



Multiple signals in chameleon contests: designing and analysing animal contests as a tournament

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Traditionally, studies of intrasexual selection have focused on single traits that are more exaggerated in males. Relatively little is known about systems in which traits are larger in females or the role of multiple traits in male contests. We used a tournament design in which each male encounters a series of different opponents, in conjunction with the structured Bradley–Terry model, to examine the role of multiple male traits in contests between male Cape dwarf chameleons, *Bradypodion pumilum*. Females are larger but males have relatively longer tails, larger and more ornamented heads and a larger central flank patch, all of which are emphasized during agonistic displays. We found no evidence that larger body size confers an advantage in male contests, despite high levels of aggression and escalated encounters. However, both the height of the casque (head ornament) and relative area of the flank patch were positively associated with fighting ability, and not correlated with each other, suggesting that they may represent independent sources of information about an opponent's ability. We discuss these results in relation to the role of male contest competition in the evolution of multiple male signals and sexual dimorphism in dwarf chameleons. In addition, we show that the use of tournament designs, in conjunction with the structured Bradley–Terry model, has important advantages over traditional designs and methods of analysing animal contests.

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Many recent studies have highlighted the need to consider multiple traits in studies of sexual selection (Møller & Pomiankowski 1993; Johnstone 1996; Brooks & Coultridge 1999; Pryke et al. 2001; Andersson et al. 2002; Candolin 2003; van Doorn & Weissing 2004). The use of multiple signals during contest competition, however, has received much less theoretical or empirical attention than female preferences for multiple male traits in mate choice (reviewed in Candolin 2003). Males may use multiple signals in agonistic interactions because different signals may convey different information regarding an opponent's fighting ability ('multiple messages'), thereby facilitating accurate opponent assessment (see also Møller & Pomiankowski 1993; Johnstone 1996; Ord et al. 2001). Alternatively, some signals may be redundant or serve as 'backup signals', each reflecting the same rather than different aspects of opponent quality with some error (Møller

& Pomiankowski 1993; Johnstone 1996). Such redundant signals may not be current targets of intrasexual selection, instead resulting from the accumulation of traits that previously conferred an advantage in male contests or in a different context. Identifying traits that currently confer an advantage in contest competition is thus necessary to understand the evolution of male trait variation and multiple male ornaments.

Size and ornamentation often predict the outcome of male–male contests in species in which these traits are larger or more exaggerated in males (Andersson 1994). Most studies of intrasexual selection have examined traits that show male-biased dimorphism because these are expected a priori to be targets of sexual selection. However, traits that are monomorphic or are more exaggerated in females may also play a role in male–male contests (Maklakov et al. 2004; e.g. Legrand & Morse 2000; Prenter et al. 2003; Kraaijeveld et al. 2004). In several species of arthropods in which females are larger than males, larger size is advantageous in male contest competition (Fairbairn & Preziosi 1994; Kraushaar & Blanckenhorn 2002; Prenter et al. 2003; Maklakov et al. 2004). In contrast, in yellow-pine chipmunks, *Tamias amoenus*, one of relatively few mammals with female-biased sexual size dimorphism

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(SSD), male contest competition favours smaller male size because smaller males are more aggressive (Schulte-Hostedde & Millar 2002). In these systems, selection for larger or smaller male size through male contest competition is offset by opposing natural or sexual selection on male body size (Schulte-Hostedde & Millar 2002; Schulte-Hostedde et al. 2002). For instance, in the case of the web-building spider *Stegodyphus lineatus*, smaller, early maturing males have an advantage obtaining matings with virgin females early in the breeding season even though larger males win physical contests over access to mates (Maklakov et al. 2004). Male size is consequently under balancing selection, while selection for fecundity favours larger female size, thereby maintaining female-biased SSD (Schulte-Hostedde et al. 2002; Maklakov et al. 2004). As these contrasting examples show, the role of body size in male contest competition in species with female-biased SSD remains controversial, but has so far been examined in very few species, and especially few vertebrates.

