stimuli were each assembled from several display clips, with intervals depicting the lizard basking on the perch between them. When clips finished with a lizard jumping from the perch, we selected a following clip showing the lizard climbing on to the perch or used a 1-s fade into position, whichever produced the smoother transition. The stimulus lizard was never absent from the perch for more than 2 s.

One hundred unique push-up/body-rocks were available for each of the lizards filmed in 2004; this large library allowed us to create playback sequences without reusing clips. Fewer push-up/body-rocks had been obtained from each of the lizards filmed in 1999 (45 apiece), so we were obliged to use 35 push-up/body-rocks twice and 10 push-up/body-rocks three times. Even so, we were able to ensure that no push-up/body-rock exemplar was repeated within a playback sequence.

Playback Experiment

Design

Our approach was modelled on the well-established habituation–dishabituation paradigm (Gheusi et al. 1994; Evans 1997). Two series of paired playbacks were conducted. These tested sensitivity to variation in morphology (morphology series) and to the combination of morphology and display behaviour (display series), respectively. All 20 subjects participated in both series. We used a randomized split-plot design to control for order effects. Each lizard was first assigned an initial playback type (morphology or morphology + display), and then allocated a playback treatment within this (same or different stimulus lizard viewed in the first probe trial). We randomly assigned 10 animals to each of the four possible combinations of these factors.

Each playback series comprised two 5-day blocks. The familiarization phase of each block involved the presentation of a different randomly selected video sequence of the same lizard once every day, for 4 successive days. This design ensured that the only consistent attribute of the familiarization process was the identity of the stimulus animal depicted, and not a particular video sequence or order of sequences. On the fifth day, we conducted a probe trial. Half of the subjects were presented with the remaining sequence of the familiar stimulus lizard, while the other half viewed a randomly selected sequence of an unfamiliar male.

After a 2-day rest period, we repeated the test procedure, showing subjects the same set of sequences as during the previous familiarization phase, followed by whichever

