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ARTICLE

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Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*)

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Abstract Two potential signals used during male–male agonistic encounters were examined for signal content in the territorial agamid lizard *Ctenophorus decresii*, or tawny dragon. Males have black chest patches, which are apparent when they posture during agonistic encounters. Patches are not condition or size dependent. The area of the patches is positively associated with levels of aggression and likelihood of winning a fight. The patch thus functions as a "badge of status" indicating male aggression. The complex dynamic displays given by males contain information on male endurance and size. The number of push-ups given during a display reflects the aggressiveness of an animal. There was no relationship between patch size and endurance. There is some overlap in the content of the two signals, both contain information on aggressiveness, suggesting that they may function as back-up signals. The multiple-message hypothesis is not ruled out as endurance and size are only related to the dynamic displays. However, it is not clear that endurance is an important determinant of contest outcomes in this species, and so it is not certain that the receiver uses this information.

Key words Male–male contests · *Ctenophorus decresii* · Quality · Badges of status · Signal reliability

Introduction

Many animals have a repertoire of signals and displays that may function simultaneously in social interactions. Two main hypotheses have been proposed for multiple signals in animal displays: (1) The back-up hypothesis where multiple components signal the same quality to account for receiver error in detection and discrimination; and (2) the multiple-message hypothesis where different display components signal different qualities (Johnstone and Grafen 1992; Johnstone 1996). However, few model systems investigated in the context of male–male contests have revealed multiple signalling components. Signals used in male–male contests may be assigned to their task by arbitrary convention and thus may not be directly linked with the attribute they represent. This is known as conventional signalling – badges of status are an example (Maynard Smith and Harper 1988; Guilford and Dawkins 1995). Other signals may be more directly associated with the type of attribute they represent and are known as assessment signals (Maynard Smith and Harper 1988). Both types of signals can be found in a single species and as conventional signals are often static, that is always present, they often occur simultaneously with assessment signals.

Badges of status should theoretically be of low cost to produce and thus be a conventional signal of male quality. Isolated patches of pigment are often found to act as a badge of status in vertebrates. The information conveyed by the badge may be the social ranking of the animal; for example, the melanic chest patches of the house sparrow increase in size as social ranking increases (Gonzalez et al. 2002; Hein et al. 2003; McGraw et al. 2003). The red colouration of three-spined sticklebacks also acts as a signal of male dominance (Baube 1997; Candolin 1999). Other badges may reflect the aggressive motivation of an individual, for example the white wing patches of the chaffinch, where increased exposure of the patch during an interaction reflects increasing aggressive motivation (Jablonski and Matyjasiak 1997). The badge of these species allows males to identify the dominance status of another individual without having to engage in physical combat (Baube 1997; MacLeod 1998; Jones and Hunter 1999). Badges of status also are known in lizards. The size of the orange and yellow ventral badges of *Platysaurus broadleyi* is correlated with the number of times an animal wins in contests staged in the field, thus signalling male dominance (Whiting et al. 2003). For the agamid lizard *Ctenophorus ornatus*, the size of the black chest badge predicts territory size and therefore the number of females in a territory; it does not predict

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reproductive success, but may reflect male social dominance (LeBas 2001).

Assessment signals of male quality relate more directly to the attribute signalled, with the type of information conveyed being a direct function of the signal. Thus the display directly signals male quality by letting a male directly assess the fighting ability of the opponent. For example many species use vocal signals. The energetic calls of baboons, for example, are correlated with male dominance, with more dominant animals giving longer bouts and more calls per bout (Kitchen et al. 2003). Likewise for many frogs the deepness of the call reflects male size, which influences contest outcomes for many species (Davies and Halliday 1978; Wagner 1989; Burmeister et al. 2002). Many animals such as iguanid lizards also give dynamic and presumably energetically expensive displays (DeCourcy and Jenssen 1994; Macedonia and Clark 2001). Fighting is energetically expensive for a variety of species and so the endurance capacity of an animal may well have an impact on its ability to engage in sustained activity in display bouts, or physical combat (Smith and Taylor 1993; Hack 1997; Neat et al. 1998). The displays used by *Anolis cristatellus* in an anti-predator contest have been found to be a reliable indicator of male endurance capacity (Leal 1999). Threat displays of *Uta stansburiana* also have been found to reliably signal endurance capacity (Brandt 2003). There is evidence that for male lizards from the iguanid and phrynosomatid families dominance and display production are also correlated with endurance capacity (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004).