We examined the role of multiple male traits, including traits showing both male-biased and female-biased sexual dimorphism, in the Cape dwarf chameleon, *Bradypodion pumilum*. Female dwarf chameleons are larger than males (female-biased SSD) but several other traits are relatively larger in males than females: males have longer tails, relatively higher, more rugose ornamental casques and wider heads (Burrage 1973). During both social and agonistic interactions, male dwarf chameleons perform a display with their body laterally compressed, the skin behind the bony casque stretched tight, the gular region extended and the tail coiled. In the centre of the flank, which is generally bright green in this population, there is an irregularly shaped pink-orange patch. Whether this colour pattern is sexually dimorphic or has a role in male contests has not been determined. Hence, in this study we had two goals: (1) to quantify sexual dimorphism and (2) to examine the relation between fighting ability and multiple male traits including body size and condition, head dimensions, casque height, tail length and size of the central flank patch. These traits are the most likely candidates for sexual selection because communication in chameleons is almost exclusively via the use of visual signals (Cooper & Greenberg 1992; Necas 2001). Although chameleons are famous for their ability to change colour and the spectral properties of colour patches are likely to be an important component of visual signals used during male–male contests, we were primarily interested in fixed (rather than labile) traits thought to influence contest competition in a wide range of taxa (e.g. body size, head size, size of ornaments or colour patches). Furthermore, quantifying coloration from videotaped interactions can be problematic (Fleishman et al. 1998), especially as this species shows some UV reflectance (D. Stuart-Fox, unpublished data).

To estimate the relation between male traits and fighting ability, we designed our experiments as a tournament and applied a structured Bradley–Terry (B–T) model for paired comparisons (Bradley & Terry 1952; Firth 2005). Tournament designs, whereby each male contests several other males in a series of paired encounters, allow much

larger sample sizes and, consequently, greater statistical power, as each individual is used more than once. Tournament designs, however, are not widely used because such a design results in males having different agonistic experiences and the effects of unmeasured differences in fighting ability and ‘experience effects’ can be difficult to disentangle. That is, a winner may keep winning because he has a series of attributes that make him a better fighter or because of a self-reinforcing ‘winner effect’ and vice versa for losers. We show how this problem can be circumvented through use of a generalized Bradley–Terry model.

Traditionally, the B–T model has been used to assign ranks to individuals within a linear hierarchy based on paired observations. The only two previous applications of the B–T model to animal dominance or aggression used the model to estimate a complete hierarchy, then tested whether position in the hierarchy was associated with individual traits in subsequent analyses (Appleby 1983; Haley et al. 1994). However, individual-specific covariates (in this case, male traits) can be incorporated directly into a single structured model of B–T form, thereby circumventing the problem of having to derive a linear hierarchy first (Tufto et al. 1998; Firth 2005). We provide a case study for the application of the structured B–T model for paired comparisons and discuss its utility and the utility of tournament designs for experimental studies of male contests.

METHODS

Study Species, Collection and Husbandry

The Cape dwarf chameleon is a small (up to 90 mm snout–vent length) lizard with a distribution restricted to the southwest Western Cape, South Africa. It occurs in a variety of habitats including fynbos, riparian vegetation and wetlands. These chameleons can occur at high densities (up to 200 individuals/ha; Burrage 1973), suggesting that encounter rates between individuals are likely to be high. Males are very aggressive and escalated fights have been observed in the field, with males locking jaws and falling from perches to the ground in prolonged wrestles. Males vigorously defend perches although they do not necessarily defend home ranges (Burrage 1973). The high level of costly male–male aggression, and potentially high encounter rates between males, suggests that male–male competition is likely to be important in gaining access to receptive females and preventing other males from doing so.

We captured 36 adult male *B. pumilum* by hand from the region within and immediately surrounding Stellenbosch in the Western Cape Province, South Africa (33°56'S, 18°52'E) in April 2003, overwintered them to ensure no recent contest experience, conducted experiments the following spring (September–November 2003), then released them at their site of capture (November 2003; see Ethical Note below). To ensure that they were sexually mature, we avoided capturing very small males. Chameleons were housed individually in enclosures (40 × 40 cm and 80 cm high) with no visual contact. Each enclosure contained a live native shrub and additional perches (dowel

sticks). These enclosures were kept in constant temperature (CT) rooms with day–night light and temperature cycles approximating (or slightly warmer than) those in their natural environment (April–May: day 28°C, 13 h; night 15°C; June–August: day 23°C, 12 h; night 10°C; September–November: day 28°C, 14 h; night 15°C). Lighting was with Osram L36W/72-965 Biolux fluorescent lights, which emit appropriate levels of both UVA and UVB (for reptiles) and approximate natural sunlight in terms of wavelength range. All chameleons were misted daily and fed on a diet of live gut-loaded crickets provided three times per week, as dwarf chameleons eat only active, live prey. Crickets were dusted with multivitamin and calcium powder on a fortnightly basis.