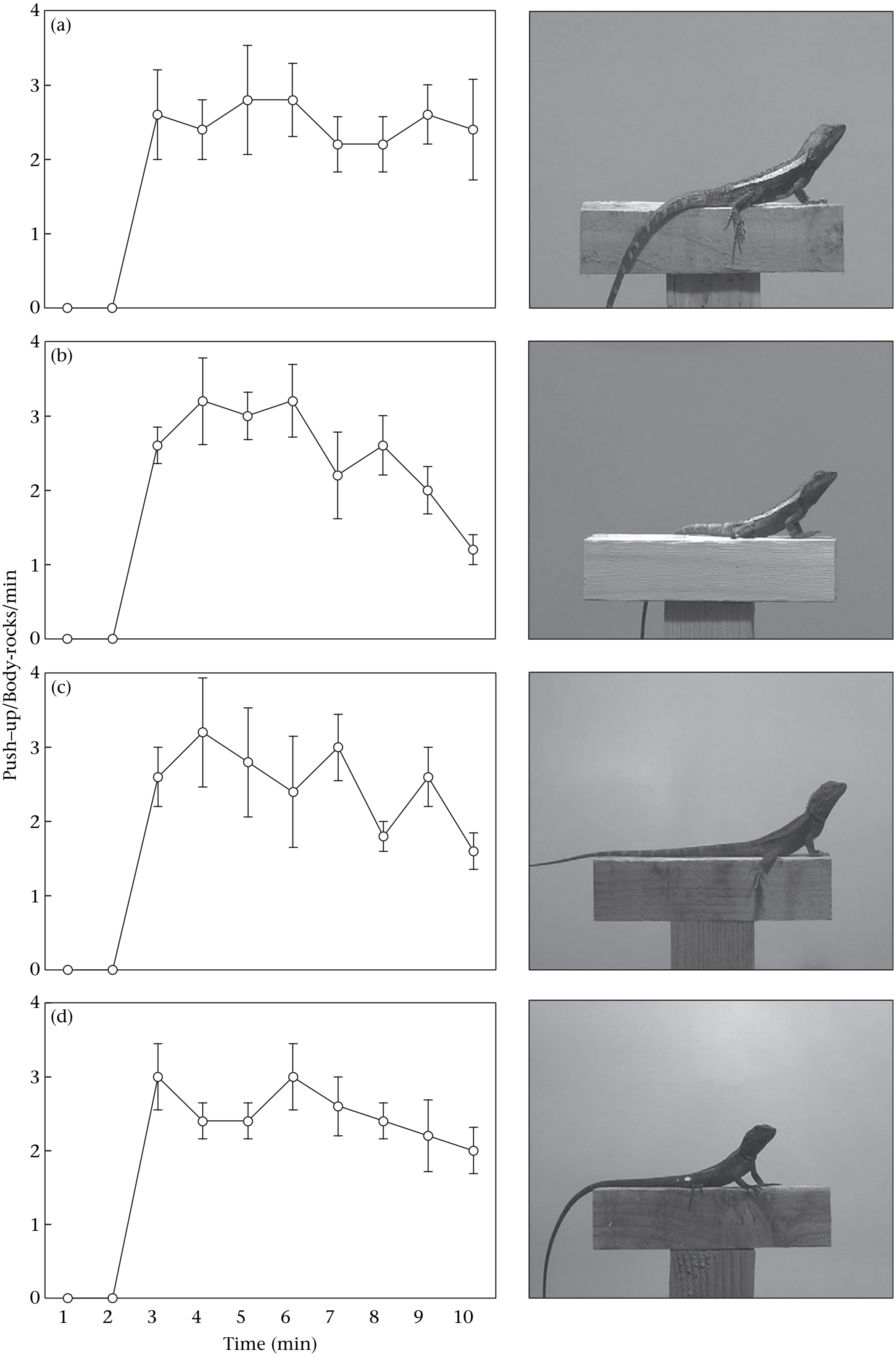

Figure 1. Characteristics of the display series playback sequence for each of four males. Push-up/body-rock display rates ($\overline{X} \pm$ SE) and representative video frames illustrating variation in morphology are shown; (a–d) correspond to stimulus identity, A–D, in Table 1.

type of probe trial they had not seen previously. The two treatments, familiar and unfamiliar, thus differed only in the identity of the stimulus lizard presented during the probe trial on day 5.

To eliminate differences caused by subtle differences in the filming set-up, we paired playback exemplars by the year in which they had been recorded. Half of the subjects were shown lizards filmed during 1999, while the other half were shown lizards filmed in 2004. Within each of these groups, the stimulus lizard used for the familiarization phase was viewed by five subjects. Each subject was randomly assigned a different unfamiliar lizard sequence. We also ensured that each subject saw a different pair of lizards in each of the two playback series, so that each stimulus exemplar was entirely novel at the beginning of the familiarization phase.

Test procedure

Subjects were moved into experimental pens and allowed to acclimate for at least 2 weeks prior to a playback series. Testing commenced between 0800 and 0900 hours each day and ran for approximately 5 h.

We mounted some of the test equipment on a trolley, so that it could be positioned in front of each of a line of pens with minimal disruption (Fig. 2). This included the stimulus presentation monitor (Sony PVM-1450; resolution 450 lines), a video camera (Panasonic WV-CP240) fitted with a wide-angle lens (Panasonic WV-LA210CSE) and a second monitor (Panasonic TC-1470Y) repeating the camera signal, to function as a viewfinder. Before testing, we calibrated the presentation monitor using PAL standard pluge bars (Final Cut Pro 3.0, Apple Computer).

The remaining test equipment remained static at one end of the room, allowing the experimenter to remain concealed behind the end wall of the lizard pens. This was linked by 5-m cables to the presentation system (Fig. 2) and included an S-VHS deck (Panasonic AG-MD830) for recording subject responses, the digital video deck (Sony DSR-11) that played stimulus sequences, and a monitor (Sony Trinitron Color PVM-14N6A) repeating the playback signal.

At the beginning of each playback session, the trolley was moved into position and adjusted so that the entire pen was visible on the viewfinder. A black cloth covering the stimulus monitor was then removed and filming commenced. Lizards were tested in the same order every day, so the intertest interval remained constant at approximately 24 h.