The tawny dragon, *Ctenophorus decresii*, is a small, arid-zone agamid lizard from South Australia (Gibbons 1979). Males are highly territorial and aggressive towards other males. Agonistic encounters in *C. decresii* have a number of signalling components. In this study I examine the information contained in two potential signals, the dark chest patches and the dynamic displays, which are available simultaneously during male–male encounters. Males have dark chest patches that vary from light grey to black. A previous study found no relation between patch colour and male contest outcomes (Stuart-Fox 2002).

The displays used by males in agonistic encounters are highly elaborate and are assumed to be energetically expensive and time consuming (personal observation; Gibbons 1977, 1979). The display elements seen in agonistic encounters include threat postures such as elevation of the body with the back arched, lateral compression, lowering of the gular region (or dewlap) and erection of nuchal and vertebral crests. *C. decresii* also performs a unique agonistic display termed the hind-leg push-up display where the rear of the animal is lifted in the air with the tail coiled over the back. Often during this display the back feet leave the ground. These push-up displays are often combined with head bobbing and forearm waving (personal observation; Gibbons 1977, 1979).

I test whether the dark chest patches function as a badge of status: Do males with bigger patches tend to win more fights and/or are they more aggressive? I also test if the agonistic displays are reliable indicators of endurance capacity. Finally, I test whether features of the display or endurance are related to aggression or likelihood to win, and whether endurance is related to badge size. Thus the present study also aims to answer the question: Is there overlap in the signal content or do the signals convey different information on male quality?

Materials and methods

Encounters

All animals were collected from the Flinders ranges in South Australia as mature adults (snout-vent length >65 mm) (Gibbons 1977). Animals were caught by noosing, using waxed dental floss on the end of a 5-m telescopic fishing pole. Animals were immediately transferred to calico bags. All individuals were recognisable by their unique gular patterns and colouration, and so it was not necessary to mark animals. All animals were housed individually in outdoor enclosures for the duration of spring, summer and autumn in Canberra, Australia. The enclosures were 2 m in diameter and divided in half with one male on each side. The divider was made from 2-mm opaque plastic and was buried 10 cm into the ground and extended to 1.5 m in height thus preventing males from visual or chemosensory contact with other males while in their home enclosures. Enclosures had a natural soil substrate, with tussock grass, refugia and basking sites provided in the form of rocks and roof tiles. Food and water were available ad libitum in the lizards' home enclosures. Wild insects were available as a food source, which supplemented the diet of captive crickets. Animals were retained in captivity for further studies.

Experiments were conducted outdoors during November and December 2002, and the animals were exposed to natural spring/summer light cycles and temperature ranges. Contests were conducted in glass aquaria that measured 150 × 50 × 50 cm and were protected by shade cloth.

Thirty-two adult males were used in this study. Males were assigned to size-matched groups of four individuals according to a size index, thus producing eight groups. The index was calculated by running a principal components analysis with data for mass, snout-vent length (SVL) and head width, and ranking the regression factor scores obtained. Using this index to size-match males was preferred to using any one size variable because it incorporated any differences in variability of the different measures of size, and because SVL, mass and head-width have all been shown to be important in determining male contest outcomes in lizards (Vitt and Cooper 1985; Olsson 1992; Stuart-Fox 2002).

Two size-matched males were placed in a glass tank with an opaque divider down the middle, so that they were unable to see each other. Each side had a refugium and a heat source. The lizards were allowed to acclimatise overnight. Prior to removal of the divider, a central platform with a heat lamp over it was placed in the centre of the tank providing a resource over which the animals could contend.

The divider was then removed and the resulting interaction between male pairs filmed and timed. Filming was done using a Panasonic NV-DS28 digital video camera mounted 20 cm from the side of the tank. Interactions were ended at 20 min or when an animal repeatedly tried to escape. This was sufficient time for a winner to be decided. All contests were carried out between 1000 and 1300, when the animals are naturally active.

