

# Lizard threat display handicaps endurance

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Honest-signalling theory asserts that threat displays reliably advertise attributes that influence fighting success. Endurance, as measured by treadmill performance, predicts the outcome of agonistic interactions among lizards. If threat displays in lizards function to advertise endurance capacity then variation in threat displays should correlate with endurance. I tested this prediction for the duration of threat posturing in male side-blotched lizards (*Uta stansburiana*) and examined whether threat displays act as quality handicaps, reliable signals that expend the attribute that is advertised. Individual variation in the duration of threat posturing correlated with endurance, while an experimental reduction of endurance diminished the duration of threat posturing. As expected of a quality handicap, endurance fell below baseline after display production. A restriction of aerobic metabolism can account for this effect. In threat posturing, lateral compression of the thorax may interfere with respiration or with circulation, limiting aerobic metabolism and causing a compensatory increase in anaerobic metabolism, thereby generating lactate and diminishing locomotor capacity. Concentrations of lactate measured after display production were higher than baseline, consistent with the proposed mechanism. By restricting aerobic metabolism, the threat posture can act as a quality handicap, simultaneously advertising and expending the endurance capacity of displaying lizards.

**Keywords:** signalling; handicap; threat display; endurance; lizard; *Uta stansburiana*

## 1. INTRODUCTION

During the course of agonistic encounters, animals produce a diversity of movements, postures, sounds and chemical signals (Huntingford & Turner 1987). Zahavi (1975, 1977) proposed that communicatory structures and behaviours provide honest information that facilitates assessment. Honest-signalling theory predicts that intraspecific variation in threat display characteristics should reflect an underlying variation in attributes that affect the motivation (Enquist 1985) and the capacity to fight (Enquist & Leimar 1983; Payne 1998). Body size (Davies & Halliday 1978; Riechert 1978), weaponry (Hughes 1996, 2000; Sneddon *et al.* 1997, 2000) and energetic reserves (Marden 1990; Marden & Rollins 1994; Fitzstephens & Getty 2000) are attributes that can influence fighting ability, and may be advertised in threat displays. Fighting is supported by substantially elevated aerobic and anaerobic metabolic activity (Smith & Taylor 1993; Hack 1997; Neat *et al.* 1998; Sneddon *et al.* 1999), indicating that endurance capacity may have a significant impact on fighting ability. Despite some suggestive evidence (Clutton-Brock & Albon 1979; Briffa & Elwood 2000), the prediction that threat displays vary in concert with endurance has not been tested directly. A direct test of this prediction requires a reliable measure of endurance capacity that is obtained independently of display behaviour, as well as quantitative measures of display production elicited in a standardized context.

The locomotor endurance of lizards is routinely measured as the duration of sustained exercise on a motorized treadmill (Bennett & Huey 1990). Individual variation in treadmill endurance is repeatable (Huey *et al.* 1990; van Berkum *et al.* 1989), with much of the variation accounted for by variations in morphological, enzymatic and physio-

logical variables (Garland & Else 1987). Endurance in fighting should be correlated with locomotor endurance if the same metabolic pathways support both activities. Therefore, locomotor endurance can serve as a measurable proxy for the capacity to sustain vigorous fighting activity.

Among male lizards, locomotor performance, dominance and display production appear to be linked. Encounters staged in a neutral arena between pairs of size-matched males were won more often than expected by chance by the individual who was faster and possessed higher locomotor endurance (Garland *et al.* 1990; Robson & Miles 2000). Compared with healthy individuals, male lizards infected with malaria suffer from a reduction in aerobic scope and endurance capacity, spend less time in social interactions, display less frequently, have lower dominance scores and are less successful in obtaining access to females (Schall *et al.* 1982; Schall & Dearing 1987; Schall & Sarni 1987; Schall & Houle 1992). Field-active males implanted with testosterone enjoy improved sprint speed and endurance, increased home-range size and enhanced access to females, at the cost of reduced growth rates and diminished fat stores (Klukowski *et al.* 1998; Sinervo *et al.* 2000). Considering that endurance influences fighting ability in lizards, honest-signalling theory predicts that display elements that are employed in agonistic interactions should vary in concert with endurance capacity.

