Locomotor performance and social dominance in male *Anolis cristatellus*

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The proximal mechanisms determining social dominance are not well understood. We used the highly territorial lizard *A. cristatellus* to test two main hypotheses: (1) that male social dominance is associated with locomotor abilities; (2) that locomotor abilities (maximal performance), as measured in the laboratory, are correlated with behaviour in the field. In the field, we recorded locomotor behaviours and assertion displays, then characterized microhabitat use and thermal relations. In the laboratory, we measured maximum sprint running speed, endurance and morphometric characters, and assessed dominance by pairing males of similar body size in an experimental arena. In 72 of 77 interactions, one lizard (the 'winner') was unequivocally determined to be dominant over the other (the 'loser'). Winners performed more assertion displays than losers before capture and also had higher endurance in laboratory tests. Although contestants were matched for snout–vent length, winners had significantly deeper and wider heads. However, we found no significant differences in field locomotor behaviours, perch or thermal characteristics, head length, or maximal sprint speed. Our findings support those of previous studies, and extend them in several ways. This is the first demonstration that assertion displays in the field are related to both locomotor performance and laboratory-assessed social dominance. Locomotor performance may directly affect social dominance by allowing some males to perform better in dyadic interactions. Alternatively, both locomotor performance and social dominance may be linked to a common underlying mechanism, such as variation in hormone levels, which are known to affect aggression, locomotor performance and morphology.

The influence of behavioural choices and repertoires on the outcome of agonistic interactions has received considerable attention in recent years (e.g. Andersson 1994; Jenssen & Nunez 1998). However, the behavioural options available to an individual may be constrained by its whole-organism performance abilities and, in turn, by the underlying morphological and physiological traits that determine those abilities (e.g. Arnold 1983; Bennett 1983; Garland et al. 1990a; Garland & Losos 1994; Irschick & Garland 2001). Therefore, the relationship between physiological performance abilities and success in agonistic interactions has also begun to receive attention (Garland et al. 1990b; Chappell et al. 1999; Hammond et al. 2000; Robson & Miles 2000).

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Physiological performance most affects individual fitness when it directly impacts survival or reproduction (Pough 1989; Bennett & Huey 1990). Locomotor performance, the focus of the current study, can directly affect foraging abilities, predator avoidance and reproductive success (references in Garland & Losos 1994; Clobert et al. 2000; Irschick & Garland 2001). We focus on the potential impact of locomotor performance on the ability of male lizards to acquire and control territory. A large number of studies have shown that controlling a territory can have a major effect on Darwinian fitness (reviews in Dewsbury 1982; Ellis 1995), and should thus be under strong selection. However, the processes by which a territory is established remain unclear (Maynard Smith 1982; Stamps & Krishnan 1995, 1998).

Lizards are common models in both behavioural ecology (e.g. Huey et al. 1983; Vitt & Pianka 1994) and locomotor biology (e.g. Gleeson & Harrison 1988; Losos & Sinervo 1989; Garland & Losos 1994; Irschick & Losos 1998; Autumn et al. 1999; Irschick & Jayne 1999; Zani 2000; Irschick & Garland 2001; Vanhooydonck et al.

2001). Interspecific comparisons demonstrate that locomotor performance is related to morphological traits (Bonine & Garland 1999 and references therein) and to activity patterns in the field (Garland 1999).

Many lizard species are territorial, and male dominance is generally considered important in controlling a territory (e.g. Stamps 1997; Sinervo & Lively 1996; Jenssen & Nunez 1998; Stamps & Krishnan 1998). In lizards, two studies have found that locomotor performance ability is positively related to the ability of male lizards to establish social dominance in experimental arenas (Garland et al. 1990b; Robson & Miles 2000). In the field, males with larger territories are likely to enjoy higher fitness, as demonstrated by Haenel et al. (2003a, b) and suggested by Sinervo & Lively (1996). Thus, locomotor performance may be important in determining the Darwinian fitness of male lizards (Stamps 1994). However, the generality of these findings is unclear. First, in the study of Garland et al. (1990b), only speed was a significant predictor of dominance, whereas Robson & Miles (2000) found that both endurance and sprint speed were positive predictors of the outcome of experimental encounters. Second, the species examined, *Sceloporus occidentalis* and *Urosaurus ornatus*, are rather closely related (Reeder & Wiens 1996). Finally, the relationship between laboratory and field measures of dominance is unknown (Robson & Miles 2000).