Males were then rematched with a new unknown lizard. Each new pairing was in a new clean tank (see Russell 1980), with animals allowed to acclimatise in each instance overnight before the experiment was repeated. Thus interactions with new rivals occurred 24 h after the last fight. All tanks were identical and were cleaned before swapping animals. There were three interactions in total per lizard with males being paired in a "round robin" fashion (where each animal meets every other animal in its group in succession) so as to eliminate possible carry-over effects (Russell 1980). In total 48 interactions were carried out, with six contests per group of lizards.

Thus for four individuals, d1, d2, d3, and d4, the successive pairings were as follows:

Round (1) d1 × d2 & d3 × d4
Round (2) d1 × d3 & d2 × d4
Round (3) d1 × d4 & d3 × d2

The recording of each interaction was analysed by taking behavioural observations from the tapes and noting the contest winner. Winners were those who continued assertive behaviour such as an alert or aggressive posture. Losers were recognised by a lack of aggressive posturing, for example crests being lowered, and retreating animals would flee when the winner postured or approached. In order to keep results comparable with other studies on male aggression in this species, behaviours were scored according to the following index to obtain an aggression score (modified from Stuart-Fox 2002). The following aggressive behaviours were noted (scores in parentheses): biting (3); hind-leg push-up display (3) (this includes lowering of dewlap, lateral compression, slow push-ups, and tail coiling); chasing (2); aggressive posturing (2) (this includes raising of nuchal or vertebral crests, back arching, lateral compression, lowering dewlap); tail flick (1); and taking possession of central resource (1). Submissive behaviours were scored as follows: fleeing (–2); and lying prostrate (–2). Each instance of a behaviour was scored during a trial and the total aggression score used. As interactions were ended when an animal became prostrate (they do not become active again until the aggressor is no longer visible) or attempted to escape, the negative component of the index due to submissive behaviour was generally small, thus preventing aggression score differences from becoming inflated (as the negative submissive score reduces an animal's over-all aggressive score). Most contests were resolved without physical fighting; biting occurred infrequently, and involved a short nip to the base of the tail. No scale damage or other physical trauma resulted and all animals recovered fully within 10–15 min of the contest ending, returning to normal behaviour such as basking and feeding. All interactions that were ended early due to repeated escape attempts (5 of 48) were adjusted to be comparable to the 20-min interactions in a simple linear fashion. This was achieved by calculating the average aggression score for 1 min and multiplying it by the number of minutes required to make up a 20-min interaction period.

Badge size

To measure badge size, digital pictures of badges were taken using the macro lens of a digital camcorder (Panasonic NV-DS28), and stills were extracted as bitmap files. Animals were constrained against clear Perspex in order to film their badges, and a guide ruler was included in the film for scale. The bitmaps were imported into Scion Image Beta 4.0.2. and an outline of the badge drawn; the area was then calculated in mm^2. It was then tested if badge size correlated with measures of animal size (snout-vent length, head width, or mass), or body condition (mass/snout-vent length^3) (Olsson 1994). Badges were measured both in autumn 2002 (March) and spring 2002 (November), when the experiments were conducted, to determine if badge size varied between seasons. The relationship between badge size and animal aggression and the likelihood of winning was explored.

Agonistic displays and endurance capacity

Ctenophorus decresii is an arid-zone species and its habitat is prone to occasional flooding, so populations will be adapted to swim. Swimming is instinctive, providing a strong motivational drive, and it is easy to gauge with accuracy when a lizard is tired as it simply ceases to swim. This means we can get more accurate measurements of endurance than by using measurements of running ability, which often result in sub-maximum performance by lizards (Losos et al. 2002). *C. decresii* also do not engage in prolonged bouts of running but instead use short bursts to escape predators, always being close to a refuge site (personal observation). Thus swimming is an appropriate measure of endurance for the study species.

To measure endurance capacity, a heated water bath (50 × 40 cm) filled to a depth of around 10 cm was used. Males were brought into the lab and housed individually in plastic boxes (50 × 30 × 28 cm), with water available ad libitum, and allowed to acclimatise overnight. The containers were placed on heat tape set to 40°C. It was ensured that all animals had been basking for the same period of time so that all test subjects were at the same body temperature. Additionally the room was temperature controlled so that the night-time temperature was also constant (15°C). The temperature of the water was maintained at the species-preferred optimum, 36°C (Gibbons 1977). Trials were started by releasing the test subject in the water. Animals would begin to swim immediately. Animals were stimulated to keep swimming with a tap at the base of the tail when necessary. Swimming time was measured with a stopwatch from the time the animal was placed in the bath until the trial was ended. Trials were terminated when the animal failed to respond to five taps to the base of the tail. When exhausted, animals would gulp air and float; thus there was no risk of sinking or drowning. The time that the animal could continuously swim was noted, and used as a measure of endurance capacity. Three trials were conducted for each animal with at least a week between trials to ensure animals had fully recovered. The average swimming time over the three trials was noted.