The display elements that are observed most frequently in agonistic interactions among iguanian lizards comprise a threat posture and a dynamic component, the 'push-up' display, performed simultaneously or separately (Carpenter 1978*b*). The threat posture can be maintained for extended time-periods and includes elevation of the body, lateral compression of the thorax and extension of

the throat flap (Carpenter 1962*b*). Push-ups are performed singly or in series, with a stereotyped species-specific cadence of rapid vertical movements (Carpenter 1962*a*, 1978*a*; Hunsaker 1962). Push-ups are produced in a wide variety of contexts, while the threat posture is used in a much narrower spectrum of contexts (Martins 1993), limited primarily to intraspecific aggression but also appearing as a component of predator deterrence in some species (Leal & Rodriguez-Robles 1995). Research on the communicatory displays of lizards has traditionally focused on display stereotypy and its role in species and sex recognition. Individual variation in display behaviour, where studied, has been considered as a cue for individual recognition (Martins 1991; Rothblum & Jenssen 1978) or linked to contextual variation (Martins 1993; DeCourcy & Jenssen 1994), for example in the value of the contested resource (McMann 1993). More recently, the number of push-ups produced in the context of predator deterrence was found to correlate with endurance capacity (Leal 1999), presumably providing a reliable indication to the predator of the capacity of the displaying lizard to evade predation.

As in many communication systems, the maintenance of signal reliability among selfishly motivated individuals presents a puzzle (Krebs & Dawkins 1984). Considering the potential benefits of signalling greater endurance, be it to competitors or to predators, what could prevent an individual from advertising a level of endurance that is higher than its actual level of endurance? Some signals may simply be impossible to cheat, while in other cases signalling may engender costs that make dishonest signalling unprofitable (Maynard-Smith & Harper 1995). Signal costs can be broadly divided into signal-production costs and costs contingent on receiver response (Bradbury & Vehrencamp 1998). Displays that are stabilized by signal-production costs can be further divided into quality handicaps, which reflect signaller quality, and general handicaps, which reflect resource value or the 'need' of the signaller (Hasson 1997). Uniquely among the factors that can stabilize reliable signalling, quality handicaps are expected to 'use up' or diminish the specific attribute that the signal is advertising (Hasson 1997; Vehrencamp 2000). The hypothesis that threat displays in lizards act as quality handicaps is directly testable, since it predicts that the production of threat displays should be followed by a transient decrement in endurance capacity. Aerobic interference can account for this effect mechanistically: the laterally compressed threat posture may interfere with ventilation or with circulation, thus disrupting aerobic metabolism and causing the displaying individual to rely on glycolysis for energetic support, thereby generating lactate and diminishing endurance.

Using adult male side-blotched lizards (*Uta stansburiana*), the present study tested whether threat displays reliably advertise endurance capacity and whether these displays act as quality handicaps. The first experiment examined the prediction that threat displays correlate with endurance by measuring threat-posture duration and counting the number of push-ups elicited in a standardized context by individuals with known endurance capacity. In a second experiment, the possibility that display behaviour is influenced by an unknown variable rather than by endurance was controlled for by manipulat-

ing endurance and measuring the effect on display production. A third experiment tested whether display production diminishes endurance capacity, thus testing whether these displays act as quality handicaps. Finally, the effect of display production on lactate concentration was assessed as a test of the aerobic-interference mechanism.