Data Analysis

Jacky dragons produce three distinct movement-based visual signals (Carpenter et al. 1970). The aggressive display consists of a highly stereotyped sequence of rapid motor patterns (Peters & Ord 2003). The core element of the display is a push-up, in which the head is raised by the coordinated action of the neck and forelegs, followed

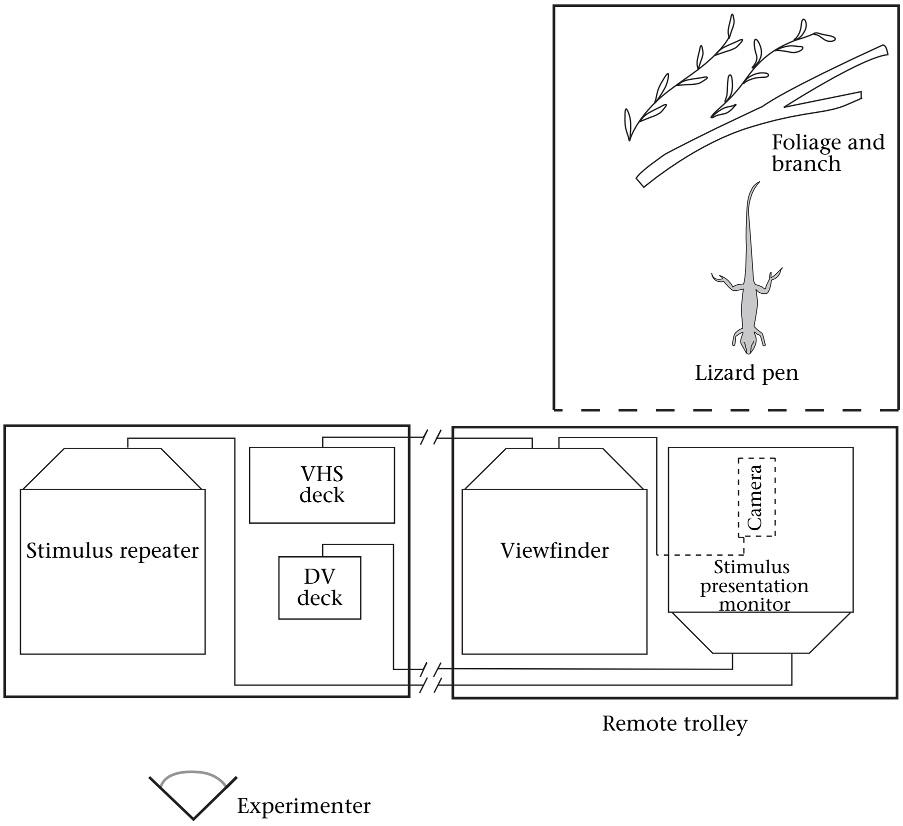

Figure 2. Plan view of experimental set-up. Drawing not to scale.

by a body-rock involving sharp downward and usually forward motion of the body. Tail-flicks of variable duration and a fast foreleg wave often precede the first push-up in a bout. Two putative submissive signals, the slow arm-wave and slow head-bow, have been observed in both indoor and outdoor settings (D.A. Van Dyk, personal observation). In the slow arm-wave display, the foreleg moves along a circular path parallel to the lateral body surface. The slow head-bow involves a very gradual raising and lowering of the head and neck. Social interactions also commonly involve locomotion and substrate licking (Ord et al. 2002). Animals may approach the intruder when escalating the interaction, or retreat to safer locations at the back of the pen. Substrate licking is an exploratory behaviour which is typically interpreted as an attempt to acquire chemical information with the vomeronasal organ (Alberts & Werner 1993; Cooper 1998; Font & Desfilis 2002).

We scored push-up/body-rocks, slow arm-waves, slow head-bows, substrate licks and bouts of locomotion from test session videotapes. In addition, we recorded latency from the appearance of the stimulus lizard to the first response evoked. Animals that failed to respond in a particular session were assigned a latency score equal to the test duration (480 s); lizards were required to respond at least 1 day per week to be included in the analyses. This criterion resulted in five subjects being excluded from the morphology series. All data were square-root transformed to fulfil the assumption of equal variances and analysed with nonparametric tests (SPSS 11.0 for Macintosh 2003, SPSS Inc., Chicago, IL, U.S.A.).

We used the Friedman test to analyse responses across the 4 days of the familiarization phase in each block. To check that treatments were comparable, we used a Wilcoxon signed-ranks test to assess differences between the average responses during familiarization phases as a function of the type of probe trial that followed. To compare probe trial responses we used the Wilcoxon signed-ranks test. These tests were two tailed and the alpha level was set at 0.05 throughout.