Display intensity for hind-leg push-up displays was measured using data from the male–male interactions above and was graded using the following index to obtain a display intensity score: raising of nuchal crest (1); raising of vertebral crest (1); lateral compression (1); lowering dewlap (1); tail-coiling (1); head-bob (1 × no. of head-bobs); arm circumduction (1 × no. of rotations); push-up (2 × no. of push-ups). The sum of the total components of a display constitutes the index. Although more than one display may be performed per interaction, individual displays are quite distinct, with animals returning to normal posture afterwards or initiating physical combat. This index is an independent measure from the aggression index. The aggression index includes only the number of push-up displays performed, not the number of different components performed per display.

Display intensity and the display parameters with the greatest numerical variability, number of push-ups and head-bobs performed, were then correlated with endurance capacity and aggression score to look for interactions. I also tested if body size and condition correlated with endurance capacity. A correlation between endurance capacity and aggression score and/or badge size was also looked for.

Statistical analysis

All statistical tests were performed using SPSS 11.0, except for the generalised linear model which was created using Genstat 6.1. All comparisons are two-tailed. Linear regression was performed using the difference in aggression score and the difference in badge area between opponents in order to control for opponent effects. The relation is constrained to be symmetric as the chance of winning is constrained to 50% if the differences in badge area and aggression score are zero, so for modelling purposes it is immaterial which animal is chosen as the one whose result is recorded, so long as the values for the other animal are subtracted from the values of the first to give the aggression score and badge area differences. Each fight was included only once in the data set ($n = 45$) with difference in badge area used as the independent variable and difference in aggression as the dependent variable. The regression analysis excluded interactions with one animal, which did not affect significance but did have high leverage; that is, the results for this one animal had a disproportionate influence on the results ($F_{1,47} = 7.590$, $P = 0.008$, $R^2 = 0.142$). This animal lacked aggressive responses while having an exceptionally large badge. A generalised linear model was used to test the predictive power of these two variables on an animal's likelihood to win a contest. The model was constructed using multiple logistic regression on binomial data, with fight outcome as the response variable (win/lose) and difference in aggression and difference in badge area as the predictors. Group was included as an interaction term to test for possible group effects on an animal's aggression levels, but no significant effect was found ($\chi^2_7 = 1.32$, $P = 0.236$).

Measures of size, condition, endurance capacity, aggression and display parameters were analysed by computing Pearson correlation coefficients as variables were normally distributed. One animal was omitted from analyses because no accurate measures of mean endurance capacity were obtained ($n = 31$). Another was omitted from analyses of mean endurance capacity because only two measures of endurance capacity were obtained ($n = 30$).

Display data were obtained for 28 animals, as some animals were never observed to display (this includes the animal for which no accurate endurance measures were obtained and the animal for which no mean endurance data were available). The intensity score for the first display of the first encounter/interaction is presented here, as this excludes any experience effects. Although this consists of a single measurement, the opportunity for experimenter error is low as the interactions were filmed and all actions were distinct.

Twenty-three animals performed more than one head-bob in a display (this includes the animal for which no accurate endurance measures were obtained), and 23 performed more than one push-up in a display, which was enough to allow for analysis. The average number of push-ups and head-bobs performed in the first encounter for an animal is used (not all animals performed these as part of their first display).

Results

Badge size

Badge area did not differ between seasons (paired *t*-test; $t_{30} = 0.355$, $P = 0.725$), and badge size was not correlated with condition ($r = 0.106$, $n = 32$, $P = 0.565$) or animal size ($r = 0.205$, $n = 32$, $P = 0.260$).

