

Behavioural persistence during an agonistic encounter differentiates winners from losers in green anole lizards

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Abstract

Agonistic encounters featuring ritualized displays precede the establishment of dominance relationships in many animals. We investigated the predictive value of the amount of display behaviour (number and duration of displays) vs. quickness to display (latency to express a display behaviour) in determining the outcome of aggressive interactions and establishment of dominant vs. subordinate status in male green anole lizards, *Anolis carolinensis*. Similar-sized males were paired and observed for ninety minutes as they established social status. We recorded the number, duration (where appropriate) and latencies to first expression for multiple behavioural display components (head bob A, B and C, dewlap displays, open mouth displays, pushups, lateral displays) and colour changes (eyespot presence and body colour changes). Males that eventually won and became the dominant male had significantly higher counts and durations with the exception of Bob C counts, pushup counts and open mouth duration. Future dominants also maintained a green body colour longer than future subordinates, which had brown shades more often and for longer durations. Latency to first express a display component was shorter in future dominants for head bobs A and C, dewlap and open mouth displays when all data were considered. However, all significant latency differences disappeared when data only from pairs in which both males displayed a behaviour were included in the analysis. Counts, durations, and latencies were highly correlated with each other within individuals. The results indicate that behavioural display patterns during an initial display contest predict the outcome of the interaction, with the amount of display behaviour being the best predictor of whether a male will win or lose the contest and hence become dominant or subordinate. These results are consistent with the idea that displays are honest signals of a male's physiological capacity or stamina, and hence fighting and resource holding ability.

Keywords

aggression, social behaviour, reptile, agonistic displays, dominance hierarchy.

1. Introduction

Social aggression is a common phenomenon in animals, particularly when organisms defend a resource-based territory or a display site in a social aggregation (Ryan & Wilczynski, 2011). Ritualized agonistic displays are often the first phase of an aggressive encounter. They may escalate to overt fighting, but very often encounters are settled on the basis of an exchange of agonistic displays. When winners and losers of these competitions subsequently coexist a social hierarchy is established. The winner becomes the dominant individual while losers become subordinate. There are often dramatic behavioural and physiological differences in dominant and subordinate individuals, particularly in terms of stress responses (Plavicki et al., 2004; Ling et al., 2009). Furthermore, dominant individuals generally have enhanced mating success (Cowlishaw & Dunbar, 1991; Ellis, 1995; Wroblewski et al., 2009).

Multiple interacting factors contribute to an organism's expression of aggressive behaviour and to whether or not it will win or lose a particular encounter (for review see Hsu et al., 2006). The location of an encounter is important; residents on their home territories have a significant advantage over intruding opponents. Past experience, including familiarity with a competitor, contributes to the amount of aggression an individual expresses (Temeles, 1994; Yang et al., 2001; Korzan et al., 2007; Carazo et al., 2008; Garcia et al., 2012, 2014; Yoon et al., 2012). Levels of reproductive and stress hormones modulate aggressive behaviours and hence how vigorously an individual will respond in a challenging situation (Greenberg & Crews, 1990; Yang & Wilczynski, 2002, 2003; Husak et al., 2007; Cox et al., 2009; Sperry et al., 2010). Body condition can similarly modulate how well an individual can engage in display or fighting behaviour (Huyghe et al., 2005; Poisbleau et al., 2006; Husak et al., 2007), as individuals that are in better physical condition can more readily sustain vigorous behaviour. Research has also focused on whether there are general behavioural traits intrinsic to an individual that would predict the outcome of an agonistic encounter (Øverli et al., 2004; Fox et al., 2009; Dahlbom et al., 2011; David et al., 2011). One such trait is an individual's behavioural reactivity to stimuli or stressful situations, that is, how quickly it responds. Another trait is an individual's persistence in expressing a behavioural response to a challenge.

Behavioural or emotional reactivity has been described as a personality variable or behavioural style in several animals. On one end of this scale,

individuals may be described as ‘bold’ or ‘impulsive’. On the other end, individuals may be described as ‘shy’, ‘docile’, or ‘risk-averse’. Individuals on the ‘bold’ end of the emotional reactivity scale show higher levels of offensive aggression (Huntingford, 1976; Brick & Jakobsson, 2002). Moreover, evidence in a number of species shows that individuals that display bolder or less fearful responses by responding more quickly in general are more likely to be dominants in a social hierarchy (Summers, 2001; Sundstrom et al., 2004; Korzan et al., 2006b; Dahlbom et al., 2011). Consistent with this, males that initiate an agonistic contest more often win (Hsu et al., 2006).

Individuals may in principle be more persistent or vigorous in their behavioural responses whether or not they are quicker to respond. Visual and vocal agonistic displays are energy intensive behaviours, as is fighting itself. It therefore makes sense that individuals with higher strength or endurance would have an advantage in such contests as they would be able to sustain their behavioural responses to a greater degree. In various species of lizards, males that ranked higher on measures of locomotor performance including endurance and speed (Garland et al., 1990; Robson & Miles, 2000; Perry et al., 2004; Huyghe et al., 2005), or bite force (Henningsen & Irschick, 2012) were more likely to become dominant in dyadic encounters.

Reactivity and persistence are not mutually exclusive. Koolhaas et al. (1999, 2007, 2010) synthesized ideas about behavioural response types by contrasting ‘proactive’ with ‘reactive’ coping styles. Proactive individuals show rapid and active behavioural responses to challenging or stressful situations, whereas reactive individuals show more passive responses, with freezing, immobility, or avoidance as predominant behavioural reactions. Proactive individuals might therefore be expected to display faster and more vigorously in agonistic encounters, as they generally respond both more readily and more vigorously to a challenge (Summers, 2001; David et al., 2011). Nevertheless, impulsiveness and persistence each predict a different pattern of agonistic displays during a contest. If impulsiveness is a better predictor of winning a social contest, the individual that responds first would more likely become the dominant individual. If persistence is a better predictor, the individual that responds with longer or more displays would more likely become the dominant individual. Furthermore, if behavioural patterns reflect an intrinsic quality or trait of the animal, we would predict significant correlations within an individual in either the amount of behaviour or latency across different displays.