## 2. MATERIAL AND METHODS

Side-blotched lizards are small (5–10 g) visually orientating sit-and-wait insectivores with an annual life cycle (Tinkle 1967). Agonistic activity peaks during the spring, when males compete for access to females using territorial, mate-guarding and sneaky strategies (Sinervo & Lively 1996). Reproductively active adult male side-blotched lizards (*U. stansburiana*) were collected for this study during the spring in 1997, 1998 and 1999 at Los-Banos Grandes, Merced County, CA, USA (California Department of Game and Fish permit #4745 to Dr Barry Sinervo). The 1997 cohort was used in experiment 2, the 1998 cohort was used in experiment 3 and the 1999 cohort was used in experiment 1 and then three weeks later the same cohort was used in experiment 4. In each year, all experiments were completed within eight weeks of field collection. Subjects were maintained individually in terraria with a washed sand substrate and a cardboard hide. An incandescent lamp housed in a metal reflector was mounted over each terrarium to create an appropriate thermal gradient and to provide lighting for 13 h of each daily cycle. Terraria were sprayed with water daily, and subjects were offered crickets or mealworms dusted with a vitamin/mineral supplement. Husbandry and experimental procedures were approved by the animal care and use committees of Indiana University, Bloomington, and the University of California, Santa Cruz.

### (a) *Experiment 1: correlates of display production*

To test whether display production varies with endurance capacity, both endurance capacity and display production were quantified in a group of adult males ( $n = 38$ ). Displays were elicited under the standardized conditions of an experimental arena using a mirror to simulate a size-matched opponent. This design minimized the contribution of contextual and motivational differences to variation in display production. The effect of previous social experience was minimized by holding the subjects in isolation for at least two weeks prior to the experiment. The arena measured 30 cm × 40 cm × 30 cm and was furnished with a substrate of washed play sand and an incandescent light to provide suitable thermal conditions. Trials lasted 5 min, and were videotaped from behind a blind (Sugerman & Hacker 1980). Trials were subsequently transcribed using ETHOLOG 2.2 software (Ottoni 2000), yielding two display variables: the duration of the laterally compressed threat posture summed over the entire trial and the number of push-ups performed during the 5 min trial. Each subject participated in two trials, separated by 5 days, and the trial with the higher display rates was used for all subsequent analyses. The endurance capacity of each subject was determined as the time taken to reach exhaustion while running on a motorized treadmill (Sinervo *et al.* 2000). The belt of the treadmill advanced at a rate of 0.5 km h<sup>-1</sup>, similar to the velocity of movements in the field, and activity body temperature (35–38 °C) was maintained with an incandescent lamp mounted over the treadmill. Lizards were motivated to run by tapping on the hind legs and on the base of the tail until exhaus-

Table 1. Pearson correlation coefficients for threat-posture duration, number of push-ups, snout-vent length, condition index and treadmill endurance in adult male side-blotched lizards ( $n = 38$ ).

	threat-posture duration	number of push-ups	snout-vent length	condition index
number of push-ups	0.820 <sup>a</sup>	—	—	—
snout-vent length	0.219	0.040	—	—
condition index	0.399 <sup>b</sup>	0.206	-0.003	—
treadmill endurance	0.489 <sup>a</sup>	0.316	0.217	0.443 <sup>a</sup>

<sup>a</sup> Correlation is significant at the 0.01 level (two-tailed).

<sup>b</sup> Correlation is significant at the 0.05 level (two-tailed).

tion, confirmed by the loss of the righting response (Huey *et al.* 1984). Although lizards require several hours for complete metabolic recovery from exhaustive exercise (Gleeson 1991), survival rates of subjects released back into the field after recovery from exhaustive exercise were indistinguishable from survival rates of untested animals (B. Sinervo, personal communication), suggesting that there are no long-term negative consequences of this treatment. Furthermore, field-active lizards routinely support foraging and social behaviours anaerobically (Bennett *et al.* 1981; Pough & Andrews 1985).