The regression analysis showed a significant relationship between the difference in aggression scores between contestants and the difference in the size of their badges. The difference in badge area between contestants was a good predictor of the difference in their aggression scores ($F_{1,44} = 14.391$, $P < 0.001$, $R^2 = 0.251$) (Fig. 1). Aggression scores of winners were significantly higher than those of losers (paired *t*-test: $t_{44} = -8.838$, $P < 0.001$). The difference between aggression scores in paired contests was the most significant predictor of winners ($\chi^2_1 = 44.77$, $P < 0.001$) (Fig. 2). The difference in badge size between contestants was also a predictor of winners ($\chi^2_1 = 4.67$, $P = 0.031$) (Fig. 3).

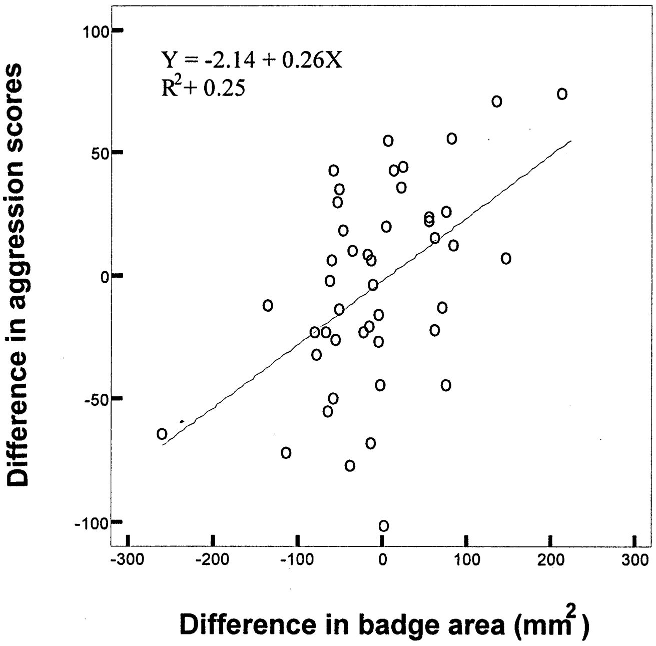

Fig. 1. The relationship between the difference in aggression and the difference in badge area (mm^2) for pairs of adult male tawny dragons ($n = 45$)

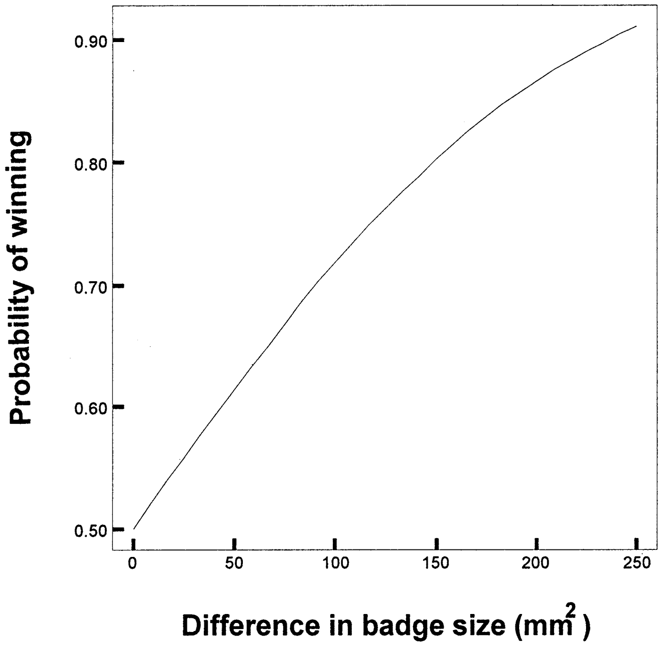

Fig. 3. The predictive power of the difference in badge size (mm^2) between adult male tawny dragons on likelihood to win, determined by a generalised linear model ($n = 45$)