We examined this using staged aggressive encounters leading to dominant–subordinate status in the male green anole lizard, *Anolis carolinensis*, to determine what patterns of behaviour during an agonistic interaction predicted the outcome of the encounter. *Anolis* lizards have been the subject of studies into animal aggression for many years (Greenberg & Noble, 1944; Crews, 1975). Endocrinological and neural correlates of anole aggression and social status are well-documented in both green and brown (*Anolis sagrei*) anoles (Adkins & Schlesinger, 1979; Tokarz, 1987; Greenberg & Crews, 1990; Baxter et al., 2001a, b; Korzan et al., 2001, 2006a; Yang & Wilczynski, 2002, 2003; Watt et al., 2007; Yang & Wilczynski, 2007; Cox et al., 2009; Kabelik et al., 2013, 2014) as are many aspects of their behaviour (Jenssen & Nunez, 1998; Yang et al., 2001; Lailvaux et al., 2004; Jenssen et al., 2005, 2012; Lailvaux & Irschick, 2007; Garcia et al., 2012, 2014). Males express a set of stereotyped displays during agonistic encounters with other males (Crews, 1975; Greenberg & Crews, 1990; Decourcy & Jenssen, 1994; Lovern & Jenssen, 2003). When paired in experimental laboratory tests, males readily form dominant–subordinate relationships after 30–90 min of behavioural interaction. In laboratory settings, the dominant–subordinate relationship is stable for several weeks with few if any further fights or overt challenges occurring once the contest is settled (Yang et al., 2001; Forster et al., 2005; Korzan et al., 2007). The interactions leading to the dominance hierarchy typically begin with stereotyped displays, and may escalate to chasing and, occasionally, fighting. Colour changes accompany behaviours and include both changes to overall body colouration and the expression of a black postorbital ‘eyespot’ located on the side of the head (Greenberg & Crews, 1990; Summers & Greenberg, 1994; Korzan et al., 2000; Yang et al., 2001; Greenberg, 2002).

Although it is assumed that some aspects of the anole agonistic displays are the basis for determining winners (who become dominant individuals) and losers (who become subordinates) the overall pattern of displays leading to social status has never been analysed. The one exception is that Korzan et al. (2000, 2002) reported that the male that first expressed the eyespot was more likely to eventually win the interaction and become the dominant male in the dyad. Plavicki et al. (2004) reported a similar result. Korzan et al. (2006b) also reported that the duration of eyespot expression was longer in the males that eventually became dominant, and the latency to begin aggressive displaying was shorter. Studies in other anole species suggest that persistence and the amount of behaviour expressed factor into winning dominant

status (Stamps & Krishnan, 1995, 1998; Simon, 2011; Garcia et al., 2012). We extended these previous findings by monitoring the display components of paired male *Anolis carolinensis* as they first interacted and established a dominant–subordinate relationship. We tested whether responding faster, responding more persistently, or both, across some or all display components differentiated individuals that would eventually become the dominant from those that become subordinate members of the pair. We also examined if the patterns of rapidity and persistence were correlated within individuals. Finally, we examined whether individuals were consistent over the different components of their agonistic display. Such reliability across display components would be expected if individuals had intrinsic behavioural styles influencing their displays.

2. Methods

2.1. Study animals

Adult male and female *Anolis carolinensis* were obtained from Charles Sullivan (Nashville, TN, USA). Males' mean \pm SE snout–vent length was 6.30 ± 0.048 cm, and mean \pm SE body weight was 5.98 ± 0.113 g. Upon arrival, anoles were immediately placed in a 10 gallon (37 l) aquarium tank separated into two compartments with an opaque wooden divider in the middle. Anole males were singly housed along with a female anole on each side of the aquarium divider. Housing with a female was done to provide a more natural social and territorial environment, which our experience indicates helps to maintain males in a more socially-responsive state. Each aquarium was covered with a mesh screen lid and the entire bottom was covered with peat moss. The peat moss was misted a minimum of twice per day. Each side of the divider had a Petri dish that contained water, as well as an artificial plant and a single wooden rod positioned diagonally from the bottom of the aquarium to one upper corner to serve as a perch. A 50-watt heat lamp that hung in front of every aquarium provided heat for basking, and a UVA bulb was suspended above each tank with lights on a 14L:10D cycle. Ambient daytime room temperature was set at 26–28°C. During the course of the behavioural experiments, the anoles were fed 3 times a week using crickets fed with calcium-enriched Fluker's cricket food. Anoles were housed for a two-week minimum acclimation period before being used in the behavioural study. All housing and experimental procedures were approved by the Georgia State University IACUC (Protocols A06051 and A09040).

2.2. Aggressive displays and colour changes

Green anole aggressive displays consist of several different movements and postures that can be expressed in various sequences (Greenberg & Noble, 1944; Decourcy & Jenssen, 1994). Anoles express three different types of head bobs during male–male interactions (A, B and C). In our animals, males generally produced A Bobs more often and before B and C Bobs. Head bobs consist of a pattern of rapid up and down head movements which can occur alone or along with a dewlap extension. Each head bob pattern is broken out into 3 phases based on duration: S1 and S2 and S3, occurring at 0–1 s, 1–2 s and 2–3 s, respectively. The S1 phase distinguishes the head bob types. Bob A consists of 3 quick bobs with two inter-bob pauses, Bob B consists of two bobs and one inter-bob pause, and the S1 phase of Bob C consists of one long bob with no pause until the S2 phase begins. For all bob types (A, B and C), the S2 and S3 phases are similar with two quick bobs and two pauses in S2 and then a series of one to nine quick bobs with declining amplitude in S3. Dewlap extension occurs when the specialized throat fan, or dewlap, is extended and held extended for several seconds. A pushup occurs when the head is held stiffly and the entire body is moved up and down by rhythmic extensions of the front legs. Dewlap displays and head bobs often include some push-up like behaviour. In our data recordings, we only counted push-ups as a separate measure when they were performed alone without coincident dewlap extension or head bob, and did not distinguish between dewlap and head bob displays that did and did not include push-up behaviour. A lateral display occurs when a male flattens his body dorso-ventrally, which increases its size from a side view. A sagittal crest along the ridge of the back may be raised during a lateral display. Anoles can intersperse their displays with less stereotyped behaviours including open mouth, in which the anole has his head bent sideways while simultaneously having his jaws widened (Greenberg, 1944). Occasionally males will engage in nipping or biting an opponent. The male will also chase or push opponents, defined in our data as wrestling.