To test whether variation in predictors of dominance, other than endurance, could account for display variation, snout to vent length (SVL) to the nearest 0.5 mm and mass to the nearest 0.1 g were measured. Mass was corrected for length by computing a condition index obtained from the residual of the regression of mass against SVL<sup>3</sup> (Jakob *et al.* 1996). Size is a ubiquitous predictor of dominance (for example, for lizards, Carpenter (1995); Tokarz (1985)), while condition may affect dominance by reflecting variations in muscular development or energetic reserves. A Pearson correlation coefficient and a corresponding  $p$  value were computed for each pairing of the following variables: number of push-ups, threat duration, endurance capacity, SVL and condition. Correlations between multiple variables were re-evaluated using partial correlation analyses.

Paired  $t$ -tests were used to detect whether behaviour differed from the first trial to the second trial. The repeatability of these behavioural variables was quantified using the intraclass correlation coefficient, calculated as  $r = s_A^2 / (s^2 + s_A^2)$ , where  $s_A^2$  is the among-individual variance component and  $s^2$  is the within-individual variance component derived from a one-way analysis of variance (ANOVA) (Lessells & Boag 1987; Falconer & Mackay 1989).

### (b) Experiment 2: effect of endurance manipulation on display behaviour

Finding a correlation between endurance and display does not indicate that endurance *per se* is advertised, since individuals differ in many attributes in addition to endurance capacity, such as aggressiveness or circulating levels of testosterone. To eliminate all factors other than endurance, I used a within-subjects design, testing the effect of an endurance manipulation on display behaviour. Endurance was manipulated by exercising each subject on a treadmill for one half of its previously determined endurance capacity. Thus, each subject was induced to display in a baseline trial with its endurance capacity intact, and in an additional trial with only one half of its baseline endurance capacity remaining. In both baseline and experimental trials displays were elicited by exposure to a mirror in a neutral arena. For each trial, I scored from the recorded videotape the total duration of threat posturing and the number of push-ups perfor-

med. Paired  $t$ -tests were used to compare baseline display levels with display levels following an experimental reduction in endurance.

### (c) Experiment 3: effect of display production on endurance

The prediction of the quality-handicap model, that display production diminishes the trait being advertised, was tested by comparing endurance capacity following display production with baseline endurance capacity, using a within-subjects experimental design. Each endurance measurement was preceded by a 5 min trial in a neutral arena: in display trials subjects displayed in response to the reflective side of a mirror, while in baseline trials lizards were exposed to the non-reflective side of a mirror, and hence did not display. Immediately after the 5 min trial in the arena, the subject's endurance was measured on a motorized treadmill (as in experiment 1). To control for order and day effects, successive subjects were alternated between the two treatments. A paired  $t$ -test was used to compare baseline endurance with post-display endurance.

### (d) Experiment 4: effect of display production on lactate concentration

The aerobic-interference mechanism proposes that the production of threat displays restricts aerobic metabolism, which prompts a compensatory increase in anaerobic metabolism, and that threat displays should be followed by elevated lactate concentrations. This prediction was tested using a paired  $t$ -test to compare baseline lactate concentrations with lactate concentrations immediately after a 5 min mirror exposure in a neutral arena. Blood samples for measuring lactate concentrations were obtained using a 50  $\mu$ l haematocrit tube inserted into the post-orbital sinus. Each sample was immediately ejected from its haematocrit tube into an Eppendorf tube, frozen and maintained at  $-80^\circ\text{C}$ . Within a week of collection, lactate was assayed colorimetrically, using reagents from a kit by Sigma-Aldrich. Absorbance is directly related to lactate concentration, allowing a determination of lactate concentration after sample dilution is taken into account.