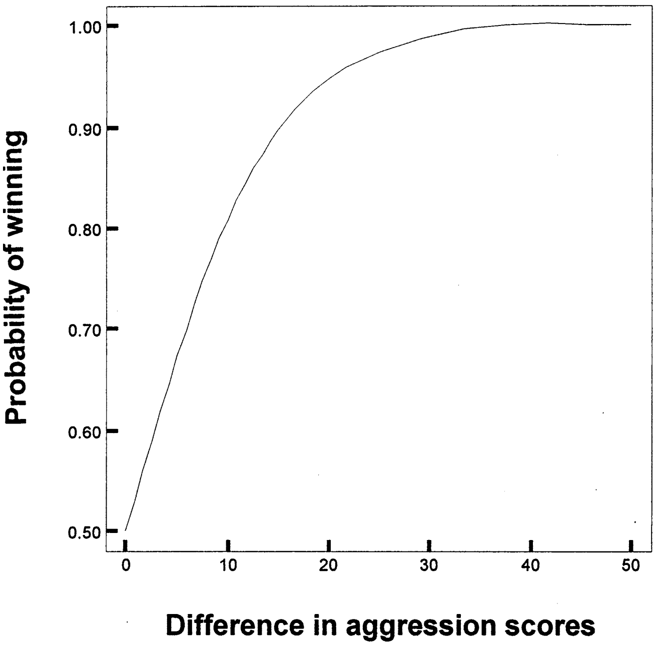

Fig. 2. The influence of the difference in aggression between adult male tawny dragons on likelihood to win, determined by a generalised linear model ($n = 45$)

Agonistic displays

There was no correlation between either animal size or condition and mean endurance capacity (size: $r = 0.286$, $n = 30$, $P = 0.126$; condition: $r = 0.173$, $n = 30$, $P = 0.361$). Display intensity was not correlated with condition ($r = 0.238$, $n = 28$, $P = 0.223$), but did correlate positively with size ($r = 0.450$, $n = 28$, $P = 0.016$). There was no correlation between either animal size or condition and the number of head-bobs performed (size: $r = 0.078$, $n = 30$, $P = 0.724$; condition: $r = -0.003$, $n = 30$, $P = 0.989$). There was no correlation between either animal size or condition and the number of push-ups performed (size: $r = 0.019$, $n = 30$, $P = 0.932$; condition: $r = 0.233$, $n = 30$, $P = 0.285$).

Display intensity correlated positively with mean endurance capacity ($r = 0.416$, $n = 26$, $P = 0.034$) (Fig. 4). There was no correlation between the number of head-bobs performed and mean endurance capacity ($r = -0.033$, $n = 22$, $P = 0.442$). There was no correlation between the average number of push-ups performed and mean endurance capacity ($r = 0.197$, $n = 23$, $P = 0.183$).

There was no correlation between badge area and mean endurance ($r = -0.022$, $n = 30$, $P = 0.908$). The difference in endurance of opponents did not relate to the difference in aggression scores ($r = 0.011$, $n = 40$, $P = 0.945$, where n = number of interactions). Aggression scores were not related to display intensity ($r = 0.303$, $n = 28$, $P = 0.117$), or number of head-bobs given ($r = 0.045$, $n = 23$, $P = 0.840$). There was a positive correlation between number of push-ups and aggression scores ($r = 0.673$, $n = 23$, $P < 0.001$).

Discussion

Badges of status

The results show that as the difference in the size of the dark chest patches of adult male *C. decresii* increases, so does the difference in aggression scores between two males.

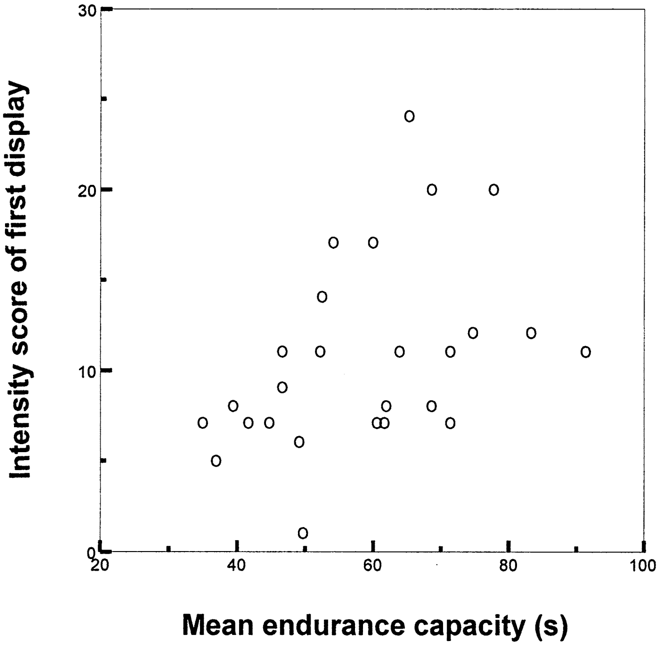

Fig. 4. The relationship between intensity of the first display given by an adult male tawny dragon and its mean endurance capacity (s) ($n = 26$)