There are also colour changes that occur during social interactions. The body colour of undisturbed anoles is usually bright green. Body colour can change from green to green-brown, light-brown, dark brown, to, in rare instances, black (not observed in our animals). Green anoles have a specialized patch of skin on the side of the head caudal to the eye that contains cate-

choline sensitive melanophores. This eyespot turns black in a variety of stressful situations, including aggressive contests.

2.3. *Experimental procedure*

The data were collected June, July and August 2007, 2008 and 2009. Prior to confrontation, male anoles were transferred to a neutral 10-gallon aquarium similar to their living quarters without the peat moss and Petri dish. Females were not present in the test aquarium. An opaque divider separated the aquarium into two equal sized compartments. One 50-watt bulb rested above the mesh screen in the middle of the aquarium to provide light and heat. Overhead lights in the room were turned off for observations. Two males were picked with a maximum mass difference of 1.5 g and a snout-vent length (SVL) difference of up to 4 mm though most were within 1 mm; these measurements were recorded prior to confrontation. Each male was placed on one side of the aquarium. Anoles were given approx. 5–10 min to acclimatise to this new tank and observations did not begin until both anoles had a steady respiration rate and were not moving rapidly around the aquarium compartment.

After acclimation, the divider was removed allowing the two male anoles to be exposed to each other. Males remained together for 90 min. This period was chosen based on previous work indicating that this was the maximum time needed for males to resolve their agonistic contest. Two observers sat on either side of the aquarium and recorded data on behavioural displays as they occurred for the entire 90-min duration of the confrontation. A video camera was used to record the behaviours for later off line, finer analysis as well. Observers manually recorded the data in Stopwatch+ Software (Center for Behavioural Neuroscience) on a laptop computer as each behaviour happened. The Stopwatch+ Software system allows behaviours and other variables to be preloaded into the software. Each behaviour in the software was assigned a pre-designated key that was pressed on the laptop keyboard to record the occurrence of the behaviour. We recorded the following behaviours: Bob A, B, C, dewlap extension, pushups, lateral display, open mouth displays, nips and wrestles. We also recorded body colour transition (from green to a dark brown/black colour; all males started the confrontation period with a bright green colour) and post-orbital eyespot darkening. We recorded the latency to the first expression of an individual display, the number of times the individual display occurred, and if warranted, the duration of the display. If an individual did not express a particular behaviour, a count

of 0 and a latency of 5400 s were entered. The same data were collected in all years, with the exception that in 2007 nips, wrestles and lateral displays were not recorded.

The paired males exchanged displays and engaged in chasing and other behaviours for a variable amount of time before winners (dominants) and losers (subordinates) became obvious. Dominant males were those that continued to produce display behaviour (dewlap and pushup displays) after their opponent ceased, moved away from the dominant male, and assumed a more crouched body position. Subordinates continued to avoid an approaching dominant after all displays ceased. Dominants also occupied a higher position on the wooden perch in the aquarium. The end of mutual displays and subsequent differentiation of behaviour generally happened within 60 min, although some males continued to exchange displays for the entire 90 min. Regardless of the time dominance was established, we recorded behaviours over the entire 90 min. At the end of the 90 min observation period, the dominant/subordinate status of each individual was noted and the males were returned to their home aquaria.

Four pairs of males did not resolve their dominance status within the 90 min interaction period and were not included in the analysis. Data were therefore obtained from 29 paired males, yielding 29 dominant and 29 subordinate males that interacted and formed unambiguous dominant–subordinate pairs at the end of the interaction. In some instances, recording errors for a particular behaviour occurred. In those cases, data for that behaviour from both members of the pair were discarded, as this prevented their use in paired *t*-tests.

2.4. Statistical analysis

Statistical analyses were run on the data summed across the 90 min observation period on the combined observations from 2007–2009 using Graph-Pad Prism software. Because males interacted during the observation period the behaviours cannot be assumed to be independent. We therefore used Wilcoxon matched-pairs signed rank test to assess mean differences for each display and colour measure. A nonparametric approach was used as most of the data were not normally distributed. Two tailed tests were performed in all cases with $p < 0.05$ considered significant. We employed False Discovery Rate (FDR) methods (Benjamini & Hochberg, 2000; Benjamini et al., 2006; Pike, 2011) to correct for multiple comparisons using the Two-Stage

Sharpened method. These methods are less conservative than Bonferroni methods, but have greater power and minimize Type II error (Pike, 2011). FDR-adjusted p values are reported throughout.

Linear regressions were performed to assess the relationship between individuals' latency and behavioural counts and between latency and behavioural durations. Regressions were assessed across the combined dominant and subordinate measures, as well as within the set of dominants and the set of subordinates for that measure. For all behaviours and colour changes measured, at least some individuals did not express the behaviour and were given a latency of 5400 s and a score of 0. Inspection of the data indicated that this may have skewed the distribution and affected the regressions. We therefore also calculated regressions including only individuals in which both members of the interacting pair expressed the behaviour or colour change. Correction for multiple comparisons was done using the FDR methods as above, and FDR-adjusted p values are reported. Finally, we constructed correlation matrices to determine the degree to which display counts, latencies, and (where appropriate) durations were related within individuals in order to assess how well performance on one variable predicted performance on others. All males (both dominant and subordinate) were included in the correlation matrices.

