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ORIGINAL ARTICLE

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Rival recognition in the territorial tawny dragon (*Ctenophorus decresii*)

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Abstract The ability to discriminate between familiar and unfamiliar conspecifics is important in territorial animals as it allows animals to distinguish neighbours from non-neighbours. This prevents wasting time and energy in unnecessary aggressive interactions. I investigated the ability of adult males of a territorial lizard, the tawny dragon (*Ctenophorus decresii*), to distinguish familiar from unfamiliar rivals in a laboratory setting. Males significantly reduced their aggression levels in repeat interactions with familiar rivals and increased their aggression levels towards unfamiliar males. The time taken for interactions to be settled was also significantly lower towards familiar than unfamiliar males. The results of this study suggest that adult male tawny dragons can discriminate familiar from unfamiliar conspecifics. Furthermore, animals were presented with three new rivals in succession and showed a robust ability to discriminate between familiar and unfamiliar males.

Keywords Rival recognition · Agamid · Territorial · Male–male contests · *Ctenophorus decresii*

Introduction

Individual recognition will evolve only if there is an associated fitness advantage. In territorial species this advantage may be the ability of individuals to distinguish rivals with which they have previously fought from those with which they have no prior experience; this prevents wasting energy and risking injury in repeating interactions with predictable outcomes (McGregor 1993; Temeles 1994; Lopez and Martin 2001).

For rival recognition to evolve there must be enough non-condition-dependent phenotypic variation in a population to provide an individual ‘fingerprint’ (Olsson 1994; Whiting 1999; Dale et al. 2001). There is evidence of rival recognition based on individual variation in a number of traits in vertebrates. For example, many bird species can distinguish the calls of neighbours from the calls of strangers (Stoddard et al. 1990; Aubin et al. 2000; Molles and Vehrencamp 2001). Plumage colouration of birds also can provide information on individual identity (Mateos and Carranza 1997; Dale et al. 2001). Rival recognition based on acoustic signals has been demonstrated in mammal species, such as the barking fox (Frommolt et al. 2003), and in amphibians (Bee and Gerhardt 2002). The use of chemicals as cues for individual identity has been noted in mammals (Vache et al. 2001; Rosell and Bjørkøyli 2002; Johnston 2003) and reptiles (Alberts et al. 1993; Aragon et al. 2000; Lopez and Martin 2002). In some lizard species, it has been suggested that enough variation in colour exists to facilitate individual recognition (Olsson 1994; Whiting 1999).

Laboratory studies show that the ability to distinguish rivals in some lizards is very robust. Some species can recognise rivals with which they have interacted only once before (Olsson 1994; Lopez and Martin 2001; Trigosso-Venario et al. 2002). This memory, however, is probably lost without social reinforcement. In *Liolaemus tenuis*, the ability to recognise a rival is lost after 20 days without reinforcement (Trigosso-Venario et al. 2002).

Among lizards, there is evidence supporting rival recognition in both non-territorial species, such as *Lacerta agilis* (Olsson 1994) and *Podarcis hispanica* (Lopez and Martin 2001), and territorial species, such as *Crotaphytus collaris* (Fox and Baird 1992; Husak and Fox 2003). The benefits of rival recognition are similar for territorial and non-territorial species since non-territorial individuals tend to meet the same individuals within their home ranges (Olsson 1994; Lopez and Martin 2001). The territorial species, *C. collaris*, is particularly interesting. It can recognise rivals over a broad range of contexts in natural and

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unnatural settings (Husak and Fox 2003). This suggests its discriminative abilities are flexible.

The tawny dragon, *Ctenophorus decresii*, is a small arid zone agamid lizard from South Australia and belongs to the rock dragon species complex (Gibbons 1979). Males are highly territorial and aggressive towards other males. The displays used by males in agonistic encounters are highly elaborate and are assumed to be energetically expensive, and initial interactions can be time consuming (personal observation; Gibbons 1977, 1979). It would seem beneficial for males of this species to be able to distinguish rivals with which they have already established a dominance ranking from unfamiliar individuals. Male tawny dragons have sufficient phenotypic variability to allow individuals to be distinguished by human observers. Males are polymorphic for colouration, with all animals having unique gular and back patterns. Individual variation may also exist in their display structure (Gibbons 1977, 1979). It is likely that *C. decresii* can also use chemical cues for rival recognition as well. Males mark rocks on their territory with faecal pellets and femoral pore exudes (personal observation; Gibbons 1977). The sister species *Ctenophorus fionii* can distinguish known from unknown males using femoral pore exudes (G. Johnston, unpublished data).