Male Traits and Sexual Dimorphism

We measured the following traits for all chameleons: snout–vent length (SVL; ± 1 mm), mass (± 0.1 g), tail length (cloaca to tail tip; ± 1 mm), jaw length (angle of the jaw to the tip of the snout; ± 0.1 mm), head width (width at the widest point; ± 0.1 mm), casque height (angle of the jaw to the highest point of the casque; ± 0.1 mm). For head width, jaw length, casque height and tail length, measurements were taken at the beginning and end of the trial period and we used the mean of the two measurements to represent male traits at the time of the trials. We measured male SVL and mass after each contest because body mass is more variable over time than morphometric measurements. We converted all traits (apart from SVL) to size-free variables by taking the residuals of these variables regressed against SVL.

We took digital photographs of each individual (perched on a dowel stick against a uniform white background, ensuring that the flank was not obscured by the limbs) for identification and to measure the proportion of pink flank markings. Pink markings in the Cape dwarf chameleon generally comprise an irregular oval patch in the centre of the flank, sometimes with

some small peripheral patches (enlarged tubercles; Fig. 1). In this species, individuals cannot vary the size of their flank patch, although the intensity of coloration can vary greatly depending on social context. Thus, the relative size of the flank patch can be considered a fixed trait. The main central patch (Fig. 1) was traced and the area calculated with the software Scion Image beta 4.02 for Windows (Scion Corporation, Frederick, MA, U.S.A.), then standardized as the proportion of the total flank area (from cloaca to casque; Fig. 1). As the final measure was a proportion, we applied the appropriate arcsine transformation. In addition, all of the above measurements were taken for 20 females captured at the same time and from the same site, to quantify sexual dimorphism.

Male Contests

We carried out trials between 26 September and 6 November 2003. This species is active year-round and male–male conflict occurs in all seasons, although it peaks in spring and summer (September–February, [Burrage 1973](#)). Trials were conducted in an arena (60 × 40 cm and 50 cm high) with four horizontal, intersecting dowel sticks 30 cm above the floor as perches. At each dowel intersection a vertical dowel led to the floor to allow the chameleons full access to the enclosure. The arena was in a CT room under the same conditions as described above. Thus, experiments were conducted at 28°C, which is slightly higher than the mean but within the range of active body temperatures in the laboratory and field (laboratory: mean = 25°C, range 7–30°C; field: mean = 22.4°C, range 3.6–39°C) for this species ([Burrage 1973](#)). A removable opaque partition divided the arena into two. Males were placed on either side of the opaque partition and allowed to acclimatize for 5 min before the partition was removed. Pilot experiments showed that 5 min was sufficient, as male dwarf chameleons are very aggressive and generally begin to display within a minute or two of seeing another male chameleon, regardless of any recent handling. We