For both behavioural characters and colour changes (including eyespot formation) we separated the data into measures of the amount of display (counts and durations) and measures of the latency to produce the display. Data were summarized in tables as means \pm SEM, with $N = 29$ dominants and 29 subordinates unless otherwise indicated.

3. Results

3.1. Behavioural characters: Counts and durations

Behaviour was highly variable across individuals. However, there was a consistent pattern across the data showing that males that eventually become dominant had higher numbers (Table 1) or durations (Table 2) of nearly all behaviours measured, with the only exception being Pushup Counts; pushups without head bobs were rarely observed in either males that became dominant or subordinate. The mean difference between future dominants and future subordinates was not significant for Bob C counts ($p = 0.076$),

Table 1.
Behavioural measures: Number of times each display behaviour was expressed during the 90 min interaction in males who became dominant or subordinate.

Behaviour	Dominants			Subordinates		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
Bob A*	35.03	4.54	29	19.62	5.36	29
Bob B*	10.86	2.58	29	5.07	1.58	29
Bob C	5.14	1.39	29	3.34	1.51	29
Dewlap*	19.07	2.60	29	9.79	3.73	29
Pushup	1.76	0.88	29	2.10	1.46	29
Open Mouth*	3.52	1.14	29	1.17	0.42	29
Lateral Display*	3.57	0.66	21	1.81	0.53	21

* Significantly higher in dominants.

pushup counts ($p = 0.360$), or open mouth duration ($p = 0.282$; all FDR-corrected p -values). Because nips and wrestling were observed in only four males (two future dominants, two future subordinates, not paired with each other) we did not perform a statistical test on those data. Analysis of the remaining behavioural data summed over the course of the 90 min observation time showed that during the agonistic interaction the males that became dominant had significantly higher average Head Bob A ($p = 0.012$) and B counts ($p = 0.030$) (Figure 1). Bob C counts were lower and more variable across both classes of males and the difference did not reach significance ($p = 0.076$). Future dominants also had a higher number of dewlap extensions ($p = 0.008$) (Figure 2). Total dewlap duration during the 90 min interaction was also higher in future dominants ($p = 0.0001$). Future dom-

Table 2.
Behavioural measures: Total duration (s) of each display behaviour expressed during the 90 min interaction in males who became dominant or subordinate.

Behaviour	Dominants			Subordinates		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
Dewlap*	56.61	7.43	29	21.53	5.82	29
Open Mouth	8.75	2.96	29	7.65	3.63	29
Lateral Display*	2525.34	409.58	21	1209.58	312.94	21

* Significantly higher in dominants.

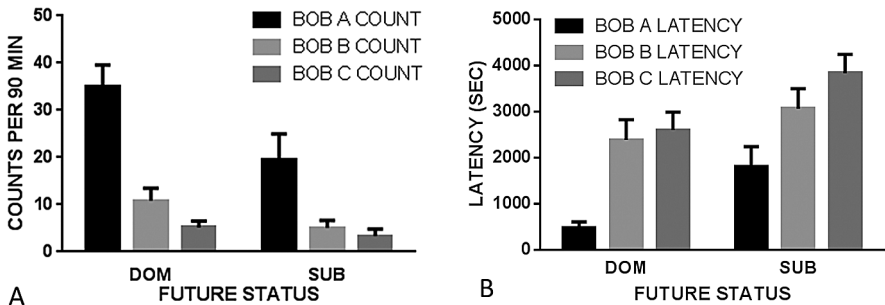


Figure 1. Head bob counts and latencies. (A) Numbers (mean \pm SEM) of Head Bobs A, B and C expressed in future dominants and subordinates during the 90 min observation period. (B) Latency (mean \pm SEM) to first express Head Bobs A, B, and C in future dominant and subordinate male anoles. Bob A data are shown in black, Bob B in light grey and Bob C in dark grey.

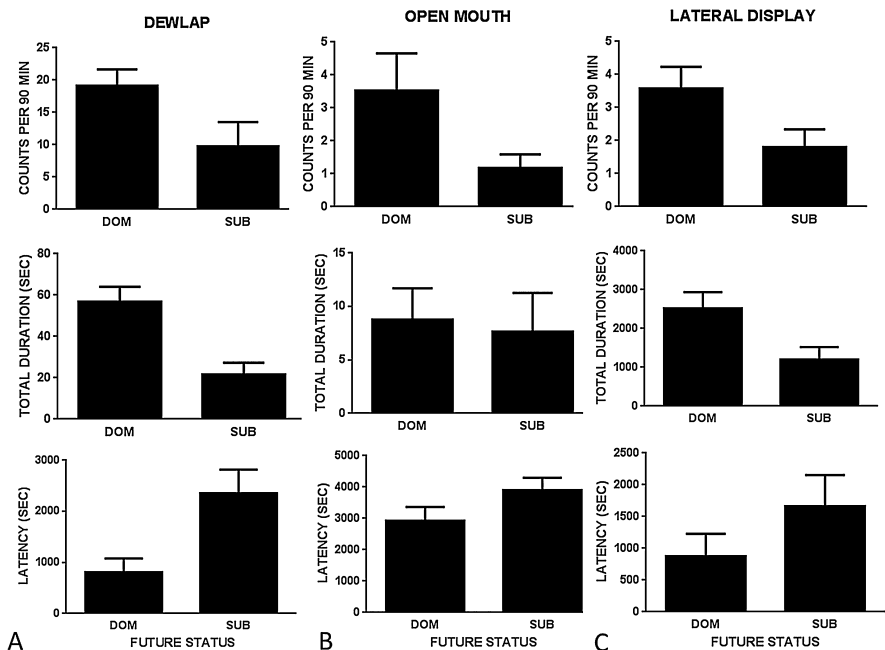


Figure 2. Durations and latencies of behavioural displays. From top to bottom, number over the 90 min observation period, total duration, and latency to first express the behaviour for three behavioural displays in future dominant and subordinate male anoles: (A) dewlap extension; (B) open mouth display; (C) lateral compression display. All graphs show mean \pm SEM.

inants also had significantly higher open mouth counts ($p = 0.003$) (Figure 2). Finally, future dominants had significantly higher lateral display counts ($p = 0.041$) and durations ($p = 0.012$; all FDR-adjusted p -values) than future subordinates (Figure 2).