The goal of the present study was to expand upon previous studies of the relationship between locomotor performance, field behaviour and social dominance. To explore the generality of previous findings, we focused on *A. cristatellus*, a member of an iguanian clade that is only distantly related to *Sceloporus* and *Urosaurus* (Pough et al. 2001). The genus *Anolis* has received much attention, including several studies of factors related to agonistic interactions, such as body size (Tokarz 1985), communication (McMann 1993) and territoriality (Stamps & Krishnan 1995, 1998; Jenssen & Nunez 1998). *Anolis cristatellus* is common on the Greater Puerto Rico Bank (Lazell 1983; Schwartz & Henderson 1991). Only males possess the large body and tail crests that give the species its scientific name (Rivero 1978). Adult male body length is about 1.4 times greater than adult female body length (Fitch 1981). Males defend a territory typically consisting of several trees. Adults of both sexes, as well as the juveniles, show frequent aggression and territoriality, although males are especially combative (MacLean 1982). In *S. occidentalis* and *U. ornatus*, agonistic interactions typically last only a few minutes (Garland et al. 1990b; Robson & Miles 2000). In contrast, male–male agonistic interactions in *A. cristatellus* may last up to an hour, and often leave participants visibly exhausted (G. Perry and K. LeVering, unpublished observations). Such interactions involve pushup displays, dewlap extensions, body compression, biting, head butting, tail lashing and extensive chasing (Ortiz & Jenssen 1982). Interactions tend to be long, rather than rapid. Because agonistic interactions are potentially physiologically taxing, we expected that locomotor performance would be positively correlated with social dominance in this species. More specifically, we hypothesized that social dominance in *A. cristatellus* would be more closely related to endurance than to sprint speed. We also predicted that field behaviours would be positively correlated with locomotor performance and social dominance gauged in the laboratory.

METHODS

To maximize comparability with previous studies, we replicated the methodologies of Garland et al. (1990b) and Robson & Miles (2000) to the extent allowed by differences in the biology of the species. The methods used by McMann (1993) to study dyadic encounters in *A. carolinensis* were used whenever possible. Prior to collection, we conducted behavioural observations of a subsample of randomly chosen individuals. We collected the lizards immediately afterwards. Locomotor performance was measured during the following days, and morphometric measurements were taken at their completion. On the final testing day, prior to release, we measured dominance in an experimental interaction.

Study Animals

In some *Anolis* species, aggression is much more common during the reproductive season (Jenssen et al. 1995). We therefore conducted our work during October, when *A. cristatellus* are reproductively active and aggression is common in all segments of the population. In 1999 and 2000, we collected 224 male *A. cristatellus* for study. Animals were collected by noosing and immediately transported to the field laboratory on Guana Island, British Virgin Islands. Prior to collection, data on field behaviours (see below) were collected for a subsample of 50 adult males.

Of the 224 males collected, 175 exceeded the minimum snout–vent length (SVL) of 47 mm at which secondary sexual characters first appear (Philobosian 1975; G. Perry & K. R. LeVering, unpublished data). Smaller animals were released, and adult males were individually housed in large plastic bags containing wet paper towels to restore moisture lost in transit. Individuals remained isolated for less than 18 h prior to testing.

In the laboratory, each animal was first tested for sprint speed, then for endurance, and finally for social dominance (see below). Morphometric data were obtained following locomotor testing but prior to dominance testing. Depending on the size of the animal, mass was measured to the nearest 0.1 or 0.5 g using a 10-g or 30-g Pesola scale, respectively. Snout–vent length was measured to the nearest 1 mm using a metric ruler. Tail condition can affect the outcome of agonistic interactions (Fox & Rostker 1982; Fox et al. 1990; Martín & Salvador 1993). We therefore measured tail length and the regenerated length of the tail if broken, tail crest length and crest height to the nearest 1 mm using a metric ruler. Finally, we measured head length, width and depth to the nearest 0.1 mm using a calliper and the methods recommended by Goren & Werner (1993), as head dimensions can be correlated with Darwinian fitness in

some lizards (Hews 1990). Following dominance testing, all animals were released at the capture site.

Field Behaviours

For a subsample of 50 males, we recorded measures of locomotor and aggressive behaviour, body and air temperatures, and characteristics of the last-used perch prior to collection. Three measures of field locomotor behaviours were obtained during 10-min observations: number of moves/min, percentage of the time spent moving (Huey & Pianka 1981; Perry 1999) and number of jumps/min (Losos 1990a; Irschick et al. 2000). We also recorded the number of assertion displays/min (Jenssen et al. 1995).

Immediately following capture, we used a Miller and Weber quick-read cloacal thermometer to measure body and ambient temperatures at the last perch to within 0.1 °C. For the last perch used by the lizard, we measured height to within 5 cm, and diameter to the nearest 0.1 mm. To avoid observer effects, a single experimenter (G.P.) collected all field behaviour data. Animals engaged in overt social interactions or thermoregulatory behaviours (e.g. shuttling in and out of sunlight) were omitted from the analysis. In anoles, assertion displays are made without reference to a specific recipient (Jenssen et al. 1995), and were thus not considered to represent an interaction.

Locomotor Capacity

Following collection, we measured locomotor performance in captivity. General testing procedures followed those of previous studies, with multiple tests of sprint speed occurring on a single day and endurance tests conducted on separate days (Garland et al. 1990b; Robson & Miles 2000). Sprint speed, which requires a relatively brief effort, was always tested before endurance, which requires exhausting the animal. Recovery from sprint speed testing is considered to be rapid, with some researchers conducting up to eight such tests in a single day, separated by at least 1 h (e.g. Robson & Miles 2000). Consequently, we follow previous studies in expecting that a rest period greater than 12 h should minimize the impact of sprint speed testing on the results of endurance tests conducted the following day.