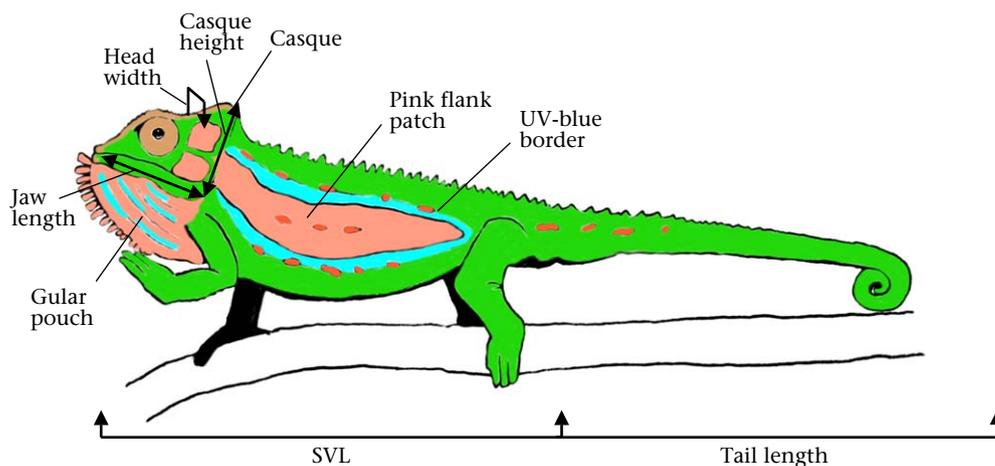


Figure 1. Diagram of male Cape dwarf chameleon in display posture indicating characters measured. The skin behind the casque is stretched tight, the body is laterally compressed with tail partially coiled, the gular pouch is extended and one arm is often raised. Traits measured: snout–vent length (SVL), tail length, casque height, jaw length, head width, relative size of the pink flank patch (thin black line; measured as a proportion of the total flank area (thick dashed white outline); see text for details).

marked individuals with a small number written in non-toxic paint-pen at the base of the tail. Contests were videotaped but monitored by an observer (D.S.F.) approximately every 5 min through a small window in the door of the CT room.

We terminated interactions once a clear winner was identified or if there was no interaction after 20 min. Most interactions escalated from lateral displays to chases, and many (53%) escalated to biting and jaw locking. The loser would flee, often dropping or climbing down from the horizontal perches to the ground. Once on the ground the loser would become very dark, while the winner would remain bright. Trials were terminated when the loser dropped to the ground or fled/retreated consistently (more than once). Contests generally lasted less than 10 min.

Ethical Note

After capture, chameleons were placed individually in cloth bags and transferred to housing in Johannesburg within 3 days of capture. No individual suffered any noticeable effects from the process of capture and transport. At the end of the experimental period, chameleons were transported in the same manner (within a day) and released at the site of capture with the permission of Western Cape Nature Conservation. During their captivity at the University of the Witwatersrand, a qualified veterinarian on the university Ethics Committee checked the chameleons on a regular basis. The study was approved by the University of the Witwatersrand Animal Ethics Screening Committee and Western Cape Nature Conservation Board.

Dwarf chameleons have no weaponry apart from their teeth, which are small and regular. We could not prevent biting because approximately half the contests escalated to biting, necessitating that we allow it to be able to determine the winner. However, we monitored contests with the intention to intervene if aggression became too severe (e.g. if serious injury such as a broken limb was a possibility because of biting in an awkward position and/or biting and twisting), but we did not have cause to intervene. Biting can cause surface bruising and short-term scarring (dark, v-shaped bite marks) but generally does not break the skin surface (in all but one case, where we applied antiseptic and which healed within 4 days). No individual suffered any permanent injury during the trials. Approximately one-third of the 36 individuals had bite marks when released at the end of the study. We do not know how long these v-shaped bite marks remain; however, chameleons with bite marks are regularly encountered in the wild because of high levels of escalated male aggression in natural populations (Burrage 1973).

Tournament Structure

Chameleons were initially grouped into size-matched quads based on SVL and mass (mean % difference between members within quads \pm SE = $2.6 \pm 0.4\%$ for

SVL and $10.4 \pm 1.3\%$ for mass). Within each quad, each member contested every other member such that each individual was initially in three contests (six contests per quad: 1 versus 2; 1 versus 3; 1 versus 4; 2 versus 3; 2 versus 4; 3 versus 4). We then conducted contests between members of different quads: members of smaller size class quads were matched against members from the next larger or smaller size class quad, depending on whether they had won or lost within-quad contests. If a winner from a smaller quad beat the winner from a larger quad, he was pitched against an individual from the next larger quad, and the converse for losers. We planned our contests according to a 'tournament structure' whereby each individual contested both similar-sized and different-sized individuals, based on our knowledge of previous wins and losses for each individual. This design ensured a robust data set for application of the B-T model (see below). To avoid stressing the animals, a minimum of 2 days, usually more ($\bar{X} \pm$ SE = 6.68 ± 0.63 days) was allowed between consecutive trials.