3.2. Behavioural characters: Latencies

When latencies were compared between future dominants and future subordinates using all the data, future dominants expressed the first instance of all measured behaviours faster, on average, than did future subordinates (Table 3). Mean latencies were significantly different for Bob A ($p = 0.045$) and Bob C ($p = 0.015$), but not Bob B. Dewlap latency was also significantly shorter in future dominants ($p = 0.031$) (Figure 1) as was open mouth display latency ($p = 0.015$; all FDR-adjusted p -values) (Figure 2). Latency differences were not significantly different for Bob B, pushups, or lateral displays (Figure 2).

For each behaviour, several individuals did not perform the behaviour and were therefore given a latency of 5400 s. These were often males that eventually became subordinate, but this was not always the case. For example, many individuals never expressed an open mouth display but still became dominant males. Nevertheless, different proportions of nonperforming males in the two social groups may influence overall means differently. Although the mean latency differences remain indicative of some type of group difference, they may obscure what happens when both members of an interacting

Table 3.
Behavioural measures: Latency (s) to the first instance of each display behaviour after introduction in males who became dominant or subordinate (includes all males observed).

Behaviour	Dominants			Subordinates		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
Bob A*	486.72	117.90	29	1814.12	427.85	29
Bob B	2389.05	438.31	29	3065.05	435.07	29
Bob C*	2603.94	390.93	29	3838.88	408.71	29
Dewlap*	813.59	261.51	29	2356.32	459.37	29
Pushup	4062.53	386.61	29	4132.16	375.62	29
Open Mouth*	2936.06	430.49	29	3906.77	392.47	29
Lateral Display	875.12	355.47	21	1661.18	494.58	21

* Significantly shorter in dominants.

Table 4.

Behavioural measures: Latency (s) to the first instance of each display behaviour after introduction in males who became dominant or subordinate (includes only pairs in which both males expressed the behaviour).

Behaviour	Dominants			Subordinates		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
Bob A	523.43	151.91	21	448.07	125.22	21
Bob B	873.04	301.28	14	1219.53	368.69	14
Bob C	1156.86	289.69	9	894.12	192.01	9
Dewlap	516.32	1789.34	16	499.76	169.33	16
Pushup	916.14	440.90	5	1446.06	589.80	5
Open Mouth	742.73	135.32	3	1872.80	892.58	3
Lateral Display	356.90	142.73	3	124.13	93.35	3

pair compete against each other using the same behaviour. To address this situation, we compared latencies for each behavioural character only in individual pairs in which both males expressed the behaviour (Table 4). In all such comparisons, there were no significant differences in mean latency. We note that in some cases the number of pairs was very low, which may have accounted for the loss of statistical significance. However, future dominant male mean latency was lower in only three behaviours (Bob B, pushup and open mouth) indicating no clear trend in the latencies when both males displayed.

3.3. Colour changes: Eyespot

Eyespot data are found in Table 5 and Figure 3. During the 90 min interaction many, but not all, males expressed a black postorbital eyespot, either once or multiple times (i.e., the eyespot would appear, fade, then reappear later in the interaction). In 5 of the 29 interacting pairs, neither male expressed an eyespot, in 7 only the future dominant expressed it, and in 2 only the future subordinate expressed it. Overall, the mean number of eyespot expressions was 1.62 ± 0.35 for future dominants and 0.93 ± 0.23 for future subordinates, with future dominants having more instances of eyespot expression during the interaction in 12 of the 29 pairs. The mean difference was not significant, although the *p* value was close to significance ($p = 0.057$). As with the number of eyespot expressions, the total duration of eyespot presence was longer in future dominants, but not significantly so ($p = 0.077$). Future

Table 5. Colour measures: Number of times each colour change was expressed during the 90 min interaction; total duration (s) of each display behaviour expressed during the 90 min interaction in males; and latency (s) to the first instance of each colour change after introduction in males who became dominant or subordinate.

Colour variable	Dominants			Subordinates		
	Mean	SE	N	Mean	SE	N
Eyespot count	1.62	0.35	29	0.93	0.23	29
Eyespot duration	1363.9	312.18	29	727.15	193.97	29
Eyespot latency (all males)	2181.9	431.80	29	2845.66	449.91	29
Eyespot latency (when both males expressed eyespot)	679.71	271.97	13	588.55	197.69	13
Light brown count*	0.81	0.23	27	2.07	0.30	27
Light brown duration	252.34	124.82	27	977.09	200.98	27
Light brown latency	3680.9	419.12	27	2045.51	357.39	27
Dark brown count*	0.22	0.12	27	1.26	0.23	27
Dark brown duration*	169.99	89.92	27	1446.32	330.73	27
Dark brown latency*	4736.66	292.77	27	2797.83	419.55	29
Green duration*	4489.50	253.61	29	1991.37	283.79	29

Includes all males observed unless otherwise indicated.
* Significantly different in dominants vs. subordinates.

dominants had longer eyespot durations than the future subordinate in their dyad in 14 of the 29 pairs.

Latency to first produce an eyespot was not significantly different in future dominants and future subordinates ($p = 0.197$; all FDR-adjusted p -values). Within pairs, future dominants expressed their eyespot first in 12 of 29 pairs.