Thus the size of the dark chest patches is positively associated with aggression scores, and the difference in the size of patches is a good predictor of contest outcomes. It is interesting that as the difference in badge size decreases the variance in the difference in aggression score increases. This suggests that as the difference in badge size gets smaller it becomes a less accurate indicator of the difference in aggression between animals. Thus in contests with males that have a small difference in the size of their badges, the probability of the male with the larger badge winning decreases. Aggression scores were an important determinant of which animal won a fight, however this is not known before a contest is initiated. Patch size is the next most important predictor of contest outcomes and could be used prior to initiating a contest.

The size of the dark chest patch of *C. decresii* may act as a signal, or "badge of status", indicating the aggressive tendencies of an individual. A relationship between the size of "badges of status" and dominance has been found in a number of bird species and some lizard species (Senar and Camerino 1998; Pryke et al. 2002; Whiting et al. 2003). The size of the patch of *C. decresii* is static, as it does not change across seasons and is not dependent on body condition or size. It is possible that the badge of *C. decresii* reflects innate aggression levels as it does not change across seasons, and examination of plasma testosterone levels may be revealing. The tree lizard, *Urosaurus ornatus*, also has a badge that is fixed during adulthood (Thompson and Moore 1991). Unlike *C. decresii*, in other species of birds and lizards badges of status are dependent on body condition (LeBas 2001; Pryke et al. 2002; Whiting et al. 2003). Dependence on body condition is seen more commonly with carotenoid badges (Badyaev and Hill 2000; Pryke et al. 2002; Whiting et al. 2003). The link between melanin-based badges and body condition is not certain, as the size of melanin badges is not altered by diet manipulations (Gonzalez et al. 1999; McGraw et al. 2002, 2003). Thus, while pigments such as carotenoids may reflect male fighting ability as determined by body condition, melanin-based patches may reflect another determinant of fighting ability such as testosterone-mediated aggression levels (Evans et al. 2000; McGraw et al. 2003; Whiting et al. 2003). Male house sparrows with higher levels of testosterone, for example, tend to be more aggressive and have bigger badges, as their melanin-based chest badges are under the control of testosterone levels during molt (Evans et al. 2000; McGraw et al. 2003).

Badges of status are thought to evolve in order to reduce the number of contests with predictable outcomes engaged in by both receiver and signaller (Maynard Smith and Harper 1988). In bird species, badges of status are most likely to evolve in non-territorial species with unstable flocks where most encounters are with strangers, while neighbouring males in territorial species presumably do not require such signals because they have prior knowledge of each other's fighting ability (Rohwer 1975, 1982; Pryke et al. 2001). Two conditions have been suggested that could relax these requisites so that badges may be beneficial in other systems. These are high costs of fighting and low costs of conspicuous signalling (Olsson 1994). For *C. decresii*, which is territorial, the risks of unnecessary fights are high. Contests can result in mouth-wrestling and biting and thus carry the risk of injury (Gibbons 1977). As *C. decresii* live on exposed rocky outcrops, fighting is likely to increase their risk of predation. Interactions are also energetically demanding and so are likely to decrease the lizard's ability to escape from predators and to engage in a future contest with a more evenly matched male (Gibbons 1977; Stuart-Fox et al. 2003). Thus a badge of status that signals male aggression may be beneficial in avoiding contests when the asymmetry in badge size is high.

While the cost of maintaining badge reliability cannot be determined from this experiment, it seems likely that costs will be low compared to the benefits of avoiding predictable contests. The badge is unlikely to incur a predation risk. Most predators of *C. decresii* are avian, and the badge is concealed ventrally (Gibbons 1977; Stuart-Fox et al. 2003). Social remediation may be a cost of having a badge as it is possible that individuals with large badges will be tested by other aggressive males through contest escalation, as seen in other species (Hurd 1997; Qvarnström 1997; Candolin 2000). Sub-adult males live on adult male territories and do not develop badges until maturity, although they do have adult gular colouration (Gibbons 1977). If increased levels of plasma testosterone are associated with badge size then the cost may be metabolic (Buchanan et al. 2001; Whiting et al. 2003), or in reduced immune function (Salvador et al. 1996; Poiani et al. 2000).