Thirty-six individuals were used in a total of 112 contests. As each contest involved two individuals, this corresponds to each individual participating in a mean \pm SD of 6.22 ± 1.77 trials (range 3–9). Four contests were discarded because contestants failed to interact or no clear winner could be identified and an additional one was discarded owing to incomplete data for morphological traits, leaving a total of 107 contests for statistical analysis. Of these 107 contests, 63 involved contestants that differed in either mass or SVL by more than 10% and 55 were between individuals from different 'quads'. Comparison of coefficients of variation (CV) in the difference between contestants for each trait ($CV = 100 \times (SD/mean)$ based on absolute differences between contestants for the entire data set of 107 contests) confirmed that variation in mass and SVL was comparable to that of other traits (SVL = 101.9; mass = 92.8; head width = 82.5; casque height = 72.8; jaw length = 85.5; tail length = 81.5; flank patch = 85.8). Thus, although a subset of our data set involved size-matched pairs, we ensured enough variability in mass and SVL to assess the effects of size on fighting ability (Brandt 1999).

Fighting Ability, Male Traits and Order Effects

The standard B-T model takes the form:

$$\text{logit}[\text{probability}(i \text{ beats } j)] = \lambda_i - \lambda_j,$$

for any contest between individuals i and j with λ_i and λ_j representing the abilities of the two individuals. We used the more general model:

$$\begin{aligned} \text{logit}[\text{probability}(i \text{ beats } j \text{ in contest } k)] \\ = \lambda_i - \lambda_j + \delta(z_{ik} - z_{jk}) \end{aligned}$$

to allow for the potential effect of experience; here the extra predictor z_{ik} summarizes the contest history of individual i at the time of contest k . The extra term is necessary since tournament designs entail using individuals in more than one contest and experience may affect the

probability of winning or losing subsequent contests (Jackson 1991; Hsu & Wolf 1999). To assess the relation between individual-specific traits and ability, we assumed the abilities to be related to measured traits x_1, \dots, x_p through a linear predictor with coefficients β_1, \dots, β_p in the familiar form:

$$\lambda_i = \sum_{r=1}^p \beta_r x_{ir}.$$

The model used is thus a structured (through the assumption of a linear predictor of ability) and generalized (through the addition of the contest-specific experience variable) version of the standard B–T model.

We coded ‘contest history’ in several different ways because the type and duration of experience effects may vary between taxa (Hsu & Wolf 1999, 2001; Khazraie & Campan 1999; Hofman & Schildberger 2001; e.g. Zucker & Murray 1996; Schuett 1997). For instance, the effects of prior wins and losses may differ, as may the effect of the most recent versus penultimate contest experience on the probability of winning or losing subsequent contests (Hsu & Wolf 1999, 2001). In addition, the strength of the effect may decrease with time such that the effect of the previous fight is stronger than the effect of the penultimate fight, which in turn has a greater effect than the fight before that (Hsu & Wolf 2001). Consequently, we separated effects of ‘prior wins’ and ‘prior losses’ and examined three different types of experience effect as follows: (1) the effect of having won or lost the previous encounter only, each contestant being assigned a score of 0 or 1 for ‘previous wins’ and ‘previous losses’ based on whether they won or lost their previous encounter; (2) the effect of the two previous encounters, each contestant being given a score ranging between 0 and 2 for previous wins and previous losses based on their two previous interactions; (3) the effect of the entire contest history (all prior contests). In this case, however, we assumed that the advantage of a previous win or the disadvantage of a previous loss decreases exponentially over time, such that each contestant was given a score of 1 for the most recent win or loss, 0.5 for the penultimate win or loss, 0.25 for the one before that, etc., through all prior contests. Thus, if male A won his most recent fight but lost the two before

that, he would get a value of 1 for previous wins and -0.75 ($-0.5 + -0.25$) for previous losses, indicating the relative advantage and disadvantage for male A resulting from prior contest experience.

As the three types of experience effect are formulations of the same phenomenon, we allowed only one type of experience effect in any one model. In addition, we assessed the following potential predictors of fighting ability (x): SVL, condition, relative proportion of pink flank patch, casque height, jaw length, head width and tail length (the latter four variables corrected for body size). To choose the most parsimonious model, we used a standard stepwise procedure, examining reduction in the model Akaike Information Criterion (AIC) as well as the significance of variables. We used the criterion of $P < 0.1$ for retaining variables in the model. For maximum-likelihood fitting of models we used the statistical package R (Ihaka & Gentleman 1996).

RESULTS

Sexual Dimorphism

As expected, females were significantly larger than males, although absolute dimorphism was relatively small (Table 1): females were on average 108% of male size. This, however, may be an underestimate of general population dimorphism because although males varied substantially in size (Table 1), we did not use very small males (see Methods). For all other traits except mass (casque height, head width, jaw length, tail length, relative size of the flank patch), males were relatively larger (Table 1).

