

Intrasexual selection predicts the evolution of signal complexity in lizards

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Sexual selection has often been invoked in explaining extravagant morphological and behavioural adaptations that function to increase mating success. Much is known about the effects of intersexual selection, which operates through female mate choice, in shaping animal signals. The role of intrasexual selection has been less clear. We report on the first evidence for the coevolution of signal complexity and sexual size dimorphism (SSD), which is characteristically produced by high levels of male–male competition. We used two complementary comparative methods in order to reveal that the use of complex signals is associated with SSD in extant species and that historical increases in complexity have occurred in regions of a phylogenetic tree characterized by high levels of pre-existing size dimorphism. We suggest that signal complexity has evolved in order to improve opponent assessment under conditions of high male–male competition. Our findings suggest that intrasexual selection may play an important and previously underestimated role in the evolution of communicative systems.

Keywords: sexual selection; sexual size dimorphism; visual communication; signal complexity; evolution; the comparative method

1. INTRODUCTION

The extraordinary diversity of animal signals has fascinated biologists since Darwin (1872; Hauser 1996; Bradbury & Vehrencamp 1998). Complex signals are known to have evolved in response to sexual selection (Andersson 1994), properties of the signalling environment (Endler 1992), predation risk (Stoddard 1999) and social organization (Blumstein & Armitage 1997). Recent studies have particularly focused on the role of intersexual selection. The cumulative effects of female mate choice decisions have caused profound changes in signal structure, producing elaborate ornaments (Basolo 1990; Andersson 1994; Endler & Basolo 1998) and complex vocalizations (Ryan 1998; Collins 1999). Much less is known about the role of intrasexual selection.

Agamid and iguanid lizards primarily communicate using visual displays. These are composed of discrete movements, often delivered in a predictable sequence, together with characteristic postures and changes in body coloration. Exchanges of such signals between males are an important component of territory defence (Carpenter 1978). Signal complexity varies across species and is quantified by the number of modifiers added to a basic head-nod or push-up display (Jenssen 1977, 1978). Modifiers include dewlap extensions, tail wagging, arm waving, crest raising, body compression/inflation, back arching, body raising/tilting and changes in colour. Variation in modifier use determines function and influences the outcome of social interactions (Jenssen 1977; Martins 1991). Signalling behaviour is known to affect the fitness of the sender because it is important in both male–male contests (Trivers 1976) and female mate choice (Jenssen 1970*a*). However, the considerable variation between species in repertoire size remains unexplained.

In many taxa, competition between males over resources characteristically produces an asymmetry in body size between the sexes. Thus, the advantages of larger size for males typically results in sexual size dimorphism (SSD). In iguanian lizards, the success of males competing for territories and other resources is positively correlated with body size (Greenberg & Noble 1944; Rand 1967; Jenssen 1970*b*; Trivers 1972, 1976; Stamps 1977, 1983; Ruby 1978, 1984; Schoener & Schoener 1980, 1982; Tokarz 1985; Cooper & Vitt 1987; Anderson & Vitt 1990; Baird *et al.* 1997; Johnston 1997; Jenssen & Nunez 1998). Male–male competition is thus the predominant factor influencing the evolution of larger-male SSD (Trivers 1976; Schoener & Schoener 1980; Stamps 1983; Vitt 1983; Carothers 1984; Vitt & Cooper 1985; Anderson & Vitt 1990; Hews 1990; Perry 1996; Baird *et al.* 1997; Johnston 1997; Stamps *et al.* 1997; Wikelski & Trillmich 1997) and this measure provides an estimate of the historical level of competitive intensity.

Jenssen (1978) speculated that large display repertoires should reduce the risk of injury for lizards when male–male agonistic interactions are frequent. If the outcome of such contests is also influenced by signal complexity, as has been demonstrated in birds (Krebs *et al.* 1978), then we should expect complex signals to evolve with increasing SSD. In the present study, we tested this prediction by exploring whether the degree of intrasexual selection in lizards, as estimated by SSD, predicts the evolution of signal complexity, as measured by repertoire size.