## 3. RESULTS

### (a) Experiment 1: correlates of display production

Significant correlations were detected among several pairs of variables (table 1): compression duration correlated with treadmill endurance ( $r = 0.489$ ,  $p = 0.002$ ) and with condition ( $r = 0.399$ ,  $p = 0.013$ ), while the correlation between the number of push-ups and endurance approached significance ( $r = 0.316$ ,  $p = 0.054$ ). In addition, threat duration correlated significantly with the number of push-ups

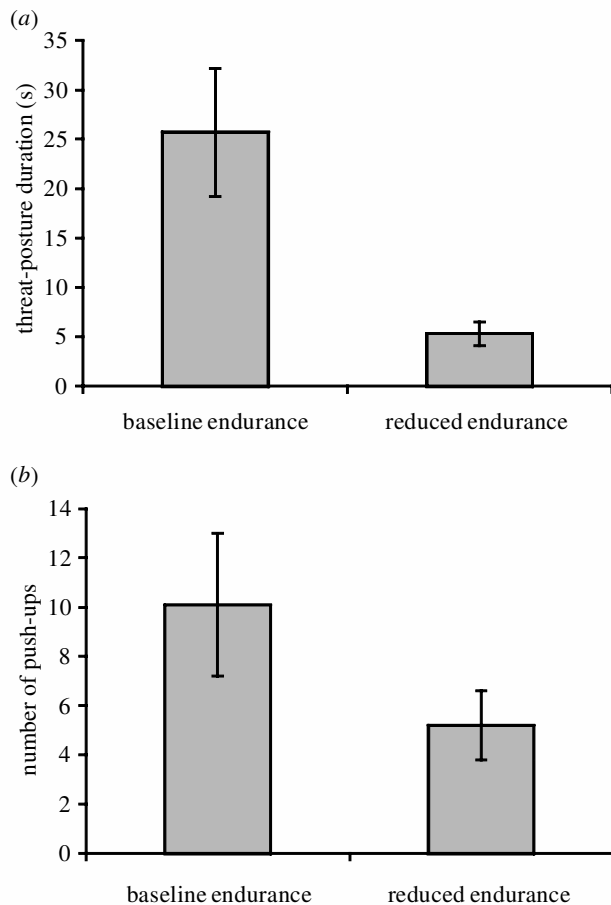


Figure 1. The effect of an endurance manipulation on display behaviours during a 5 min mirror presentation in a neutral arena. Display behaviour at baseline is compared with display behaviour after endurance was reduced to 50% of baseline by running each subject on a treadmill. Means with standard errors ( $n = 24$ ) are shown. (a) Total duration of threat posturing. (b) Number of push-ups.

( $r = 0.820$ ,  $p < 0.001$ ), and endurance correlated with condition ( $r = 0.443$ ,  $p = 0.005$ ). However, after applying the sequential Bonferroni adjustment (Rice 1989) significance at the table-wide level was maintained only for the correlations between threat duration and number of push-ups and between threat duration and endurance. Furthermore, partial correlation analysis revealed that after controlling for condition threat duration and endurance capacity maintained a significant correlation ( $r = 0.379$ ,  $p = 0.021$ ). The opposite was true when endurance capacity was controlled for: threat duration was no longer significantly correlated with condition ( $r = 0.233$ ,  $p = 0.166$ ). Similarly, while threat duration and endurance were significantly correlated ( $r = 0.426$ ,  $p = 0.009$ , controlling for the number of push-ups), the number of push-ups and endurance were not ( $r = -0.171$ ,  $p = 0.311$ , controlling for threat duration).

Neither the number of push-ups (paired  $t$ -test:  $n = 38$ ,  $t = 1.191$ , two-tailed  $p = 0.241$ ) nor threat-posture duration ( $t = 1.295$ , two-tailed  $p = 0.203$ ) varied significantly between trial one and trial two. Both the number of push-ups and threat-posture duration were highly repeatable ( $r = 0.712$  and  $r = 0.638$ , respectively).