We measured sprint speed in 2000 using a computerized racetrack equipped with infrared photocell/receptor stations at 25-cm intervals. Because *Anolis* do not respond well to flat racetracks, we followed previous workers (Losos 1990a; Losos & Irschick 1996; Irschick & Losos 1998) in angling the racetrack and treadmill (see below) at 37°. Repeatability enhances the utility of physiological performance in evolutionary analyses (Chappell et al. 1996; Dohm 2002). To assess the repeatability of laboratory measures of speed, we conducted a preliminary study using an initial sample of 31 lizards. We followed Garland et al. (1990b) in testing sprint speed on two consecutive days. Each lizard was chased up the 2.5-m-long track. The speed measured for the fastest 0.25 m was used as an estimate of maximum sprinting speed. Each lizard was tested in two bouts, conducted on the morning and afternoon of the same day. Each bout included two runs, resulting in a total of four runs each day. Using the fastest 0.25-m interval speed from each day, speed was found to significantly decline from day to day (day 1: 1.50 ± 0.39 m/s; day 2: 1.40 ± 0.47 m/s; Wilcoxon matched-pairs signed-ranks test for repeated measures: $Z = 2.293$, $N = 31$, $P = 0.022$). Moreover, maximal values obtained on the 2 days were significantly and positively correlated (Spearman rank correlation: $r_S = 0.585$, $P = 0.001$; Pearson correlation: $r_{29} = 0.676$, $P < 0.001$). We therefore eliminated the second day of testing for sprint speed.

We measured endurance in both 1999 and 2000, using a portable electric-powered treadmill inclined at 37° as described above. Speed was controlled via a rheostat, and the moving high-traction belt (effective area 50×18 cm) was surrounded on three sides by Plexiglas walls to prevent escape by the lizards. To determine the appropriate speed for distinguishing performance on the treadmill, we first tested groups of six to seven lizards at speeds of 1, 0.5, 0.35, 0.25 and 0.15 km/h. No lizard was tested at more than one speed, and lizards used for this preliminary study were not included in the analyses that follow. Based on these results (Fig. 1), we conducted all further tests of endurance at 0.3 km/h. At this speed, lizards showed a relatively wide variability in endurance time, most of them between 4 and 6 min. This period is long enough to involve substantial aerobic metabolism, yet short enough to allow efficient handling of large numbers of animals. As with speed, we also tested endurance on two consecutive days, using a subsample of 26 lizards. Each lizard was tested to exhaustion, once a day, at a treadmill speed of 0.3 km/h. Endurance measures were highly repeatable ($r_S = 0.871$, $N = 26$, $r_{24} = 0.878$, $P < 0.001$ for both) and did not differ significantly between days (day 1: 240 ± 104 s; day 2: 237 ± 96 s; Wilcoxon matched-pairs signed-ranks test for repeated measures: $Z = 1.283$, $P = 0.20$). To reduce stress on study animals, we therefore also eliminated the second day of testing for endurance and only include the results of the first day of testing in the analyses that follow.

Body temperature greatly affects locomotor performance in ectotherms (e.g. Bennett 1990; Garland 1994; Autumn et al. 1999). The problem is less severe for our study organism, because the body temperature of *A. cristatellus* closely tracks that of their relatively stable environment (Huey & Webster 1976; Hertz 1992). Moreover, the optimal temperature for sprinting is close to field body temperatures (Huey 1983). We have verified this observation on Guana Island (Table 1). Nevertheless, we avoided conducting tests outside normal activity times. As an added precaution, we used a Miller and Weber cloacal thermometer to verify that body temperatures of test animals were within the normal range of field activity temperatures for Caribbean *Anolis* (28–30 °C; Irschick & Losos 1998).

Dominance

From among the larger pool of available males, 77 pairs of *A. cristatellus* were chosen for dominance testing based
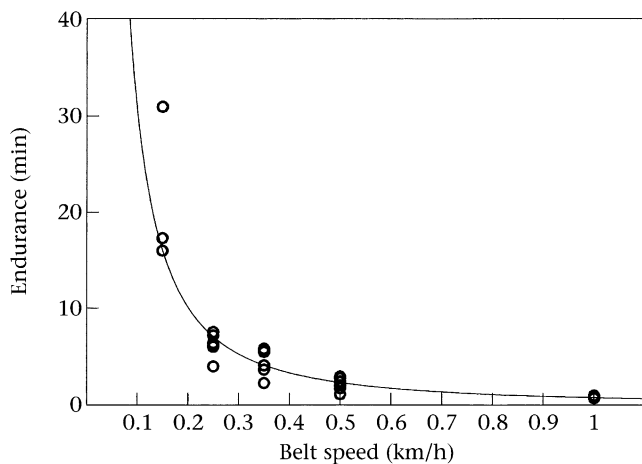
Figure 1. Endurance as a function of belt speed in adult male *A. cristatellus* from the British Virgin Islands. The treadmill was angled at 37°, and each symbol represents a single individual. Endurance can be predicted from belt speed using the equation: endurance $= 0.761 + \text{speed}^{-1.606}$ (Pearson correlation: $r_{26} = 0.96$, $P < 0.001$).

on matches in body size. Body size can strongly influence social dominance in lizards (Fox 1983; Tokarz 1985; Deslippe et al. 1990; Hews 1990; McMann 1993; Carpenter 1995; Molina-Borja et al. 1998). Paired animals were therefore chosen such that their SVLs were within 3 mm of one another. Because tail condition can also affect dominance status (Fox & Rostker 1982; Fox et al. 1990; Martín & Salvador 1993), we did not use as contenders any animals with recently damaged tails. Each lizard was only tested once. To control for possible effects of captivity (e.g. Navas & Gomes 2001), males were paired only with other individuals collected on the same day.