2. METHODS

We first examined all available published accounts of SSD and signal behaviour for iguanian lizards (205 sources covering 133 species). The subset of accounts providing complete information on both signal complexity and SSD (see electronic Appendix A available on The Royal Society's Web site) was

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identified (117 sources covering 63 species) from this larger data set (T. J. Ord, unpublished data). Visual displays of iguanian lizards are principally performed by males and invariably consist of stereotyped head and body movements commonly termed 'head-nod' and/or 'push-up' displays. These 'core' displays are elaborated by the addition of modifiers (Jenssen 1977, 1978), which vary across species and account for a considerable proportion of display diversity. We therefore used the number of display modifiers reported for each species in order to quantify signal complexity. While our hypothesis explicitly focuses upon male–male signal exchanges, some modifiers are also reported to be employed during courtship. SSD was determined from comparisons of male:female snout–vent length. Values of 1 thus indicate sexes of equal size, those greater than 1 larger-male SSD and those less than 1 larger-female SSD.

(a) Calculation of standardized independent contrasts

In order to account for possible phylogenetic non-independence of species data, we gathered additional published data on phylogeny and calculated standardized independent contrasts (Purvis & Rambaut 1995).

No single, published, phylogenetic hypothesis included all species of interest, so a composite tree was compiled from several sources (see electronic Appendix A). In some cases, several phylogenetic hypotheses were available. We 'ranked' hypotheses with those based on combined morphological and molecular data favoured over purely molecular hypotheses, which were in turn preferred over purely morphological hypotheses. While trees constructed from molecular data are not necessarily superior to those based solely on morphology and, indeed, may suffer from their own uncertainty problems (see Wiens & Hollingsworth 2000), those based on molecular data tended to be the more recently proposed hypotheses and were thus favoured. If hypotheses were still equally ranked, those based on parsimony methods of tree construction were given preference. Species synonyms were checked using the 'EMBL Reptile Database' (http://www.embl-heidelberg.de/~uetz/living_reptiles.html).

Using these criteria, the following sources were used to construct a composite phylogenetic hypothesis.

- (i) Agamidae: genera positions followed Macey *et al.* (2000) with *Acanthocercus* positioned by Moody (1980). Species within the genus *Ctenophorus* were based on A. E. Greer (unpublished data).
- (ii) Iguanidae: subfamily positions were based on Schulte *et al.*'s (1998) most resolved hypothesis. Anoles were inferred from Jackman *et al.* (1999) with additional species being positioned from other sources: *Anolis auratus*, *Anolis cupreus* and *Anolis nebulosus* (Stamps *et al.* 1997), *Anolis roquet*, *Anolis extremus*, *Anolis trinitatis*, *Anolis griseus* and *Anolis bonairensis* (Yang *et al.* 1974; Roughgarden & Pacala 1989), *Anolis opalinus* (Burnell & Hedges 1990) and *Anolis carpenteri*, *Anolis sericeus*, *Anolis intermedius* and *Anolis tropidolepis* (Etheridge 1959).
- (iii) Iguaninae were based on Sites *et al.* (1996) and on Wiens & Hollingsworth's (2000) combined morphological and molecular hypothesis with additional *Cyclura* species positioned using Martins & Lamont (1998).
- (iv) Crotaphytinae and genera level positions for Phrynosomatinae were taken from Schulte *et al.* (1998) with additional data for *Holbrookia* and *Callisaurus* from Reeder & Wiens

Table 1. *The correlation of SSD and repertoire size in iguanian lizards*

species data	d.f.	<i>r</i>	one-tailed <i>p</i> -value
raw	62	0.36	0.002
corrected for body size	62	0.37	0.001
independent contrasts	52	0.29	0.018
(polytomies unresolved)			
corrected for body size	52	0.27	0.026
independent contrasts	62	0.29	0.011
(polytomies randomly resolved)			
corrected for body size	62	0.27	0.016

(1996). Species within *Sceloporus* were positioned by Wiens & Reeder (1997). We could find no published hypothesis for *Microlophus*.

While independent contrasts can be calculated from trees possessing polytomies (i.e. where the precise relationship between species is unknown), we also wished to compare contrast-based results with those from the concentrated changes test (CCT) (see below). For this purpose, we conducted additional analyses by randomly resolving polytomies using MacClade software v. 3.08a (Maddison & Maddison 1992, 1999).