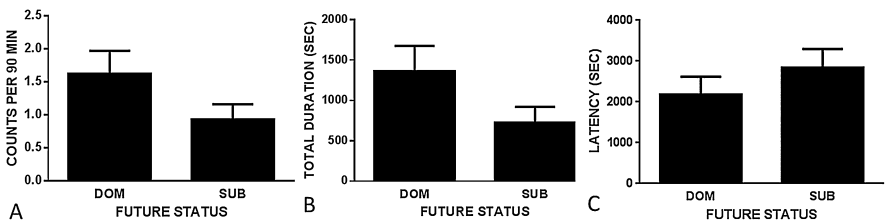


Figure 3. Eyespot expression in future dominant and subordinate male anoles. (A) Number expressed over the 90 min observation period; (B) total duration of eyespot presence; (C) latency to first express the eyespot.

3.4. Colour changes: Body colour

Body colour data are summarized in Table 5. Both males in the interacting dyad started with a green body colour. Many of the males that eventually became dominant maintained this green colour throughout the interaction (17 of 29 future dominants). As a result, the mean duration of green body colour was significantly longer for future dominants than for future subordinates ($p = 0.0001$) (Figure 4). For the other interacting animals, particularly those that eventually assumed subordinate status, males could change in and out of various shades of brown. We statistically assessed instances of light brown and dark brown body colours. Future subordinates had significantly more switches to light brown body colour ($p = 0.009$), first changed to this body colour with a shorter latency ($p = 0.015$), and maintained this colour for a longer duration ($p = 0.005$) (Figure 4). The same pattern was seen for Dark Brown body colour (Figure 4), which is the darkest brown colour we observed, with number of switches ($p = 0.001$), latency to adopt this colour ($p = 0.002$) and duration in this colour ($p = 0.003$; all FDR adjusted p -values) all being significantly different between status classes. As the means and durations suggest, very few future dominants changed to a dark brown colour, and then only very briefly. After the interaction, those males who had become subordinate generally maintained a brown body colour of some shade.

3.5. Relationship between latency and display/colour characters

To determine whether or not the amount of behavioural displays (counts or durations) that an individual produced was related to how quickly it first

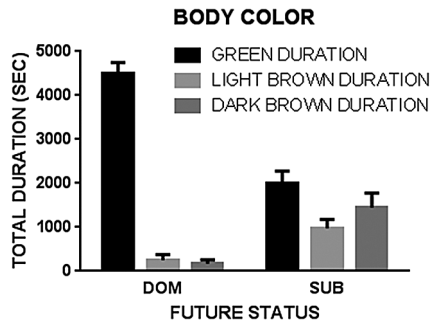


Figure 4. Body color duration. Durations of green, light brown and dark brown body colours during the 90 min observation period in future dominant and subordinate male anoles. Bars indicate mean \pm SEM.

expressed that behaviour, regressions were run between latency and count and duration (where measured) for all behaviours analysed above. When all data were included in the regressions, and regressions were calculated across future dominant and subordinate animals combined, there were significant negative relationships between the amount of behaviour and the latency to express that behaviour in all cases. The same was true when regressions were calculated separately for future dominants and future subordinates with the single exception of Head Bob A in dominants, where the regression fell just short of significance ($r^2 = 0.116$, $p = 0.074$). Inspection of the data suggested that the significant regressions may have resulted from skewed distributions caused by the inclusion of individuals that had a score of 0 for count or duration and therefore a latency of 5400 s. We therefore ran all regressions including only individuals from interacting pairs in which both males expressed the behaviour. In that case, regressions between latency and behavioural measures either across future dominants and subordinates combined or within just future dominants or subordinates were rendered non-significant with the exception of Bob C, which maintained a significant negative relationship between counts vs. latency for all males ($r^2 = 0.25$, $p = 0.04$; $N = 18$). The negative relationships between Bob A counts vs. latency for all males ($r^2 = 0.68$, $p = 0.097$; $N = 42$) and for future dominants ($r^2 = 0.17$, $p = 0.062$, $N = 21$; all FDR-adjusted p -values) approached significance.

Similar results were found for eyespot displays. Significant negative regressions were found for both eyespot count and latency for future dominants and future subordinates combined, as well as within dominants and subordinates separately. These regressions were non-significant when using only males from pairs in which both individuals displayed an eyespot. The same was found for regressions of latency against light brown body colour measures. Regressions for dark brown body colour were not performed as too few future dominants (3) expressed this colour.

3.6. Intercorrelations among variables

Correlation matrices (Tables 6–8) indicated a high degree of consistency within individuals in the expression of different aspects of their behavioural and colour (eyespot) displays during the interaction. For the correlation matrix including counts for all behaviours analysed above plus eyespot expression, most showed significant positive correlations with the main exception

Table 6.
Correlations (r values) among display behaviour and eyespot counts.

	Display component							
	Bob A	Bob B	Bob C	Dewlap	Pushup	Open mouth	Lateral display	Eyespot
Bob A		0.736457*	0.416230*	0.733838*	0.500106*	0.356667*	0.377436*	0.489222*
Bob B	0.736457*		0.469406*	0.474535*	0.287765*	0.337123*	0.429106*	0.423388*
Bob C	0.416230*	0.469406*		0.157298	0.236897*	0.168136	0.389463*	0.465075*
Dewlap	0.733838*	0.474535*	0.157298		0.700198*	0.197172	0.568795*	0.405368*
Pushup	0.500106*	0.287765*	0.236897*	0.700198*		−0.00266	0.514552*	0.384018*
Open mouth	0.356667*	0.337123*	0.168136	0.197172	−0.00266		0.172791*	0.585702*
Lateral display	0.377436*	0.429106*	0.389463*	0.568795*	0.514552*	0.172791*		0.625576*
Eyespot	0.489222*	0.423388*	0.465075*	0.405368*	0.384018*	0.585702*	0.625576*	

* Significant at $p < 0.05$.