Correlation Between Male Traits

Neither mass nor relative size of the pink flank patch was correlated with any of the other variables (Table 2). Tail length was significantly positively correlated with jaw length and head width, while all three head measurements (casque height, jaw length and head width) were positively correlated (Table 2).

Table 1. Sexual dimorphism in the Cape dwarf chameleon

Trait	Male		Female		F_{55}	P
	Mean	Range	Mean	Range		
SVL	78.1±1.0	68.5–90.4	84.7±1.4	70.3–96.8	14.66	0.0003
Mass	-0.18±0.21	-2.5–1.7	0.34±0.29	-2.5–4.2	2.14	0.15
Casque height	0.35±0.13	-1.4–2.5	-0.68±0.18	-1.6–0.7	20.71	<0.0001
Jaw length	0.27±0.10	-1.3–1.8	-0.52±0.14	-1.5–0.5	21.64	<0.0001
Head width	0.31±0.08	-2.4–2.7	-0.59±0.11	-2.4–0.6	43.98	<0.0001
Tail length	3.85±0.87	-4.4–17.6	-7.5±1.22	-14.4–1.3	57.56	<0.0001
Flank patch	29.4±0.9	20.9–44.7	21.1±1.2	9.4–28.4	31.01	<0.0001

Means are given ± SE. Mean and range of male and female values for all traits except snout–vent length (SVL) and relative area of the pink patch are the residuals of that trait regressed against body size. Statistical tests are one-way ANOVAs testing for a difference between the sexes. Values that are significant at $P < 0.01$ after Bonferroni correction for multiple tests are in bold.

Table 2. Correlations between male traits

	Mass	Casque height	Jaw length	Head width	Tail length	Flank patch
Mass	—	0.19	0.10	0.20	-0.22	0.10
Casque height	0.25	—	0.43	0.59	0.26	-0.01
Jaw length	0.57	0.008	—	0.50	0.49	-0.13
Head width	0.22	0.0001	0.002	—	0.51	0.08
Tail length	0.19	0.18	0.002	0.001	—	-0.11
Flank patch	0.55	0.97	0.46	0.63	0.51	—

Pearson correlation coefficients (r) are presented above the diagonal and P values below. Correlations with snout-vent length (SVL) are not presented as all variables except flank patch are size corrected. SVL was not correlated with flank patch after Bonferroni correction for multiple tests ($r = 0.32$, $P = 0.051$). Correlations that are significant at $P < 0.05$ after Bonferroni correction are in bold.

Predictors of Fighting Ability

Two male traits were significant predictors of fighting ability in the final model: the height of the casque and the relative area occupied by the pink patch in the centre of the green flank (Table 3). The estimated effect sizes of casque height and flank patch, as measured by standardized regression coefficients (Table 3), are roughly the same. For example, if males A and B are separated by two standard deviations in casque height, with, say, A greater than B, and all else equal, the probability that A defeats B is estimated to be $\exp(2 \times 0.51)/[1 + \exp(2 \times 0.51)] = 0.74$. For males differing in flank patch area, the corresponding probability is 0.72. Of the 'experience' formulations, the number of wins in the previous two fights explained the most variability and was a strong predictor of fighting ability (Table 3). Note that the coefficient estimate of this variable should not be interpreted as indicative of the strength of an 'experience' effect per se because it may be confounded with aspects of male fighting ability that we have not measured. The final model correctly predicted the outcome of 87 of the 107 contests (81%), suggesting that the model has good predictive capacity. Neither mass nor SVL was a significant predictor of fighting ability in the B-T model. Of the 63 contests involving males that differed by more than 10% mass or SVL, 29 (46%) were won by the larger male and 34 (54%) by the smaller male, a ratio that does not differ significantly from that expected by chance (binomial test: $P = 0.61$).

Table 3. Bradley-Terry model showing best predictors of fighting ability

Variable	Coefficient	SE	Z	$P(> Z)$	Standardized coefficient
Previous 2 wins	2.38	0.48	4.91	<0.0001	1.70
Casque height	0.61	0.28	2.19	0.028	0.51
Flank patch	0.09	0.04	2.04	0.042	0.46

The standardized coefficients allow assessment of the relative strength (slope) of each variable.