In this study I addressed the question of whether males can discriminate between familiar and unfamiliar rivals. I tested whether male aggression levels are significantly lower in encounters with familiar compared to unfamiliar rivals. I also tested whether the interaction time, defined as the time taken for one animal to display consistently submissive behaviour, is lower in interactions with familiar conspecifics compared to unfamiliar conspecifics. Animals were presented with three rivals sequentially to test how robust their ability to discriminate rivals presented in succession was, and also to see if the effect of losing interferes with an animal's reaction to a new rival.

Methods

All animals (*N*=32) were collected from the Flinders ranges in South Australia as mature adults [snout–vent length (SVL) >65 mm]. They were collected over a wide area to avoid collecting neighbours with prior knowledge of one another. Animals were caught by noosing using waxed dental floss on the end of a 5-m telescopic fishing pole, and immediately transferred to calico bags. All individuals were recognisable by their unique gular patterns and colouration so it was not necessary to mark them. All animals were housed individually in outdoor enclosures for the duration of spring and summer in Canberra, Australia. The circular enclosures were 2 m in diameter and divided in half with one male in each side. The divider prevented 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 in the form of rocks and roof tiles. Food (captive crickets) and water were available ad libitum. Wild insects were available as a food source that supplemented the diet of captive crickets. Thirty-two adult males were used in this study and 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. During the summer months the temperature regime in Canberra is similar to that of their native Flinders ranges. Contests were conducted in glass aquaria that measured 150×50×50 cm and were protected by shade cloth.

Males were assigned to size-matched groups of four individuals according to a size index. 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 from the first PCA. The first PCA accounted for 87.6% of the variation. The regression factor scores from the first PCA were highly correlated with all the direct measurements of size (SVL: r=0.931; mass: r=0.930; head width: r=0.947). This method of size-matching was preferred to using any one size variable as 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 (Vitt and Cooper 1985; Olsson 1992; Stuart-Fox 2002).

Animals were initially placed in glass tanks with an opaque divider down the middle, so that two size-matched individuals were placed in one tank but were unable to see each other. Animals were allowed to acclimatise to the new surroundings overnight. Each side had a refuge site and a heat source. 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 on a tripod placed 20 cm from the side of the tank. Interactions were terminated after 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 hours, when the animals are naturally active. For each lizard, there were six interactions against three rivals, with each male being paired in a "round robin" fashion so as to eliminate possible carry-over effects (Russell 1980) (Table 1). In total, 96 interactions were carried out. Animals were tested in one trial per day, with trials being

Table 1 Round robin tournament used to determine the occurrence of rival recognition in the male tawny dragon

Day	Pairing one	Paring two
1	d1*d2	d3*d4
2	d1*d2	d3*d4
3	d1*d3	d2*d4
4	d1*d3	d2*d4
5	d1*d4	d3*d2
6	d1*d4	d3*d2

On days 1, 3, and 5 males were paired with new unfamiliar individuals. On days 2, 4, and 6 they were paired with the male encountered on the previous day. For four individuals, d1, d2, d3, and d4 successive pairings were as follows over six consecutive days conducted over six consecutive days, thus with 24 h between interactions. On days 1, 3 and 5 males were paired with a new unfamiliar lizard with which it had no prior experience, and on each following day (days 2, 4, and 6) animals were repaired with the now familiar lizard from the previous day (Table 1). Each pairing with a new unfamiliar lizard was in a fresh tank to eliminate home and away effects (Russell 1980). All tanks were identical and were cleaned by removing any faecal material and wiping to remove chemical residue, before swapping animals.

The recording of each interaction was analysed by taking behavioural observations from the tapes and noting the contest winner. In order to keep the results comparable with other studies on male aggression in this species, behaviours were scored according to the following index (modified from Stuart-Fox 2002). For aggressive behaviours the following were noted with scores in parentheses: biting (3), hind-leg push-up display (3) (this involves lowering of dewlap, lateral compression, slow push-ups, and tail coiling), chase (2), aggressive posturing (2) (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 following: fleeing (−2), and lying prostrate (−2). All interactions that were ended early due to repeated escape attempts (five of 96) were included as a conservative representation of their aggression in that round. The latency of individuals to react and the time taken for an interaction outcome to be determined (taken as the time when one of the animals was consistently submissive) also were compared between interactions with an unfamiliar male and repeat interactions with the now familiar male.