RESULTS

All subjects performed bouts of locomotion and substrate licking on at least 1 day in each playback series, making these the most common responses. Only a minority of lizards (6/20) gave submissive slow arm-waves during the morphology playbacks, but most (16/20) responded in this way to display sequences. Push-up/body-rock displays were much less common (3 lizards in the morphology series and 7 in the display series). Slow head-bows were rare and are therefore included only in the latency analyses.

Morphology Series

None of our response measures varied significantly as a function of day during the familiarization phase of each block (Fig. 3a-e, Table 2). Comparisons between the two familiarization series confirm that average responses did not differ according to treatment (Wilcoxon signed-ranks test: morphology series: push-up/body-rocks: $Z = -1.604$, $N = 15$, $P = 0.109$; slow arm-waves: $Z = -1.153$, $N = 15$, $P = 0.249$; response latency: $Z = -0.874$, $N = 15$, $P = 0.382$; substrate licks; $Z = -0.235$, $N = 15$, $P = 0.814$; locomotion: $Z = 0.000$, $N = 15$, $P = 1.000$). Lizards were hence behaving comparably before the critical final day of playbacks.

In contrast, lizard responses during probe trials varied according to stimulus type. Unfamiliar individuals evoked significantly more bouts of locomotion (Fig. 3c, Table 3) and a significantly higher frequency of substrate licking (Fig. 3d, Table 3) than familiar ones. These changes were accompanied by a shorter response latency and an increased rate of aggressive push-up/body-rock displays that approached statistical significance (Fig. 3b, e, Table 3).

Display Series

The overall level of responsiveness during familiarization playbacks was greater than when subjects were shown a nondisplaying male (Fig. 3f–i; compare Fig. 3a–d). An upward trend is evident in the aggressive push-up/body-rock response over the familiarization phase; however, this change achieved statistical significance only in the second 5-day block (Fig. 3g, Table 2). In contrast, the submissive slow arm-wave response dropped by nearly half between days 1 and 2 and remained relatively stable thereafter (Fig. 3f). These changes are reflected in a near-significant day effect during the 4-day familiarization phase of the first 5-day block (Table 2). As in the morphology familiarization series, the average responses did not differ between treatments (Wilcoxon signed-ranks test: display series: substrate licks: $Z = -1.382$, $N = 20$, $P = 0.167$; locomotion: $Z = -0.709$, $N = 20$, $P = 0.478$; push-up/body-rocks: $Z = -0.676$, $N = 20$, $P = 0.499$; slow arm-waves: $Z = -0.673$, $N = 20$, $P = 0.501$; response latency: $Z = -0.485$, $N = 20$, $P = 0.627$).

Subjects performed significantly more substrate licks (Fig. 3i) when presented with an unfamiliar displaying male during the probe trial than when viewing a familiar one (Table 3). None of the other response measures differed significantly between the two types of probe trial, although latency scores showed a nonsignificant trend towards faster responses to an unfamiliar male (Fig. 3j, Table 3).

DISCUSSION

Our results show that Jacky dragons are capable of familiar–unfamiliar discrimination based upon static visual cues alone. When subjects were shown an unfamiliar inactive lizard, they performed significantly more substrate licks and bouts of locomotion. This is, to our knowledge, the first such finding for any species of lizard. In addition, probe trial comparisons provided unambiguous evidence that subjects were sensitive to individual distinctiveness in video sequences of simulated opponents. Although many previous studies have described differential responding based upon video stimulus characteristics such as size, speed of movement and presence of ornaments (eg. Clark & Uetz 1992; Rosenthal & Evans