Table 7.
Correlations (*r* values) among display behaviour and colour durations.

	Display component					
	Dewlap	Lateral display	Eyespot	Light brown	Dark brown	Green
Dewlap		0.365626*	0.298782*	−0.15748	−0.47255*	0.424926*
Lateral display	0.365626*		0.477384*	−0.31571*	−0.38424*	0.471865*
Eyespot	0.298782*	0.477384*		−0.09353	−0.26828*	0.290663*
Light brown	−0.15748	−0.31571*	−0.09353		0.167489	−0.62444*
Dark brown	−0.47255*	−0.38424*	−0.26828*	0.167489		−0.69953*
Green	0.424926*	0.471865*	0.290663*	−0.62444*	−0.69953*	

* Significant at *p* < 0.05.

that open mouth counts did not correlate significantly with most other display behaviour counts. For those display and colour variables for which we obtained duration measures (dewlap extension, lateral display, eyespot expression, light brown, dark brown and green), there were many significant correlations. Behavioural displays and eyespot durations were positively correlated with each other and with the duration of green body colour; they were negatively correlated with brown body colour durations. Latencies among all display variables were also significantly and positively intercorrelated, with the exception that latency to perform a lateral display did not significantly correlate with other display latencies except for Head Bob A, open mouth, and eyespot latencies.

4. Discussion

This study presents a comprehensive analysis of the behavioural and colour display patterns that distinguish future dominants and future subordinates during the critical agonistic interaction that determines winners and losers of a social contest. The most consistent finding is that individuals who eventually won and became dominant were more vigorous in their behavioural displays. They showed significantly higher mean counts and durations for nearly all of the display components measured. No mean count or duration was higher in future subordinates than dominants, and only Bob C counts,

Table 8.
Correlations (r values) among display behaviour and eyespot latencies.

	Display component							
	Bob A	Bob B	Bob C	Dewlap	Pushup	Open mouth	Lateral display	Eyespot
Bob A		0.500067*	0.401203*	0.683996*	0.281006*	0.433502*	0.477236*	0.458155*
Bob B	0.500067*		0.59668*	0.493702*	0.434876*	0.500796*	0.177135	0.447752*
Bob C	0.401203*	0.59668*		0.374656*	0.362652*	0.489981*	0.263953	0.540346*
Dewlap	0.683996*	0.493702*	0.374656*		0.343308*	0.455673*	0.266062	0.356587*
Pushup	0.281006*	0.434876*	0.362652*	0.343308*		0.291902*	0.25288	0.351467*
Open mouth	0.433502*	0.500796*	0.489981*	0.455673*	0.291902*		0.302108*	0.477082*
Lateral display	0.477236*	0.177135	0.263953	0.266062	0.25288	0.302108*		0.427658*
Eyespot	0.458155*	0.447752*	0.540346*	0.356587*	0.351467*	0.477082*	0.427658*	

* Significant at $p < 0.05$.

pushup counts and open mouth durations were not statistically significantly greater in future dominants. These behaviours were the least frequently expressed. These results strongly support the hypothesis that males that produce more display behaviour, and produce it more persistently, are more likely to emerge as social dominants.

Theoretical ideas about the nature of displays often consider them to be honest signals of an individual's general behavioural or physiological capacity (Andersson, 1994; Smith & Harper, 1995, 2003; Hurd, 1997; Searcy & Nowicki, 2005; Arnott & Elwood, 2009). In terms of aggressive displays, the argument would be that the display communicates an individual's capacity for fighting or holding resources (Wagner, 1994; Whiting et al., 2006; McGlothlin et al., 2008; Elwood & Arnott, 2012; Fawcett & Mowles, 2013). Our results are consistent with this in the simplest form. More numerous and persistent behavioural displays could directly indicate an individual with more endurance or strength. In this view, it is not the form of the behaviour, but the amount of it, that is the key signal determining the outcome of the interaction. One way to test whether the vigour of the behavioural displays represents an honest signal of a male's physical capacity is to assess whether they correlate with measures of other behaviours. This has not been done in green anoles. However, there are numerous studies in lizards and other taxa that show enhanced physiological capacity as indicated by performance in locomotor tasks or other non-social situations does predict the outcome of aggressive social interactions (Garland et al., 1990; Robson & Miles, 2000; Perry et al., 2004; Huyghe et al., 2005). Our results predict that such individuals would produce more display behaviour, and conversely predict that the winners in our experimental paradigm would test better on more general assessments of behavioural or physiological vigour.

The latency data we obtained are more difficult to interpret. When comparisons were made using all individuals, mean latencies to first express a behaviour were lower for future dominants in all cases, although not significantly so for Bob B, pushup and lateral display. For all behaviours, however, more future subordinates than future dominants did not show the behaviour at all, and thus were assigned the maximum latency of 5400 s. The statistical latency differences might therefore largely reflect differences in the proportion of individuals that expressed the behaviour rather than how quickly males produced the behaviour when they did show it. Latency would then be meaningful as an indicator that future subordinates were on average less

responsive to other individuals, that is, how reticent they were to display. If this were the case, it could be that when only the ‘boldest’ individuals are paired and both produced a display, the predictive value of latency differences would emerge. We therefore also compared latencies in future dominants and subordinates only when both produced that display component during the agonistic interaction. In these comparisons, no latency difference was statistically significant, and in only three out of seven comparisons (Bob B, open mouth and pushup) were the mean latencies lower for future dominants.

Studies in several species have suggested that individuals that are ‘bolder’ in the sense of responding faster to threats or novel stimuli have an advantage in obtaining dominant social status or winning aggressive interactions (Sundstrom et al., 2004; Dahlbom et al., 2011). This may be the case in male anoles when other factors are equal, but our latency results do not strongly support this. The most conservative interpretation of all the behavioural data is that the amount of behaviour produced, rather than how quickly it is produced, is the better predictor of which male becomes dominant. In this interpretation, when latency differences do appear, they are a reflection of the animal’s greater likelihood to behave, and hence greater amount of behavioural output, during the observation period.