All statistical tests were conducted using SPSS 11.0. Aggressive scores and times for latency to react were analysed separately using a linear mixed model based on the restricted maximum likelihood method (REML). In situations where the design is completely balanced and there is no missing data, and all the assumptions of ANOVA are met, mixed model analysis by REML gives the same result, if any of these criteria are not met, REML is the better model to use. There has been a trend in research to move to mixed models based on REML rather than ANOVA based models (e.g. see Pinheiro and Bates 2000; Littell 2002). The use of mixed models analysed by the REML method is extremely useful in situations such as repeated-measures data. It allows more flexible and robust modelling of the data. REML (and ML) use(s) quadratic forms to estimate variance components based on log likelihood functions rather than ordinary sum of square computations. Aggression or latency was included in the model as the dependent variable, individuals as random factors, and fight number and interaction outcome (win or lose) as fixed factors. Thus for fight number there are six levels and win/lose has two levels. The length of time for which the interaction lasted was also included to test for significant effects on aggression levels when contests were ended early. No effect of the length of interactions on aggression was detected ($F_{2,\ 132}$=0.125, P=0.883). Data from all 32 males was included in the analysis. The model produces paired t test statistics to compare the size and direction of fixed effect parameters. As aggression scores for one of the fighting rounds and times for latency to react were not normally distributed, the data for aggression scores and latency to react were normalised using a log transformation. The data for interaction time was pooled across rounds to either be interaction 1 (unfamiliar male) or interaction 2 (familiar male), as there was no effect of round on times for first interactions ($F_{2,\ 44}$=1.046, P= 0.360) or second interactions ($F_{2,\ 44}$=0.758, P=0.475) as determined by one-way ANOVAs. Pooled data were then compared using a Wilcoxon matched-pairs signed ranks test. One pair was left out of the analyses as no consistently submissive behaviour was seen (N=47).

Results

As the trials were conducted in sequence, rather than familiar and unfamiliar lizards being presented randomly, I tested for possible effects of order on animal aggression. There was no order effect on aggression levels in first interactions between unfamiliar lizards ($F_{2,\ 55}$=0.558, P= 0.567), as determined by REML using only aggression scores with unfamiliar males but the same factors as above.

There was a significant effect of fight number on aggression scores ($F_{5,\ 146}$=8.588, P<0.001). Animals always had a significantly higher aggression score in a first interaction with an opponent than in a repeat interaction. This was true of both winners and losers for all three pairings (Round 1 vs 2: t_{146}=4.598, P<0.001; Round 3 vs 4:

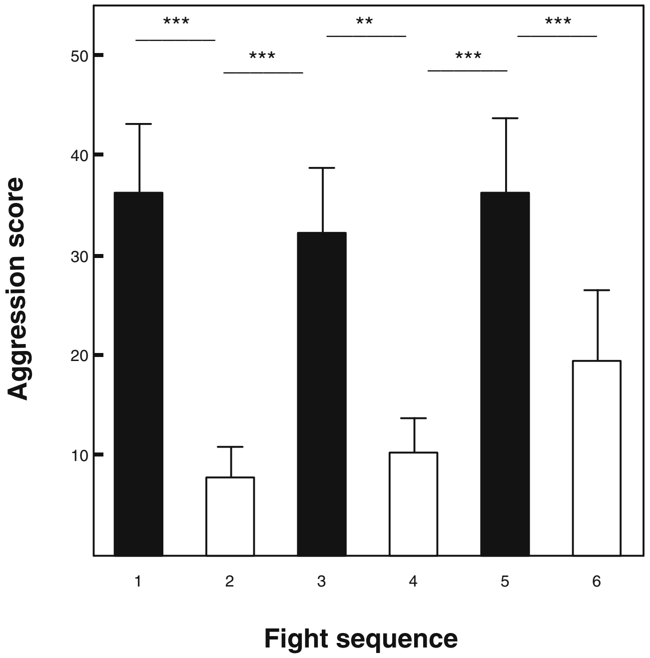

Fig. 1 Mean (+SE) aggression scores for adult male tawny dragons (N=32) over the six successive rounds against three opponents. Each opponent is met twice in succession (*filled squares*: first interactions; *open squares*: repeat interactions). Restricted maximum likelihood method: ***P≤0.001, **P≤0.005. Tests performed on log transformed data