Standardized independent contrasts are a common way of controlling for phylogenetic non-independence. We used the program CAIC, v. 2.6.2 (<http://evolve.bio.ic.ac.uk/evolve/software/caic/index.html>) (see also Purvis & Rambaut 1995) to calculate contrasts, which were then used in regression analyses. Data on branch lengths (which represent time since speciation) were only available for a small subset of species. In order to include the maximum number of species in our analyses, we set all branch lengths to be equal. We selected the 'Crunch' algorithm for contrast analyses. Regressions were forced through the origin following Purvis & Rambaut (1995) (see also Garland *et al.* 1992).

SSD in lizards is associated with overall body size (Stamps 1983). Using additional published data (see electronic Appendix A), contrasts for body size (male snout–vent length) were regressed against contrasts for SSD. The residuals from this analysis were then used to control for possible body-size effects in subsequent tests (Losos 1990; Martins & Garland 1991; Blumstein & Armistage 1998).

(b) Calculation of the concentrated changes test

Our hypothesis specifically predicts that the evolution of SSD should precede or occur simultaneously with that of signal complexity. We tested this coevolutionary hypothesis using the CCT (Maddison 1990), which calculates the probability of the observed distribution of two traits on a phylogenetic tree having occurred by chance alone. While the CCT has become increasingly popular (Donoghue 1989; Oakes 1992; Martins 1993; Höglund & Sillén-Tullberg 1994; Hunter 1995; Mitani *et al.* 1996; Pyron 1996; Janz & Nylin 1998; Ortolani & Caro 1998; Nunn 1999; Ortolani 1999), it is still relatively new and has consequently not received as much sensitivity testing (although see Werdelin & Sillén-Tullberg 1995; Lorch & Eadie 1999) as more traditional contrast-based methods (e.g. Díaz-Uriarte & Garland 1996, 1998; Price 1997; Garland & Díaz-Uriarte 1999). However, the CCT allows investigation of the direction of

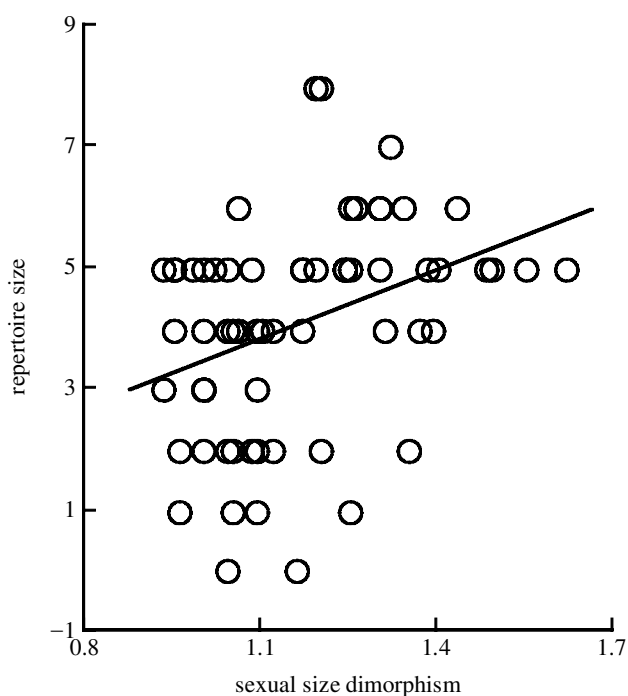


Figure 1. The relationship between repertoire size and SSD (male:female snout-vent length) for iguanian lizards. Data were obtained from a variety of sources (see electronic Appendix A).

evolution and, thus, provides a powerful complementary test of the above prediction.

The CCT can only be conducted with dichotomous data. We created frequency distributions for each variable and then split these at the median value. Hence, species with greater than the median number of display modifiers (median = 4 and range 0–8) were scored as having large repertoires, while those with less than or equal to this value were scored as having small repertoires. Similarly, species with greater than the median SSD (median = 1.12 male:female snout-vent length and range 0.93–1.62) were classified as highly dimorphic.