Dominance was tested under neutral conditions similar to the symmetric low-level contests of McMann (1993). Animals were not familiar with the test enclosure or with each other. Contestants were placed in a three-dimensional test enclosure ($120 \times 50 \times 70$ cm, L × W × H), containing a centre perch with a light over it (cf. Garland et al. 1990b; Robson & Miles 2000). Enclosures were made of nylon mesh and had entrances at each end. Placement of lizards at either end was simultaneous and was randomized to avoid location effects. Animals were allowed to interact until resolution was reached, a process that took 1–8 h.

At the end of each interaction, a single experimenter (G.P.) assigned a 'winner' or 'loser' status to each lizard based on posture, location within the cage, and overt signs of aggression. We also followed Fox & Rostker (1982), Garland et al. (1990b) and Robson & Miles (2000) in quantitatively scoring the behaviour of both participants during the interaction. For each interaction, a range of behaviours was recorded during at least 30 min and up to 1 h. Measurements occurred during active interactions between contestants. Because some interactions occurred slowly, longer observations were sometimes used to better represent the behavioural repertoire displayed. Aggressive behaviours, identified based on McMann (1993) and Leal & Rodríguez-Robles (1995, 1997), were assigned positive scores, whereas submissive behaviours were assigned negative ones. Pushups and dewlap extensions were assigned a weight of 0.5. Performing lateral displays (Leal & Rodríguez-Robles 1995, 1997), and chasing and biting an opponent each received a score of 1. Crouching (Leal & Rodríguez-Robles 1995) and escape merited a score of −1. Following the interaction, a single numerical score, summing all observed agonistic behaviours, was computed for each contestant.

In the statistical analyses that follow, all comparisons were made within dyads of interacting individuals. Recording was carried out, by a single observer not aware of individual endurance measurements, for both contestants simultaneously. If more than 3 h passed with no interaction between the lizards ($N = 5$), the dominance trial was terminated and the data were omitted from the

Table 1. Measures of behaviour and microhabitat use for a subsample ($N = 50$) of adult male *A. cristatellus* in the British Virgin Islands

Parameter	Winners ($N = 17$)				Losers ($N = 17$)				Z	P
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD		
Activity levels										
Moves/min	0.2	0.0	0.9	0.31	0.4	0.0	1.8	0.53	0.94	0.35
% Time moving	0.5	0.0	2.5	0.79	0.6	0.0	2.0	0.77	0.53	0.59
Jumps/min	0.02	0.0	0.2	0.05	0.08	0.0	0.5	0.15	1.71	0.09
Displays/min	0.2	0.0	1.0	0.28	0.05	0.0	0.4	0.13	1.78	0.037
Thermoregulation										
T_a (°C)	29.7	26.6	32.6	1.7	29.6	26.6	32.6	1.5	0.19	0.85
T_b (°C)	28.6	24.8	32.4	2.2	28.3	26.1	33.0	1.7	0.36	0.72
Perch characteristics										
Height (cm)	141	35	600	246	85	25	135	37	1.19	0.23
Diameter (mm)	346	31	2000	546	231	43	2000	445	0.59	0.55

T_b: body temperature. T_a: ambient temperature. Values for winners and losers, determined in subsequent laboratory tests, were compared using the Wilcoxon matched-pairs signed-ranks test. *P* values were two tailed except for assertion displays/min, where the prediction was for winners to have a higher value. Data for animals that participated in interactions that had no clear resolutions ($N = 16$ individuals) are not presented.

analysis. Thus, only interactions that had a clear resolution ($N = 72$) were included in the analyses that follow.

Statistical Analyses

To avoid assumptions about normality, all statistical comparisons were performed using nonparametric statistical tests. Qualitatively similar results were obtained from parametric tests, which are reported in a few places to enhance comparability with previous work. Because lizards were tested as pairs, measures of winners and losers were nonindependent, so we used a matched-pairs test (Wilcoxon signed-ranks test) for comparing winners and losers (Garland et al. 1990b; Zamudio et al. 1995; Robson & Miles 2000). The same test was also used to compare field behaviours, observed prior to capture, between winners and losers. To fully account for differences among individuals regardless of interaction outcome, we also used a Spearman rank correlation to relate laboratory locomotor performance to field behaviours. The reported *P* values are two tailed unless stated otherwise. Means are reported with standard deviations throughout.