t_{146}=2.889, P=0.004; Round 5 vs 6: t_{146}=3.631, P< 0.001) (Fig. 1). Also, aggression scores were significantly higher in the first interaction of a new pair compared to the second interaction of the last pairing (Round 2 vs 3: t_{146}= 3.626, P<0.001; Round 4 vs 5: t_{146}=3.616, P<0.001) (Fig. 1). The effect of fight number was significant for winners ($F_{5,\ 64}$=5.068, P=0.001) and losers ($F_{5,64}$=5.599, P<0.001) analysed separately also using the REML model described above, with losers having negative or submissive scores in repeat interactions and returning to a positive score in interactions with unfamiliar males (Fig. 2). Animals were consistently losers or winners within pairings. In 48 rounds animals remained losers and in 48 animals remained winners. No animals that lost became winners and none that won became losers. This was significantly different from that behaviour seen across pairings as determined by chi-square tests (χ_3^2=38.319, P<0.001). Across pairings 20 animals remained winners, 22 remained losers, 11 changed from winning to losing and 11 changed from losing to winning. There was no difference in the tendency to change behaviour from days 2–3 compared to days 4–5 when pairings changed (χ_3^2=0.182, P=0.975).

There was no effect of fight number ($F_{5,\ 148}$=1.850, P=0.107) or whether an animal won or lost ($F_{1,\ 65}$=0.268, P=0.607) on times for latency to react. There was a trend however, for the times to be shorter in second interactions within any pair (Fig. 3).

Interaction times, taken as the time in seconds for one contestant to show consistently submissive behaviour, were significantly shorter for second interactions (X±SE= 232 ±43.3, N=47) than first interactions (X±SE=575±81.1, N= 47) (T=−4.306, N=47, P<0.001). Thus, the time taken to settle a contest was much shorter for animals that had previously interacted.

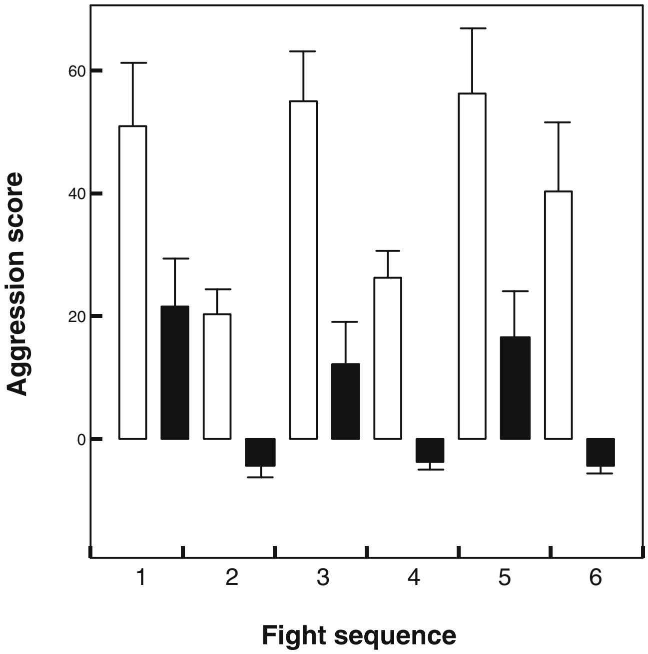

Fig. 2 Mean (+SE) aggression scores for adult male tawny dragons over six successive rounds with winners and losers listed separately (*open squares*: winners; *filled squares*: losers) (N=16 males for each *bar*, except fight three where for winners, N=15 and losers, N=17)

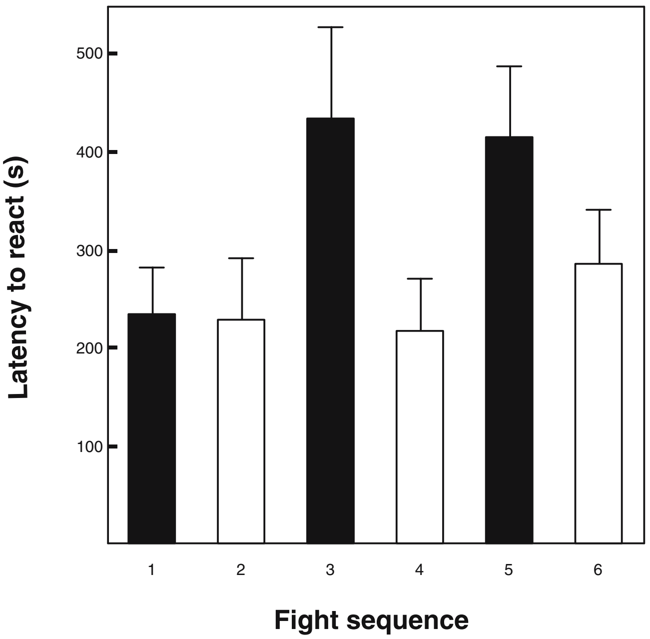

Fig. 3 Mean latency to react (+SE) (s) in aggressive encounters for adult male tawny dragons (N=32 each round, *filled squares*: first interactions: *open squares*: repeat interactions). All comparisons are non-significant