We employed the same phylogenetic hypothesis used in contrast analyses in order to reconstruct ancestor states for use in the CCT using the phylogenetic program MacClade, v. 3.08a (Maddison & Maddison 1992, 1999). However, the CCT can only be applied to a fully bifurcating tree. We implemented the recommended procedure of randomly resolving polytomies (Maddison & Maddison 1992).

The CCT assumes an equal probability of change along all branches of the tree (Maddison 1990). However, problems may arise when trait reconstructions result in distributions of change that deviate from this null model. In order to ensure that our results were not influenced by this sort of error (Maddison 1990; Lorch & Eadie 1999), we reconstructed five alternative, parsimony-based ancestor states and applied the test to each one. First, we reconstructed ancestor states from continuous data using Swofford & Maddison's (1987) linear parsimony MINSTATE and MAXSTATE and Maddison's (1991) squared-change parsimony algorithms, which were designed specifically for continuously distributed variables. MINSTATE and MAXSTATE reconstructions reflect the smallest and largest sets of equally parsimonious values at each node, respectively. Squared-change parsimony minimizes the sum of the squared changes on branches and forces changes to spread out more evenly over the tree. We then defined areas of the tree

Table 2. The influence of SSD on the evolution of large repertoire size in iguanian lizards

(The numbers of evolutionary gains and losses were calculated following alternative ancestor state reconstructions by parsimony using MacClade, v. 3.08a (Maddison & Maddison 1992, 1999). Maddison's (1990) CCT was used both for determining the number of gains in large repertoires occurring on branches of the tree also possessing high SSD and also whether this distribution could be attributed to chance alone. The number of gains and losses column is the total number of gains (G) and losses (L) in large repertoire size against the number of gains (G) in large repertoire size on branches also possessing high SSD.)

reconstruction	number of gains and losses	<i>p</i> -value
linear parsimony		
MINSTATE	G9 + L3/G6	0.031
MAXSTATE	G6 + L6/G4	0.078
ACCTRAN	G7 + L5/G5	0.023
DELTRAN	G8 + L4/G5	0.045
squared-change parsimony	G11 + L4/G8	0.017

representing large repertoires or high SSD manually using the 'fix state' option in MacClade. Finally, for dichotomously transformed data we also applied ACCTRAN (which accelerates changes towards the root and, thus, maximizes early gains and forces subsequent reversals) and DELTRAN (which delays changes away from the root and, thus, maximizes parallel changes) linear parsimony algorithms (Swofford & Maddison 1987). Repertoire size reconstruction at the root was determined by outgroup analysis (see electronic Appendix A) with additional taxa positioned by Estes *et al.* (1988).

The CCT has low statistical power and is therefore likely to be conservative (Lorch & Eadie 1999). Following Ortolani & Caro (1998) and suggestions by Lorch & Eadie (1999), we considered associations with $p < 0.05$ as highly significant, while p -values falling between 0.05 and 0.1 were considered to be marginally significant. The large number of species being investigated prevented us from calculating an exact probability; we report p -values using simulations (Maddison & Maddison 1992, 1999) based on a sample size of 10 000 replicates. This method randomly generates evolutionary changes on the tree, counting those in areas distinguished as possessing high SSD and on the tree in total, until the specified sample size has been reached. Tests have shown that this method gives similar results to exact p -value calculations (Maddison 1990). Several alternative options are available for randomly generating evolutionary changes on the tree when conducting concentrated changes analyses using simulations. We selected the 'actual changes' simulation option for analyses based on ACCTRAN, DELTRAN and squared-change parsimony reconstructions, while the alternative MINSTATE or MAXSTATE options were selected for analyses based on corresponding trait reconstructions.