RESULTS

Field Behaviours

Field measurements of behaviour and microhabitat usage are summarized in Table 1. Male *A. cristatellus* are sedentary foragers who maintain a body temperature near that of their immediate environment, and normally occupy a perch typical of trunk-ground species in the Williams (1983) ecotype scheme. Winners of subsequent laboratory dominance tests (see below) gave assertion displays at a significantly higher rate than losers (Table 1).

Locomotor Capacity

We found considerable variation between males in both maximal sprint speed ($N = 112$; mean $\pm$ SD: 1.6 ± 0.35 m/s; range 0.6–2.6) and endurance ($N = 144$; 280 ± 79.8 s; range 84–502). Neither speed ($r_S = -0.115$, $N = 87$, $P = 0.291$; $r_{85} = -0.207$, $P = 0.055$) nor endurance ($r_S = 0.064$, $N = 127$, $P = 0.473$; $r_{125} = 0.050$, $P = 0.579$) were correlated with SVL within the size range examined in this study. Endurance ($r_S = 0.188$, $N = 127$, $P = 0.034$; $r_{125} = 0.167$, $P = 0.06$) but not speed ($r_S = -0.024$, $N = 87$, $P = 0.824$; $r_{85} = -0.058$, $P = 0.595$) was significantly positively correlated with body mass.

Laboratory sprint speed was not significantly correlated with any of the four measures of field behaviour taken before capture (moves/min, percentage of time moving, jumps/min and displays/min). Endurance was positively correlated with the number of displays/min recorded in the field ($r_S = 0.31$, $N = 50$, $P = 0.027$; Fig. 2), but not with any of the other three traits (NS in all cases). We obtained data on both sprint speed and dominance for 52 pairs of lizards. The distribution of sprint speeds for both
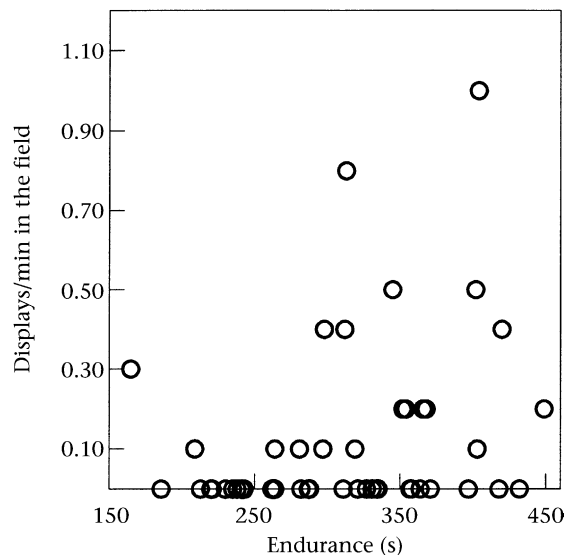

Figure 2. The relationship between endurance of adult male *A. cristatellus* in the laboratory and the rate at which they performed assertion displays before capture (Spearman rank correlation: $r_S = 0.31$, $N = 50$, one-tailed $P = 0.027$).

winners and losers did not differ significantly from normal (Kolmogorov–Smirnov tests: $D = 0.110$ and 0.107, NS for both). Similarly, the distribution of endurance for both winners and losers did not differ significantly from normal ($D = 0.062$ and 0.077, $N = 72$, NS for both).

Dominance

Lizards typically initially froze at opposing sides of the test enclosure. Once interactions began, they took a variety of forms. Some involved very subtle actions that were barely discernible, whereas others became obvious fights involving displays, chasing and biting. Escalated interactions involving biting were uncommon, compared with interactions limited primarily to displaying and posturing. The repertoire used by captive lizards was very similar to that of free-ranging animals. A dominant individual was identified, based on the observer's assessment of the interaction, in 72 of 77 staged interactions. Most interactions were prolonged, and determination of winners usually occurred more than 1 h after the interaction began. We obtained numerical dominance scores for 52 of the fights. In most cases, the numerical dominance scores agreed well with subjective assessments (Fig. 3). Winners had significantly higher scores than did losers (Wilcoxon matched-pairs signed-ranks test: $Z = 5.822$, $P < 0.001$), corroborating the qualitative assessments.

Overall, tested animals showed considerable variation in body size (Table 2). However, within a dyad, winners and losers did not differ significantly in SVL (difference between winners and losers: 1.0 ± 1.1 mm), reflecting our criterion for size-matched combatants. Paired animals also did not differ significantly in mass, tail length, crest length, crest height, head length or head width. Differences in these traits cannot, therefore, explain the winner or loser status of a lizard in our study. However, winners
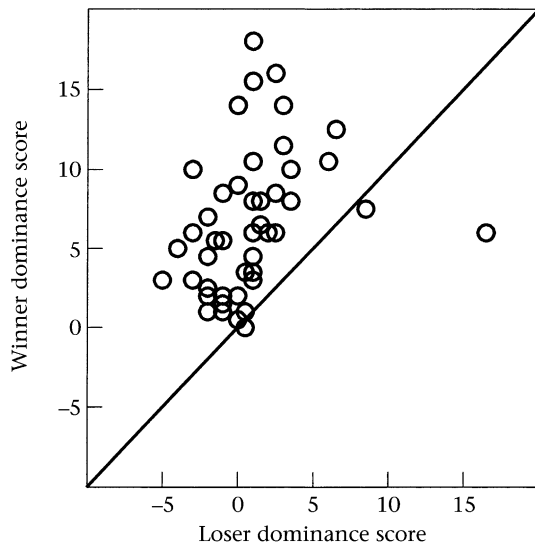
Figure 3. Dominance scores of winners and losers in experimentally matched pairs of male *A. cristatellus* in which an agonistic interaction occurred. The diagonal line represents equal values for the winner and loser in a pair. Winners had significantly higher dominance scores than losers (Wilcoxon matched-pairs signed-ranks test: $Z = 5.822$, $N = 52$ pairs, two-tailed $P < 0.001$).