Although the results show that animals with larger badges are more aggressive and thus more likely to win an encounter, they do not show that this information was actually used by the receiver in this experiment. Further studies would need to be carried out using manipulations of badge size and looking for differences in the response of the receiver.

Agonistic displays

The results show that the displays given in agonistic encounters are correlated with a male's endurance capacity. Individual components such as push-ups and head-bobs are not indicative of endurance capacity. Rather it is the sum of the energetic components of a display that reflect mean endurance capacity, that is the total number of actions such as push-ups, head-bobs and arm waves performed in one display. Side-blotched lizards, *U. stansburiana*, also show no statistically significant relation between the number of push-ups or head bobs performed and endurance capacity (Brandt 2003). However, the side-blotched lizard performed fewer push-ups and head-bobs when endurance was experimentally decreased prior to contests (Brandt 2003). Additionally a study on tree lizards found no relationship between endurance or dominance and behavioural components, but rather found a relationship with the total behavioural score similar to this study (Robson and Miles 2000). A significant relationship was found between number of push-ups performed and endurance capacity in an anti-predator context in an anole species (Leal 1999).

Endurance and display intensity were not condition dependent; endurance was also not related to size. This is reasonable as condition is a measure of mass relative to body length and so represents fat storage whereas endurance depends on energy stores that are immediately accessible. A lack of correlation between condition and endurance capacity or dominance has also been found in other lizards (Brackin 1978; Brandt 2003). Larger males of *C. decresii* gave displays of higher intensity. Size differences in display behaviour have been noted in anole lizards where larger lizards gave more displays, which may provide a means of size assessment (Tokarz 1985). As the animals in this study were size-matched, the possible effects of size in determining contest outcomes were ruled out, but larger males of *C. decresii* are more likely to win in contests with size asymmetries (Osborne, submitted).

Of the behavioural components, the number of push-ups given during a hind-leg push-up display did correlate with the aggression score of an animal. As this is likely to be the most demanding component of a display, it may reflect an animal's aggressive motivation and thus its likelihood to win. No relation was found between an animal's endurance capacity and its aggression score, which is a strong predictor of its likelihood to win a contest. Endurance capacity is related to dominance in other lizard species (Schall et al. 1982; Schall and Dearing 1987; Robson and Miles 2000; Perry et al. 2004), although one study found no relation between this measure of locomotor performance and dominance (Garland et al. 1990). It is uncertain why no relationship was found for *C. decresii*. It may be that the display does not intentionally carry information on endurance as this information is not used by or is not useful to the receiver. Perry et al. (2004) hypothesised that for the anole species, *Anolis cristatellus*, endurance did not directly determine the outcome of contests between males, but was linked to dominance through another underlying factor such as hormone levels. Experimental reduction of endurance, such as by prior exercise, and subsequent analysis of effects on contest outcomes would determine more directly if endurance is important and thus if the information may be utilised. It is possible that in arena trials such as this, where contests occur in a confined space, that contests escalate more rapidly than in a natural environment. Thus displays do not have time to function as a handicap as this part of the contest is cut short; on occasions animals were interrupted during a display by their opponent. Additionally, endurance may not be a primary determinant of contest outcomes, but in the event of all other determinants being equal, including size and aggression score, it may become important.

Conclusions

The results suggest that for *C. decresii* there are multiple signals used in the single context of male–male interactions, and that some of the information carried by the signals refers to different aspects of male quality. The black chest patch of *C. decresii* functions as a "badge of status" signalling male aggression and social dominance but is not related to endurance or size, and the hind-leg push-up displays signal endurance capacity, size and aggression. However, both signals carry information on male aggression suggesting some redundancy in the contained information which supports the back-up hypothesis. As the badges are static signals of aggression, the hind-leg push-up displays may be used in conjunction to modify information on a male's current aggressive motivation. Also, it seems endurance is not an important factor in winning contests and so the receiver may not use this information. Further studies into the information content of these displays will be carried out in order to determine this.

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