DISCUSSION

Both the height of the casque and the relative size of the pink markings in the centre of the flank predicted fighting ability in *B. pumilum*. Although body size (length or mass) commonly determines contest outcome in many species, our results suggest that even moderate size asymmetry is a poor predictor of fighting ability in dwarf chameleons (although evidently large asymmetries are likely to influence contest outcome). In species in which females are the larger sex, results on the role of body size in male contest competition are varied although aggression between males is often low (Zamudio 1998; Hagelin 2002; Schulte-Hostedde & Millar 2002). Why might size not be a good predictor of contest outcome despite high levels of aggression and the prevalence of escalated contests in dwarf chameleons? In many other systems, factors such as weapon or ornament size, gonad size, behavioural syndromes and strategies, motivation, agonistic experience, subjective value placed on the resource and even developmental conditions have all been shown to be more important to the resolution and outcome of contests than body size (Zamudio et al. 1995; Zucker & Murray 1996; Barki et al. 1997; Hernandez & Benson 1998; Neat et al. 1998; Daws et al. 2002; Hoefler 2002; Leiser et al. 2004). In addition to casque height and flank patch size, we identified a strong effect of experience and unmeasured differences in ability (see below) suggesting that, in dwarf chameleons, contest outcome is likely to be determined by the interaction of numerous factors, including aspects of fighting behaviour, rather than body size. That body size is not a good predictor of fighting ability may have facilitated the evolution and/or maintenance of female-biased SSD, although female-biased SSD is likely to be maintained by a combination of selection pressures acting on male and female size independently. For instance, female size is likely to be under fecundity selection (see Zamudio 1998; Olsson et al. 2002; Cox et al. 2003) as larger females have larger litters in this species (Burrage 1973).

Males with relatively higher casques and larger areas of pink-orange on their flanks tended to be better fighters and, in contrast to body size, both these traits are larger in males. Sexual dimorphism in colour pattern has not previously been reported in dwarf chameleons. This may be because individuals tend to be highly variable in coloration and, consequently, sexual dimorphism in

coloration has not been examined quantitatively. Sexually dimorphic colour ornaments have been shown to affect the outcome of male contests in some lizard species (reviewed in Olsson & Madsen 1998; Whiting et al. 2003), although several studies have reported no relation or a relation in some populations but not others (Zucker & Murray 1996; Kwiatkowski & Sullivan 2002; López et al. 2004). In *B. pumilum*, the central pink-orange patch on the flank is usually surrounded by a thin UV-blue border (D. Stuart-Fox, unpublished data). Pink-orange and UV-blue are complementary colours that maximize contrast because they are at opposite ends of the visual spectrum (Endler 1992). The flank patch thus represents a conspicuous signal of competitive ability that may facilitate opponent assessment. The constraints to expression of flank coloration, such as dietary acquisition of pigments (e.g. carotenoids, Olson & Owens 1998) or association with testosterone levels or immune function (Roberts et al. 2004), are not known in this system, although flank patch size was not correlated with relative mass, suggesting that this trait is not condition dependent. Further work on factors affecting trait expression is required to understand the maintenance of signal honesty.

The casque is similarly a form of ornamentation in dwarf chameleons but casque height (measured from the angle of the jaw) also reflects head depth. Many other studies have reported a relation between contest outcome and a measure of head size, including head depth, in lizards (Hews 1990; Kratochvil & Frynta 2002; López et al. 2002; Perry et al. 2004). Head size is associated with bite force in lizards (Herrel et al. 2001; Verwajen et al. 2002) and, consequently, may convey information on potential costs of fighting. This could be especially important in dwarf chameleons because in our study, 57 (53%) of the 107 fights escalated to biting. However, males began most contests with lateral displays and chameleons in the wild first display from a distance while approaching each other, before conflicts escalate (personal observation). This raises the possibility that the flank patch may convey information during initial phases of the contest, whereas casque height may be used to assess opponents during later escalated stages of the contest. Thus, multiple signals may communicate different aspects of fighting ability.