had significantly deeper heads than did losers (Table 2), raising the possibility that relative head size helps determine the outcome of agonistic interactions between males.

As expected, winners of laboratory encounters performed more assertion displays in the field before capture than losers (winners: 0.21 ± 0.279 displays/min; losers: 0.05 ± 0.133 displays/min). However, both body and ambient temperatures were nearly identical for winners and losers prior to capture (Table 1). Winners typically used higher and wider perches than did losers, but the differences were not statistically significant. Winners and losers also did not differ significantly in the number of moves/min, the percentage of the time spent moving or the number of jumps/min.

The sprint speeds of winners (1.61 ± 0.39 m/s) were not significantly different from those of losers (1.57 ± 0.34 m/s; $Z = 0.537$, $N = 52$ pairs, $P = 0.591$; Fig. 4). In contrast, the endurance of winners (300 ± 87.7 s) was significantly higher than that of losers (268 ± 69.1 s; $Z = 2.447$, $N = 72$ pairs, $P = 0.014$; Fig. 5).

We used two methods to search for a correlation between speed and endurance. At the level of individuals, we found no significant correlations between sprint speed and endurance within either winners or losers ($P > 0.6$ in both cases). Similarly, comparing members of each dyad, we found no correlation between the difference between winners and losers in speed and the difference in endurance (Spearman rank correlation: $r_S = -0.09$, $N = 52$ pairs, $P = 0.524$).

DISCUSSION

Our study is the first to link social dominance, locomotor performance, morphological traits and field behaviours. Experimentally assessed social dominance in *A. cristatellus* was positively and significantly related to relative head depth, laboratory-measured endurance and display frequency in the field, but was not related to most morphometric traits, microhabitat and thermoregulation measures, most field locomotor behaviours, or laboratory sprint speed. Both endurance (Garland 1994; present study) and dominance (Fox 1983; Tokarz 1985; Deslippe et al. 1990; McMann 1993; Carpenter 1995; Molina-Borja et al. 1998) often covary with body size within lizard species. However, our contestants were matched for SVL and did not differ significantly in mass, thus removing size as a possible influence on our findings.

To the extent that results obtained under artificial conditions in captivity reflect natural behaviours, social dominance in male *A. cristatellus* was positively related to locomotor performance in the present study. This result is consistent with previous work on lizards (Garland et al. 1990b; Robson & Miles 2000), suggesting that locomotor performance is a widely important correlate of social dominance in this group. Studies of social dominance in junglefowl, *Gallus gallus spadiceus*, also show a relationship between organismal performance (aerobic capacity, in this

Table 2. Morphometric measures taken from adult male *A. cristatellus* in the British Virgin Islands

Parameter	Winners ($N = 17$)				Losers ($N = 17$)				Z	N	P
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD			
Mass (g)	7.8	4.0	13.5	1.71	7.6	3.0	11.5	1.66	1.08	71	0.28
Tail length (mm)	100	33	145	23.6	95	25	145	28.1	0.21	72	0.84
Crest (mm)											
Length	45	0	73	20.4	46	0	72	19.1	0.21	72	0.84
Height	7	0	17	3.6	6	0	15	3.5	1.07	72	0.28
Head (mm)											
Length	19.7	16.7	22.3	1.18	19.5	15.9	22.2	1.43	1.38	72	0.17
Width	11.9	9.9	13.9	0.88	11.9	8.7	13.7	0.95	1.54	72	0.12
Depth	9.4	7.8	11.5	0.85	9.2	6.9	10.9	0.91	2.35	35	0.019

Values for winners and losers were compared using the Wilcoxon matched-pairs signed-ranks test. *P* values are two tailed. *N* refers to the number of dyads used in each comparison.
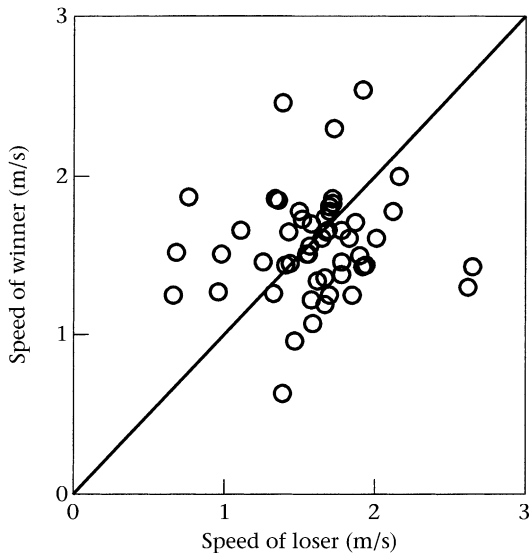
Figure 4. Maximum sprint speed of winners and losers in pairs of male *A. cristatellus* matched for body size. Sprint speed was measured on a 2.5-m racetrack angled at 37°. The diagonal line represents equal values for the winner and loser in a pair. Differences between winners and losers were not significantly different (Wilcoxon matched-pairs signed-ranks test: $Z = 0.537$, $N = 52$ pairs, two-tailed $P = 0.591$).