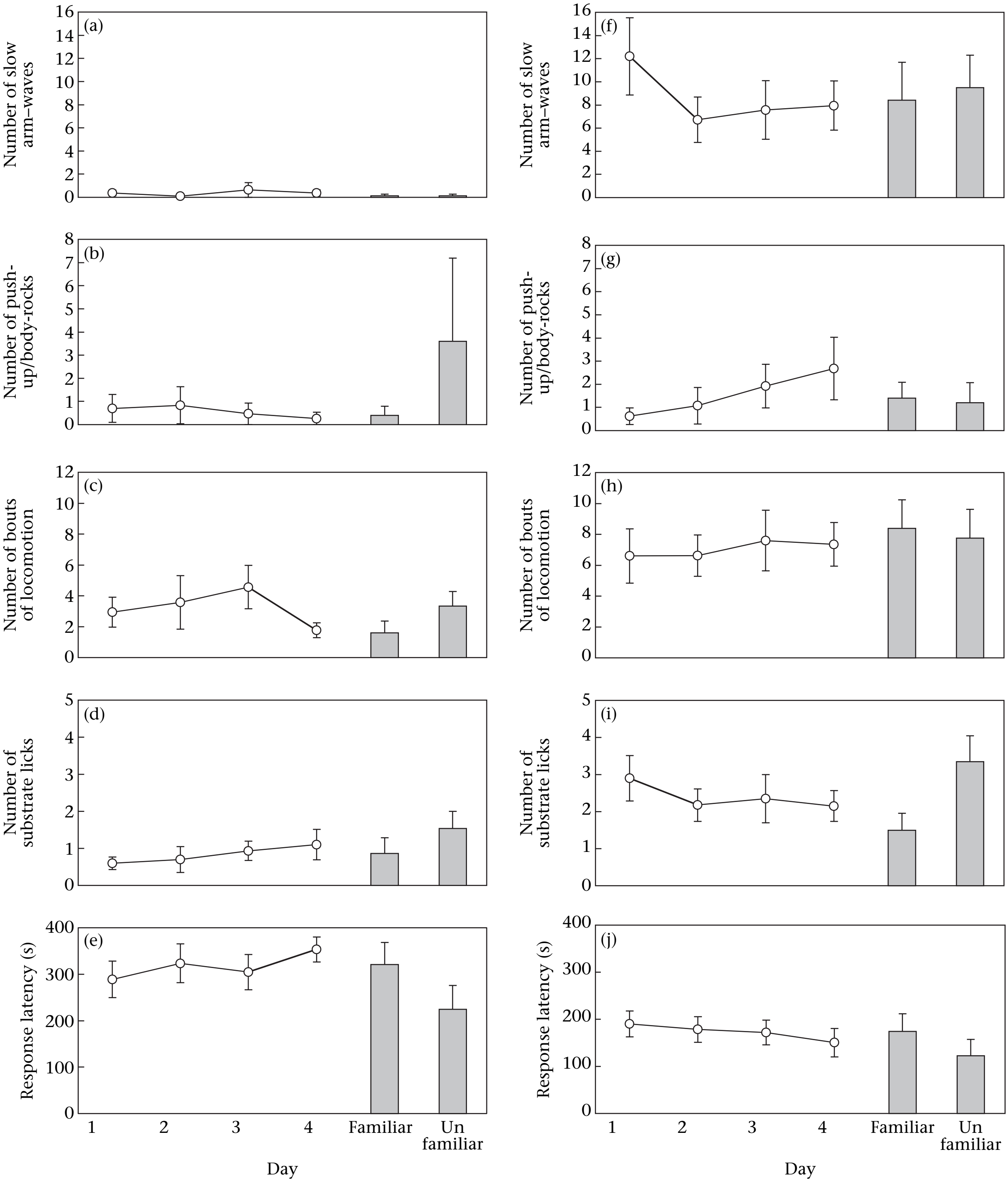

Figure 3. Lizard responses ($\overline{X} \pm$ SE) to video stimuli in familiarization phases (black line) and probe trial (grey columns) of each playback series. Morphology series: (a) slow arm-waves, (b) push-up/body-rocks, (c) locomotion, (d) substrate licks and (e) response latency. Display series: (f) slow arm-waves, (g) push-up/body-rocks, (h) locomotion, (i) substrate licks and (j) response latency.

1998; Nicoletto & Kodric-Brown 1999), our experimental design allowed us to separate the attributes of any particular exemplar from the more general property of individual identity. As in analogous habituation–dishabituation experiments using sound playbacks (Blumstein & Daniel 2004), the only possible basis for differential responding was detection of a difference between the stimulus lizard seen during the preceding 4 days of familiarization sequences and one of the two novel probe stimuli.