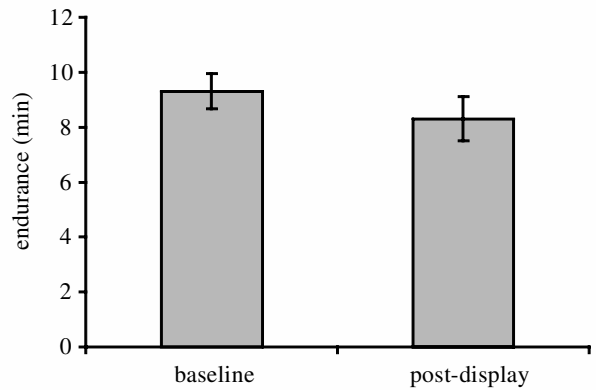


Figure 2. The effect of display production on treadmill endurance. Baseline endurance is compared with endurance immediately after a 5 min exposure to a mirror in a neutral arena. The change in endurance was judged to be significant using a paired  $t$ -test ( $t = 2.53$ ,  $p = 0.019$ ,  $n = 22$ ).

#### (b) Experiment 2: effect of endurance manipulation on display behaviour

Compared with baseline levels of display, both threat-posture duration and the number of push-ups decreased as a consequence of experimentally halving the endurance capacity of the subjects through treadmill exercise (figure 1). Threat duration dropped from a baseline of  $25.7 \pm 6.5$  s (mean  $\pm$  s.e.) to  $5.3 \pm 1.2$  s after endurance was halved (paired  $t$ -test:  $n = 24$ ,  $t = 3.1$ , two-tailed  $p = 0.0047$ ). The number of push-ups performed decreased from a baseline of  $10.1 \pm 2.9$  to  $5.2 \pm 1.4$  after endurance was halved, but this change was not statistically significant ( $t = 1.9$   $p = 0.067$ ).

#### (c) Experiment 3: effect of display production on endurance

Post-display endurance measurements averaged  $8.3 \pm 0.81$  min, while baseline endurance values averaged  $9.3 \pm 0.65$  min (figure 2), a significant difference (paired  $t$ -test:  $n = 22$ ,  $t = 2.53$ , two-tailed  $p = 0.019$ ) corresponding to an 11% decline from baseline endurance levels.

#### (d) Experiment 4: effect of display production on lactate concentration

Post-display concentrations of lactate averaged  $4.32 \pm 0.17$  mM, a 12% increase over baseline concentrations of  $3.86 \pm 0.16$  mM (figure 3; paired  $t$ -test:  $n = 18$ ,  $t = 2.6$ , two-tailed  $p = 0.019$ ).

## 4. DISCUSSION

The results of this study are consistent with expectations of honest-signalling theory. The demonstration, in this study, that threat-posture duration varies with endurance capacity provides the first direct evidence (to my knowledge) that threat displays are capable of advertising endurance. Confounding effects of contextual variation and social experience were minimized by the design of this study, in which display behaviour was recorded in a controlled setting and elicited by a standard stimulus. The possibility that variation in traits other than endurance can account for variation in threat duration is diminished by the finding that neither size nor condition correlate with

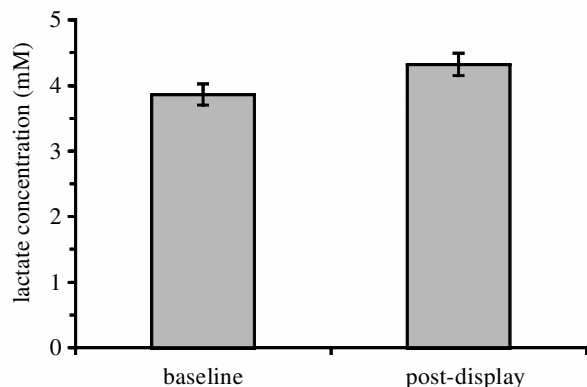


Figure 3. The effect of display production on lactate concentration. Baseline lactate concentration is compared with lactate concentration measured immediately after a 5 min exposure to a mirror. The change in lactate concentration was judged to be significant using a paired  $t$ -test ( $t = 2.6$ ,  $p = 0.019$ ,  $n = 18$ ).