case) and the social rank of males (Hammond et al. 2000). No such relationship exists in female junglefowl (Chappell et al. 1999; Hammond et al. 2000), and it would be interesting to test for such a relationship in female *A. cristatellus*, which appear to be aggressive but not territorial (G. Perry, unpublished data).

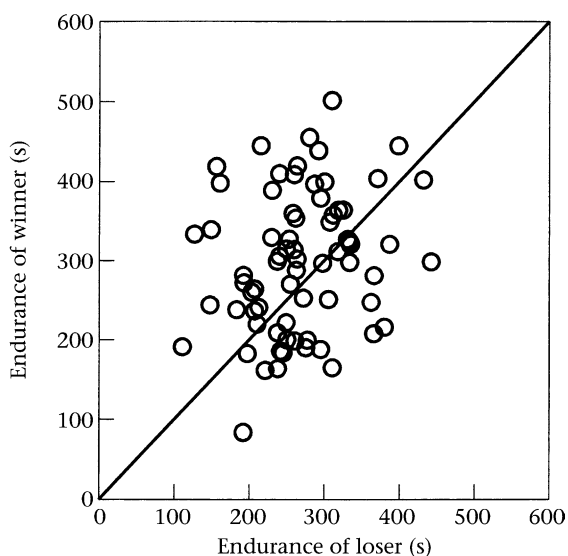As predicted, winners of dyadic encounters had greater endurance than did losers. However, most of the inter-

Figure 5. Endurance of winners and losers in pairs of male *A. cristatellus* matched for body size. The diagonal line represents equal values for the winner and loser in a pair. Winners had significantly higher endurance values than losers (Wilcoxon matched-pairs signed-ranks test: $Z = 2.447$, $N = 72$ pairs, two-tailed $P = 0.014$).

actions we observed in the test arenas were not very intense, perhaps because males tend to match the level of aggression displayed by the other individual (McMann 1993). Endurance in our study was measured under conditions intense enough to exhaust lizards in a few minutes, whereas the dominance interactions apparently lasted much longer. Thus, although our findings could be interpreted to mean that endurance directly determines social status, maximal endurance is unlikely to have directly determined the outcome of observed fights. At least some of the processes involved in territorial acquisition in *Anolis* appear to rely more on persistence than on active aggression, and winning an interaction may not be essential to controlling a territory (Stamps 1994, 2001; Stamps & Krishnan 1995). Animals can use subtle cues to evaluate each other (McMann 1993). Such assessment of aggressive potential is predicted by evolutionary theory (Maynard Smith 1982), although the specific cues used have rarely been identified (Hofmann & Schildberger 2001). Males may be able to use the frequency or amplitude of aggressive displays as a proxy for the endurance of an opponent. That field display rates are correlated with endurance (see below) suggests that display rates may serve as honest signals of male physical prowess (sensu Zahavi 1977).

Winners in our study, matched in size to losers, had significantly deeper heads. Hews (1990) also found greater head depth in male *Uta palmeri* that won experimental dyadic interactions. She also observed a positive correlation between head depth and territory quality. Her findings that head width and length were not so correlated (Hews 1990) suggest that head length, width and depth are not necessarily part of a single evolutionary suite, but may evolve in response to separate selection pressures. Our data also support this interpretation. Two interspecific comparative studies (Carothers 1984; Kratochvíl & Frynta 2002) also reported an association between male–male aggression and sexual dimorphism in lizard head sizes, suggesting that this might be a general phenomenon associated with intrasexual selection. Head dimensions are directly related to bite force (Herrel et al. 1998, 1999). As biting is an occasional element in *A. cristatellus* agonistic interactions, head dimensions may be important for determining social dominance during male–male interactions. However, biting was rarely observed in our experimental arenas, and was not a common element during interactions we observed in the field. We therefore do not believe that head dimensions of contestants directly affected the outcome of our contests. As with endurance, head dimensions may provide information on opponent biting ability, thus providing cues that help to determine the outcome of an interaction, even in the absence of overt aggression.

An alternative interpretation of our findings would be that higher endurance and greater head size are not the direct causes of winning fights, but rather are affected in parallel by an underlying physiological trait. Testosterone levels are well known to be associated with dominance and display behaviours in lizards (Cooper et al. 1987; Moore & Marler 1987; Marler & Moore 1989; DeNardo & Sinervo 1994; Smith & John-Alder 1999; Sinervo et al.