The strongest evidence for familiar–unfamiliar discrimination in the present study comes from rates of substrate licking. In both the morphology and the display series,

Table 2. Friedman tests for the effect of day in the 4-day familiarization phase of each 5-day block

	Block 1		Block 2	
Behavioural response	χ^2_3	*P*	χ^2_3	*P*
Morphology series (*N*=15)				
Slow arm-waves	0.455	0.929	6.0	0.112
Push-up/body-rocks	2.455	0.484	1.286	0.733
Locomotor bouts	4.150	0.246	1.359	0.715
Substrate licks	4.763	0.190	0.110	0.991
Latency to respond	1.049	0.789	2.571	0.463
Display series (*N*=20)				
Slow arm-waves	6.841	0.077	2.469	0.481
Push-up/body-rocks	1.071	0.784	8.333	0.040
Locomotor bouts	2.064	0.559	0.878	0.831
Substrate licks	3.810	0.283	0.523	0.914
Latency to respond	3.063	0.382	0.979	0.806

Data are square-root transformed.

the rate of this response was significantly higher when subjects were confronted with an unfamiliar stimulus lizard (Fig. 3d, i, Table 3). Licking the substrate transfers molecules to the tongue and thence indirectly to the sensory epithelium of the vomeronasal organ (Halpern 1992). This characteristic reptilian chemosensory behaviour has been used extensively as a response assay with biologically relevant stimuli such as predators, prey and conspecifics (reviewed in Cooper 1998). In our experiment, substrate licking was particularly useful because it was not dependent upon the type of signalling response evoked, a limitation that sharply reduced sample size (and hence statistical power) for some other measures. This pattern also implies that gathering chemical information is a priority for lizards engaged in a territorial contest, and that this is true whether the response is to approach with threat displays, or to withdraw with appeasement signals.

Familiar–unfamiliar discrimination based upon chemical cues is well established in lizards (Alberts & Werner 1993; Cooper 1996; Hanley et al. 1999; Aragon et al. 2001a,b; Font & Desfilis 2002). All of these studies, with the exception of Aragon et al. (2001a) and Font & Desfilis (2002), reported relatively higher rates of substrate licking in the presence of odours from an unfamiliar conspecific. The common conclusion has been that individuals sample unfamiliar odours more often because they require more information about a new individual. The results of our playback experiments extend this previous work by showing that visual cues from an unfamiliar conspecific, presented in isolation, can be sufficient to evoke an olfactory investigative response.

Table 3. Two-tailed Wilcoxon signed-ranks tests comparing the behavioural responses to a familiar and unfamiliar stimulus lizard in probe trials

Behavioural response	*Z*	*P*
Morphology series (*N*=15)		
Slow arm-waves	0.000	1.000
Push-up/body-rocks	−1.604	0.109
Locomotor bouts	−1.960	0.050
Substrate licks	−2.103	0.035
Latency to respond	−1.726	0.084
Display series (*N*=20)		
Slow arm-waves	−1.490	0.136
Push-up/body-rocks	−0.734	0.463
Locomotor bouts	−0.155	0.877
Substrate licks	−2.173	0.030
Latency to respond	−1.590	0.112

Data are square-root transformed.

We do not yet know how much Jacky dragons and other agamids rely upon chemical cues during territorial interactions in nature, but ecological factors provide some hints about the likely importance of this modality. For example, Alberts & Werner (1993) offered an environmental explanation for the ability of green iguanas, *Iguana iguana*, to discriminate between the femoral gland secretions of familiar and unfamiliar conspecifics. They suggested that communication via chemical secretions might supplement visual communication in structurally complex habitats such as tropical forests. Similar logic would apply to Jacky dragons, which live in densely vegetated coastal heath and forests (Harlow & Taylor 2000). A secondary mechanism for detecting and assessing intruders would clearly benefit territory holders in conditions that limit the effective range of visual signals.

Male–male competition may also be relevant for understanding the use of multiple sensory channels for territorial communication. Ord et al. (2001) uncovered an evolutionary link between the intensity of intrasexual selection and the complexity of threat displays, as measured by the number of display modifiers present, in the Iguanian lineage. This relationship suggests that signal complexity can be driven by assessment of the opponent, but there is no reason why such a phenomenon should be restricted to vision. It seems equally plausible that selection for either increased rates of information transfer or robust signalling under noisy conditions could engage additional modalities. A similar prediction has been made in the context of multimodal signal design more generally (Partan & Marler 1999).

The only other response to differ significantly between probe trials was bouts of locomotion. Subjects moved around their pens more when facing an unfamiliar basking lizard. This behaviour encompassed both rapid charges towards the stimulus lizard and efforts to increase the separation distance. This result thus probably indicates a change in the general level of arousal, regardless of the subject's decision to confront or avoid the simulated intruder.