In addition to the behavioural components of the displays, we assessed colour changes, with a particular emphasis on the expression of the postorbital eyespot, which has been argued to be an important sign stimulus in anole social encounters (Korzan et al., 2000, 2002). Our results provide little support for the hypothesis that eyespot expression distinguishes winners and losers in anole aggressive interactions. Individuals could obtain dominant status without showing an eyespot, which occurred in 7 interacting pairs. There was a trend for future dominants to have a greater number of eyespot expressions (FDR adjusted $p = 0.057$) and a longer total duration of eyespot appearance (FDR adjusted $p = 0.077$) than future subordinates. While this gives the impression that the amount of eyespot expression could be important, the fact that neither difference was statistically significant prevents us from accepting that with any confidence. Furthermore, the future dominant expressed an eyespot more often in just 12 of the 29 interacting pairs (including 7 cases where only the future dominant expressed it), and the total eyespot duration was greater in the future dominants in 14 of the 29 pairs. The latency to produce an eyespot was not significantly different in the two

groups, and in only 12 of the 29 pairs did the future dominant express the eyespot first. As with other latency analyses, we examined whether latency differences would emerge in cases ($N = 13$ pairs) where both interacting males produced the signal during their competition. The latency difference between ultimate winners and losers in those contests was also nonsignificant.

Whole body colour changes more reliably differentiated future winners and losers. Males that eventually won contests generally maintained a bright green body colour throughout the contest and into their eventual dominant status. Some future dominants did transition into brown shades during the agonistic interactions, but this was rare and not persistent. Males that eventually lost and became subordinate had more and longer transitions into brown shades during the contest and ultimately settled into a duller and browner shade when they became subordinate. The socially-related colour difference has long been noted (Greenberg et al., 1984; Greenberg & Crews, 1990; Yang et al., 2001; Greenberg, 2002). It is not clear whether body colour carries a signal to other males or is a consequence of losing the contest; both may be true. Brown body colour is controlled by skin melanocytes that are sensitive to circulating catecholamines (Hadley & Goldman, 1969). For that reason, all males can become duller and browner during periods of stress. It may be that acute stress associated with losing an encounter or chronic stress associated with being subordinate is the cause for the colour differences.

If the intrinsic vigour of an individual was responsible for its level of behaviour this should be reflected in the consistency across the behaviours measured. This is in fact reflected in the correlations among display behaviours measured (including eyespot expression) in both the amount of the display (count and duration) and its latency. The one exception was the relatively infrequent open mouth display, where counts did not correlate significantly with many other variables. Similarly, except for lateral display, latencies among display components were highly intercorrelated. As with the analysis of latency differences between social groups, the significant relationship between the amount of behaviour (counts or durations) and latency is difficult to interpret. When a comparison is done with all individuals, including those that did not produce the behaviour and hence were assigned the maximum latency, there are significant negative relationship between latency and all behavioural displays and eyespot expression. However, the

significance again is lost when the analysis is done only with those pairs in which both individuals expressed the display (with one exception, Head Bob C counts). At this point, we can say with confidence that an individual's persistence in one display behaviour predicts its persistence in other display behaviours while remaining cautious in whether the same is true for the quickness in which it starts displaying.

Our study identifies patterns of display behaviours that predict whether an individual will emerge as a dominant in an interacting dyad, but it is important to note that it does not identify how a receiving individual perceives and reacts to those displays. For that reason, our results cannot determine whether some displays are more important than others in signalling aggressive or other characteristics of the displaying male. The vigour with which display elements are produced is intercorrelated among all behavioural and eyespot displays, and all are significantly elevated in males that eventually win contests. It may be, for example, that observers judge their opponents on all display elements together and that the assembly of signals enhances the impact of the behaviour beyond a simple sum of its component parts. Alternatively, one or two behaviours may be signalling a quality such as physical capacity to the observer, but that elevated capacity spills over to increase all elements of the display, including those that carry no meaning to an observer. At this point, only eyespot expression has been experimentally manipulated to discern its meaning to observing males (Korzan *et al.*, 2000). The eyespot studies concluded that decreased latency to produce the eyespot, and persistent eyespot presence were important to males winning aggressive interactions. Our data do not provide strong support for the latency results, but some nonsignificant trends in the eyespot count and duration data are consistent with the idea that the amount of eyespot expression predicts future dominant status. More systematic experimental manipulations of displays are needed to resolve this discrepancy as well as to dissect the roles of other behavioural displays in influencing observers.

It is also important to note that our analysis summed behaviour over the entire 90 min observation period. It is certainly possible that behaviour over a much shorter time predicts the outcome as well, if not better. It is also possible that there is meaningful temporal variation in displays over the course of the encounter and that this is important in determining the outcome. A more fine grained analysis of the time course of agonistic interactions would be valuable extension to the current study.

Koolhaas et al.'s (2007) idea that individuals differ in coping styles is an important one for understanding the outcomes of challenging social encounters such as the agonistic competitions we examined here. Several studies have concluded that individuals with a 'proactive' behavioural style have an advantage in social contests (Øverli et al., 2004; Korzan et al., 2006b; David et al., 2011). In our study, an individual's performance measures were highly correlated across multiple display components, and individuals that displayed more vigorously and persistently won aggressive contests. This is one component of what Koolhaas termed a 'proactive' behavioural style. The second component of a proactive style, responding more rapidly when faced with a challenge, did not seem as important in determining winners, but bears more study. Overall, the results suggest that the more display behaviour a male produces, rather than how quickly it responds, better ensures that the male will win an agonistic competition and become the dominant individual of a social pair.

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