2000). Testosterone levels are higher in males during the reproductive season (Tokarz et al. 1998). Experimentally modified testosterone levels cause changes in activity levels (Marler & Moore 1989; DeNardo & Sinervo 1994; Sinervo et al. 2000) and locomotor performance (John-Alder et al. 1996; Klukowski et al. 1998). Similarly, male *S. occidentalis* infected with malaria show lower testosterone levels, lower stamina, reduced courtship display rates, less success at territorial defence and lower social status (Schall et al. 1982; Schall & Dearing 1987; Dunlap & Schall 1995). Thus, a reasonable hypothesis would be that testosterone levels affect social dominance in male *A. cristatellus* through both increased aggression and greater locomotor performance (see also Garland et al. 1990b). Androgen levels are well known to affect changes in secondary sexual characteristics (e.g. Shine & Crews 1988; Oliveira & Almada 1998; reviewed in Thornhill & Gangestad 1999). The observed differences between winners and losers in head depth might be interpreted as another effect of increased testosterone. However, there are two potential problems with this interpretation. First, the known organizational effects of testosterone occur during development, whereas behavioural effects are the result of short-term hormone levels. Second, data on the organizational effects of hormones such as testosterone and corticosterone on lizard head dimensions are not available. Further studies of the hormonal processes involved in dominance and locomotion in *A. cristatellus* are needed before this hypothesis can be evaluated.

Both Garland et al. (1990b) and Robson & Miles (2000) found that sprint speed is positively correlated with social dominance in the species they studied. We predicted that speed would not be as important in *A. cristatellus*, because agonistic interactions in this species are rarely high-speed. We therefore did not find it surprising that maximum attainable speed was not an important predictor of social dominance in *A. cristatellus*. All *Anolis* species studied to date normally move at speeds much below their maximum levels (Irschick & Losos 1998; Irschick 2000), and all are sedentary foragers that move relatively infrequently (Perry 1999). Thus, it is also not surprising that winners and losers showed no differences in sprint speed and all field locomotor behaviours measured (moves/min, percentage of time moving and jumps/min). Nevertheless, in the distantly related *Lacerta vivipara*, Clobert et al. (2000) found that endurance (measured at birth) is associated with subsequent field activity level, growth rate and parasite load, but not survivorship. It would be of interest to conduct similar studies in the ecologically very different *A. cristatellus*.

We did not find a trade-off between speed and endurance, although it has often been predicted based on first principles (e.g. Losos 1990b; Garland & Losos 1994). Moreover, Vanhooydonck et al. (2001) found such a trade-off when comparing lacertid lizard species. However, Garland et al. (1988) did not find it among mammals, and intraspecific studies of lizards have generally failed to identify such a pattern (e.g. Garland et al. 1990b; Sorci et al. 1995; Robson & Miles 2000; this study). Perhaps the limited amount of variability available intraspecifically, compared with interspecific differ-

ences, makes identifying such correlations and trade-offs difficult.

Our second important finding was the presence of a significant positive relationship between agonistic behaviours in the field and laboratory-measured endurance and social status. Previous studies of lizards did not include measures of field behaviour (Garland et al. 1990b; Robson & Miles 2000), so the relationship between laboratory findings and aspects of fitness in the field has not been explored. That winners in dyadic encounters had both a higher display rate before capture and greater endurance greatly strengthens the likelihood that laboratory-based findings on locomotor performance and social dominance are truly instructive about natural interactions in the field. Moreover, greater signalling frequency in dominant males has also been documented in other lizard species (Deslippe et al. 1990; Molina-Borja et al. 1998).

The lack of a correlation between field locomotor activity and laboratory-measured locomotor capacity differs from what might have been expected based on interspecific comparisons conducted in the past. Garland (1999) showed that laboratory endurance capacity and field locomotor behaviour are positively correlated among lizard species, and G. Perry, K. E. Bonine & T. Garland (unpublished data) showed that endurance and home range size are positively correlated in phrynosomatid lizards. Previous work has shown that the activity levels of territory-holding male lizards might be higher (DeNardo & Sinervo 1994) or lower (Perry 1996) than those of subordinate or nonterritorial individuals. However, we found no such differences. In a similar vein, dominant individuals might be better able to monopolize preferred microhabitats than losers, resulting in differences in body temperature. However, this seems unlikely to occur in *A. cristatellus*, which is a thermoconformer (Huey & Webster 1976; Hertz 1992). Indeed, winners and losers occupied similar microhabitats and thermoregulated to a similar degree before capture (Table 1). It thus seems that the impacts of social dominance might be highly species and/or context specific. Our findings also serve to emphasize that behavioural factors can make typically realized locomotor activity differ greatly from what is physiologically feasible (Garland et al. 1990a; Garland & Losos 1994; Irschick 2000; Irschick & Garland 2001).

Reproductive success, a crucial element of fitness, is often greatly impacted by the social status of an individual. Thus, the increasing body of evidence indicating that dominance is correlated with locomotor performance abilities emphasizes the potential multilevel nature of selection. In combination with previous studies, our findings also suggest that different aspects of locomotor performance are important in different species, presumably as a function of variation in ecology and social behaviour.

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