Discussion

Male tawny dragons can distinguish unfamiliar rivals from rivals with which they have had prior experience. There was no order effect on the aggression levels between first interactions with unfamiliar lizards. Males showed increased aggression to new rivals compared to aggressive scores in repeat interactions with rivals with whom they had already interacted. Animals that lost interactions had a negative submissive score in repeat interactions with a familiar lizard and a positive aggressive score in first round interactions with an unfamiliar lizard. Animals may also maintain some memory of their previous interactions and respond more cautiously in interactions with a new male (Jackson 1991). Animals were consistent in roles within a pairing but across pairings animals changed from losers to winners and vice versa. In addition, the length of time it took for one animal to be consistently submissive was significantly lower (by 59%) in repeated interactions with familiar rivals compared to contest length in response to unfamiliar rivals. Latency to react was also shorter in repeat interactions compared to interactions with new rivals; however, the difference is not statistically significant. Decreased aggression levels and interaction times against familiar rivals were most likely due to animals that lost the first interaction accepting this role in the second interaction; thus, repeat interactions do not escalate to the same degree as initial interactions. It is unlikely that animals experienced fatigue in repeat interactions, as there was a tendency for animals to react more quickly in the repeat interaction with a familiar rival. Additionally, if decreased aggression were due to fatigue, then in subsequent trials with unfamiliar males high levels of aggression would not be expected. In the neutral arena used in this study there was likely to be little motivation for an animal to persist in a contest he has lost since perceivable gains are likely to be low (Trigosso-Venario et al. 2002). This may lead to contests being resolved in a shorter time with fewer repeats necessary than in a natural contest.

It is interesting that the animals used in this study were able to distinguish multiple unfamiliar and familiar rivals presented in succession. They showed a consistent change in behaviour between responses to the second presentation of a rival and the subsequent initial presentation of an unfamiliar rival. The pattern of decreasing aggression to the familiar lizard and then increasing again to an unfamiliar lizard was consistently repeated. This ability to continually reassess the presented rival has not been investigated previously, as most prior studies presented only one familiar and one unfamiliar rival to each subject (e.g. Waas and Colgan 1994; Whiting 1999). This provides evidence of a strong ability to distinguish rivals. As agamid lizards are visually orientated, and *C. decresii* has a great degree of morphological variation and is highly territorial, it seems appropriate that males can distinguish one another with a reasonable degree of accuracy.

The results of this study are consistent with other studies of rival recognition. Decreased levels of aggression have been noted in other species across different taxa in response to familiar conspecifics, for example the Eurasian beaver (Rosell and Bjørkøyli 2002), rainbow trout (Johnsson 1997), lizards (Whiting 1999; Lopez and Martin 2001; Husak and Fox 2003), and also in bird species (Stoddard et al. 1990; Molles and Vehrencamp 2001). Decreased contest times have been noted in response to familiar individuals in *L. agilis* (Olsson 1994). As male tawny dragons are highly territorial, their ability to distinguish familiar from unfamiliar rivals may allow territory holders to decrease the energy and time risk associated with repeatedly fighting neighbours.

For territorial species with repeated interactions between certain individuals, it is predicted that the benefits of recognising rivals should outweigh any costs (McGregor 1993; Temeles 1994). As male tawny dragons are highly territorial and aggressive it would be advantageous for members of this species to be able to distinguish neighbours from non-neighbours or at least known rivals from unknown rivals. Repeating contests in this species is likely to carry heavy penalties on energy and time. The benefits of recognising rivals would allow males to minimise their risk of injury in unnecessary contests and avoid wasting time that could be used in other pursuits.

The cues used by male tawny dragons to recognise rivals were not elucidated by this study. There is some evidence that the highly variable colouration and gular patterning is a cue used by their sister species, *Ctenophorus fionii* (Johnston 1997). The agonistic displays of tawny dragons also have been shown to vary between individuals and this may carry some information on individual identity (Gibbons 1977, 1979). Femoral secretions are used by males to mark their territories and may also hold identity cues. Further experimentation to investigate the role of these potential identity cues may be enlightening as to the mechanism of recognition in this species and thus provide clues to possible identity cues in other vertebrates.

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