display behaviour. Furthermore, when endurance was experimentally diminished the duration of threat posturing was significantly reduced, suggesting that endurance and threat duration are specifically linked. Although the test sequence was not randomized in this experiment, an order effect is unlikely to account for these results given the lack of such an effect in the first experiment. Remarkably, after performing threat displays, endurance is significantly lower than baseline, as expected for signals that act as quality handicaps (Hasson 1997; Johnstone 1998; Vehrencamp 2000). Although this study did not test whether lizards attend to variation in threat duration, the results show that the production of threat displays in lizards varies in a manner that could allow these displays to advertise endurance capacity, while engaging in display production causes a transient reduction in endurance capacity. How can the detrimental effect of display production on endurance capacity be accounted for mechanistically? Why does threat duration correlate with endurance capacity while the number of push-ups does not?

A restriction imposed on aerobic metabolism by the threat posture provides a plausible physiological pathway linking display production to the subsequent decrease in endurance capacity. Lateral compression of the thorax is a ubiquitous component of the threat posture in iguanian lizards (Carpenter & Ferguson 1977). In some cases, this posture is maintained for extended periods of time: from minutes in eastern fence lizards (Carpenter 1962*b*) to over an hour in adult green iguanas (Dugan 1982). Ventilation in lizards is achieved by aspiration, whereby muscular contractions move the hypaxial muscles of the thorax, alternately increasing and decreasing pulmonary pressure, thereby moving air in and out of the lungs (Carrier 1987, 1989, 1990). Lateral compression is likely to interfere with the movements of the ribcage that are executed during normal breathing cycles, thereby compromising aerobic metabolism. This, in turn, would prompt a compensatory increase in anaerobic glycolytic metabolism to meet energetic requirements. Lactate, the metabolic product of glycolysis, is an important agent of muscle fatigue, most probably through its effects on  $H^+$  concentration (Fitts 1994). Similarly, lateral compression may elevate the

pressure within the thoracic cavity, thereby restricting circulation by reducing venous return (Farmer & Hicks 2000), and forcing a transition to anaerobic metabolism. By causing a shift to anaerobic metabolism, lateral compression can lead to increased lactate production resulting in fatigue and a reduction in endurance capacity. Anaerobic metabolism augments aerobic metabolism to support vigorous activity in lizards (Bennett 1982; Pough & Andrews 1985), and post-exercise lactate elimination is slow (Gleeson 1991). Therefore, the production of threat displays is likely to restrict substantially the capacity of the displaying individual to engage in activities such as fighting, courtship and evasion of predators during the period required for metabolic recovery. The finding that post-display lactate concentration is higher than baseline lactate concentration is consistent with the proposed mechanism, although further experiments are necessary to test directly whether the laterally compressed threat posture indeed restricts ventilation and circulation.

The aerobic-interference mechanism proposed here implies that, unlike the laterally compressed threat posture, push-ups do not restrict aerobic metabolism, and thus push-up production should be less costly than engaging in threat posturing, and therefore less reliable as an indicator of endurance. Thus, the aerobic-interference mechanism is consistent with the finding that threat duration, but not push-up number, is significantly correlated with endurance. Furthermore, threat duration significantly decreased in response to the endurance-reducing manipulation, while the decrease in push-up number was judged to lack significance at the 5% level. In contrast to the current study, an earlier study reported a significant correlation between the number of push-ups performed in the context of predator deterrence and endurance capacity (Leal 1999). This correlation may have arisen as a result of the relationships of these two variables with threat-posture duration, as observed in the current study. Although threat-posture duration was not quantified in relation to endurance, numerous individuals adopted a threatening posture and persisted in this behaviour for up to 8 min (Leal 1999; Leal & Rodriguez-Robles 1995, 1997).

Alternatively, the threat posture may interact with push-ups to advertise endurance capacity. Under this scenario, the restriction that lateral compression imposes on aerobic metabolism causes push-ups that are produced while threat posturing to be more metabolically taxing than push-ups that are produced in a normal posture. Yet another alternative is that breath holding itself is a costly signal, while threat posturing does not carry production costs. If this is the case then threat posturing may simply make more apparent the breath-holding signal, suggesting that the threat posture can be classified as an amplifier (Taylor *et al.* 2000).