Not all traits that were larger in males were associated with fighting ability. Although neither head width nor jaw length predicted fighting ability, both were positively correlated with casque height, indicating possible signal redundancy and/or that the three aspects of head size and shape are functionally or developmentally linked (Badyaev et al. 2001). Male chameleons may assess the overall head size and shape of prospective opponents even though our results suggest that of the three head characteristics that we measured, casque height is the best predictor of fighting ability. Tail length was not correlated with either casque height or relative size of the pink flank patch and was not independently associated with fighting ability, suggesting that sexual dimorphism in tail length is not maintained by selection as a result of male contest competition. Instead it may be an incidental consequence of inherent differences in growth and physiology between

the sexes (e.g. the presence of hemipenial pouches at the base of the tail in males) or a by-product of fecundity selection on female trunk length (Kratochvil et al. 2003). Alternatively, sexual dimorphism in tail length may be maintained through either natural selection operating differentially on tail length of the two sexes or female preference for longer tails (Marchetti 1998; Andersson et al. 2002; Patricelli et al. 2003).

We also identified an association between prior wins and predicted fighting ability. This is likely to reflect a winner effect as in many other taxa (e.g. Jackson 1991; Zucker & Murray 1996; Schuett 1997; Hsu & Wolf 1999, 2001; Khazraie & Campan 1999; Hofman & Schildberger 2001). However, it may also reflect a difference in male abilities associated with attributes that we did not measure in this study, such as hormone levels, physiological traits or behavioural profiles. Although the strong indication that winners kept winning is suggestive of an effect of prior experience, in particular winning the previous two contests, experience effects are inevitably confounded with unmeasured differences in fighting ability.

Utility of Tournaments and the B–T model

We designed our experiments as a tournament in order to allow analysis using a B–T model to identify significant predictors of contest success. The B–T model has several advantages. First, like multiple regression techniques (e.g. multiple logistic regression), the B–T model allows the relative importance of multiple independent variables to be assessed simultaneously. Second, the B–T model takes proper account of dependency among contests involving the same individual. Third, the B–T model can be applied to data on male–male interactions where each male may encounter several different opponents but not all males encounter every other male; that is, it can accommodate an incomplete matrix of possible interactions. Although biologically realistic, such a design can result in the effects of unmeasured differences in ability and ‘experience effects’ being difficult to disentangle. To distinguish experience from ability, a sequence of contests is needed involving the same individual, in which the probability of that individual’s winning or losing changes with its accumulated experience (experience and outcome change while ‘ability’ remains constant). Our data set contained too few such contests to isolate the effects of experience per se. Nevertheless, the structured B–T model as used here allows the identification of (measured) traits associated with fighting ability while controlling for effects of contest history and other potentially confounding traits.

The B–T model implicitly assumes a transitive hierarchy whereby if A is more able than B (that is, A is the more likely winner of a contest between A and B) and B is more able than C, then A is more able than C. A recent simulation study showed that both experience effects and asymmetries in resource-holding potential (RHP) can result in transitive hierarchies (Beaugrand 1997). However, Beaugrand also concluded that when the effect of fighting experience (number of previous wins or losses) was combined with individual differences in RHP, the

same biological conclusions were reached regarding traits associated with fighting ability. As the importance of fighting experience increased and the initial variation in individual RHP decreased, the lower the correlation between initial RHPs and position in the hierarchy (Beaugrand 1997). Thus, the presence of an experience effect is unlikely to result in spurious associations between fighting ability and individual traits (Type I error), although under some circumstances (very strong experience effect) it may result in failure to detect effects of subtle individual differences in RHP (Type II error). The effects of casque height and flank patch area emerge as being statistically significant in the present study, even under this potential loss of sensitivity caused by experience effects.

The B–T model is a useful tool for analysing contest data because it maximizes the information that can be obtained from a limited number of individuals. For instance, with 36 individuals, using each individual only once would result in 18 contests (18 dyads of unfamiliar males). This is similar to the sample sizes used in many studies of animal contests but results in poor statistical power and a greatly inflated chance of Type II error in a multiple regression context (Cohen & Cohen 1983; Cohen 2000; MacNally 2000). In contrast, the B–T model allows the simultaneous estimation of the relative influence of several individual traits, while controlling for ‘contest history’, based on a robust sample size (in this case, 107 contests); yet it does not require that every individual contests every other, thereby minimizing stress to the test subjects. In addition to identifying the role of male contest competition in the evolution of multiple male signals and sexual dimorphism in dwarf chameleons, our study highlights the utility of tournament designs and the structured B–T model for analysing contest data.

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