We found little evidence of habituation during the familiarization phases of the experiment (Fig. 3). Although the frequency of slow arm-waves in the display series showed a near significant downward trend in one of the 5-day blocks (Fig. 3f, Table 2), this effect was principally due to a sharp drop between the first and second day of playbacks. It is not altogether surprising that most subjects responded with submissive signals when first confronted by a simulated aggressive intruder at close range. Rapid recovery, which included a significant increase in the number of push-up/body-rock displays during one of the 5-day blocks (Fig. 3 g), probably reflects reassessment of the video opponent in the absence of a resolved dominance relationship. Conventional playbacks necessarily lack natural social contingencies, so approach by subjects was never followed by an aversive outcome such as being attacked (Rowland 1999). Interactive video playback offers a partial solution to this limitation (Ord & Evans 2002), but this approach would have been inappropriate for our purposes in the present study because we wished to retain precise control over both appearance and display.

Our playback protocol was designed to provide subjects with sufficient experience of a particular conspecific for them to generalize successfully to a novel exemplar of the same male and detect the switch to a different individual. To maintain responsiveness, and to eliminate any possibility of lizards simply learning the characteristics of particular exemplars, we incorporated natural levels of variability into the playback sequences, each of which was unique. The morphology series sequences showed the lizard basking in different orientations on the perch. Similarly, each of the display series sequences presented a different signalling pattern, with variation in both inter- and intradisplay characteristics.

Like the songs of territorial birds, Jacky dragon displays are often produced spontaneously as ‘broadcast’ signals, when no opponent is visible (D. A. Van Dyk, unpublished data). It is therefore functionally important to maintain responsiveness in a population of potential receivers. The lack of habituation during our playback series is consistent with the idea that Jacky dragon threat displays are designed to minimize receiver habituation (Hartshorne 1956).

Each stimulus lizard presented a suite of potential physical cues, including size, shape, colour and skin pattern. Further experimental tests, in which individual attributes are selectively manipulated, will be necessary to isolate the subset of morphological features that mediate discrimination. The question of whether signal structure facilitates recognition of rivals similarly remains unresolved. Subjects might have been using a combination of morphological and behavioural cues to discriminate between stimuli in the display probe trials, but in the absence of direct evidence, we adopt the working hypothesis that this effect was dependent upon morphology alone. Planned experiments will use 3-D animation and rotoscoping (Peters & Evans 2003) to hold the appearance of a simulated opponent constant and define movement based upon the push-up/body-rocks of different individuals. Dynamic cues will thus provide the only basis for discrimination and a positive result will reveal distinctiveness in display structure.

A compelling demonstration of the dear enemy effect would require increased aggressive responses directed selectively towards unfamiliar individuals (see Introduction). The only hints of such a phenomenon were the near significant decrease in response latency and increase in push-up/body-rocks when subjects viewed the unfamiliar basking lizard (Fig. 3b, e, Table 3) and the slight trend towards shorter response latency when subjects viewed the unfamiliar displaying lizard (Fig. 3j, Table 3). However, in both playback series, the number of subjects performing submissive slow arm-waves was double the number performing aggressive push-up/body-rocks. Our effective sample size for detecting a dear enemy effect was consequently too small to provide adequate statistical power. Two previous captive studies have found lizards to be more aggressive when housed in an enclosure with a female (Leuk 1995; Lopez & Martin 2002), so it is possible that the low frequency of threat displays reflects the absence of such defensible resources.

It is common for familiar–unfamiliar discrimination studies in a variety of taxa to invoke the possibility of individual recognition (Glinski & Krekorian 1985; Morris et al. 1995; Lopez & Martin 2001a; Blumstein & Daniel 2004). While it is certainly true that evidence of discrimination between these two classes is consistent with an ability to classify conspecifics into many individual categories, it is also consistent with the ability to classify them into only two. This latter explanation demands far less in terms of perceptual and cognitive capabilities and is hence more parsimonious. Stronger evidence of individual recognition requires some indication of discrimination between members of the familiar category as well (Gheusi et al. 1994; Husak & Fox 2003). For this reason, we interpret our findings as evidence for discrimination between familiar and unfamiliar conspecifics, but remain neutral about the precise nature of the categorization process underpinning this phenomenon.

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