The present study did not investigate whether recipients attend to the variation in threat display production and use this variation in rival assessment. However, studies in other lizard species, as well as more phylogenetically distant taxa, indicate that assessment of such signals is a likely possibility. Behavioural responses to video playback indicate that lizards may extract species-identity and push-up rate information from visual displays (Macedonia *et al.* 1994; Macedonia & Stamps 1994; Ord *et al.* 2002), sug-

gesting that visual displays can be used in assessing rivals. Roaring rate in red deer stags has been suggested to indicate endurance, and playback experiments show that high roaring rates contribute to successful harem defence (Clutton-Brock & Albon 1979). Among hermit crabs, the signalling rates of attacking individuals appear to be influenced by fatigue (Briffa & Elwood 2000), while the probability of the defender to give up its shell increases with signalling rate (Briffa *et al.* 1998). Anaerobic metabolism appears to play an important part in powering these signals (Briffa & Elwood 2002), and high lactate concentrations constrain the signalling ability of hermit crabs (Briffa & Elwood 2001). Given that lizards appear able to assess visual signals, and that signals of endurance seem to be used in opponent assessment in animals such as red deer and hermit crabs, it is very likely that lizards can use the duration of lateral compression, or perhaps the rate and the number of push-ups performed while threat posturing, as a means of assessing the endurance capacity of a displaying rival.

The role of glycolytic anaerobic metabolism in supporting agonistic behaviours in lizards remains unclear. Measurements in field-active animals showed higher than baseline lactate concentrations after engaging in display and fighting behaviours (Bennett *et al.* 1981; Pough & Andrews 1985). By contrast, measurements of males paired in metabolic chambers revealed elevated lactate concentrations and increased respiration rates in the absence of physical activity (Wilson & Gatten 1989). Furthermore in caged trials lactate concentrations after agonistic activity did not differ significantly from initial lactate concentrations, and both of these values were much lower than lactate concentrations in exhausted individuals (Wilson *et al.* 1990). While Wilson and co-authors offered that display behaviour does not rely on anaerobic metabolism, and that fatigue does not play a role in determining contest outcome, an alternative interpretation is suggested by the findings of the present study. The increases in anaerobic and aerobic metabolism noted for apparently inactive lizards (Wilson & Gatten 1989) might have been caused by the subjects engaging in breath-holding behaviour that went unnoticed by the investigators. The lack of difference between initial and final lactate concentrations (Wilson *et al.* 1990) may be explained by relatively high variability in resting lactate concentration coupled with small sample sizes.

In summary, endurance, a predictor of dominance, was found to correlate with signal production, while signal production appeared to result in diminished endurance, as predicted of a quality handicap. The deleterious effect of display production on endurance capacity may be responsible for maintaining the reliability of this signal, perhaps mediated by inhibition of aerobic metabolism, which leads to a compensatory increase in anaerobic metabolism. The aerobic-interference mechanism proposed here for lizard threat posturing may not be restricted to threat displays in lizards. The threat postures employed by various fishes are a case in point, as suggested by Zahavi for Siamese fighting fishes (*Betta splendens*) (Zahavi & Zahavi 1997). Ventilation in fishes is powered by movements of the buccal cavity and the gill covers (Ballintijn 1969), while threat displays involve erection of the gill covers and depression of the branchiostegal rays

on the floor of the buccal cavity (Baerends & Baerends-van Roon 1950; Simpson 1968). It follows that these threat displays should interfere with ventilation and therefore the production of these displays is expected to be detrimental to fighting ability. Consistent with this prediction is the report that individuals trained to over-display lost contests against normally displaying individuals (Halperin *et al.* 1998). If aerobic interference is an important component of threat displays in a multitude of species then interspecific differences and similarities in the design of threat displays may well be explainable by relating them to structural and functional variation in features of the ventilatory and circulatory systems.

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