3. RESULTS

There was a significant positive relationship between the number of display modifiers and SSD in all regression analyses (table 1 and figure 1). These results demonstrate a reliable association between signal complexity and SSD. However, they do not reveal either the specific historical

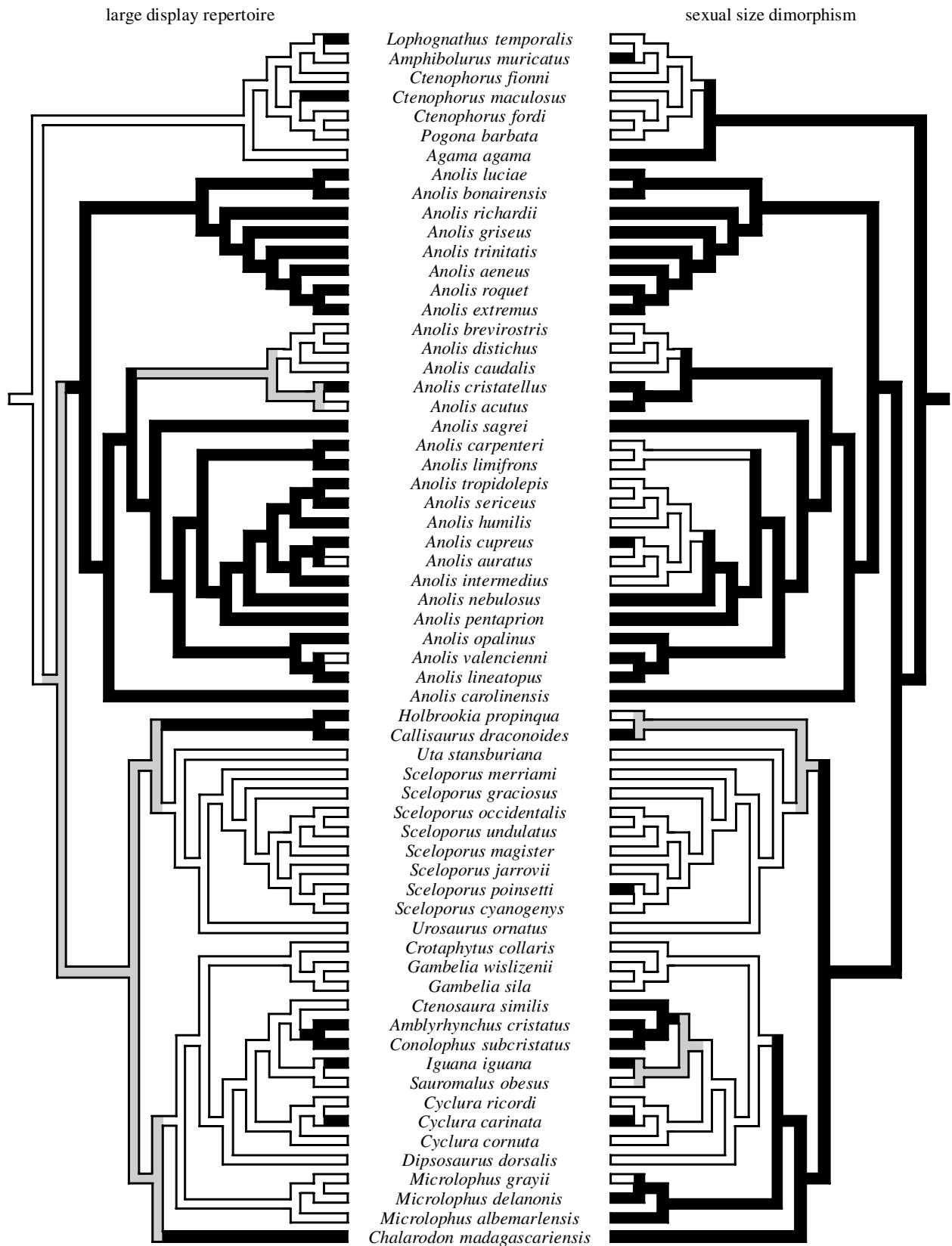


Figure 2. The evolution of large display repertoires and SSD reconstructed from dichotomously transformed data assuming linear parsimony. Data were obtained from a variety of sources (see electronic Appendix A). Filled bars indicate trait present; open bars indicate trait absent; hatched bars indicate equivocal reconstruction resolved in concentrated changes analyses using ACCTRAN or DELTRAN algorithms (see the text for details). Large repertoire size was assumed to be absent at the ancestral node (see electronic Appendix A).

events responsible for this association or the direction of evolutionary change. Four out of five trait reconstructions using the CCT had significantly more gains for large repertoire size on branches of the phylogenetic tree characterized by high levels of SSD than expected by chance (table 2 and figure 2). This relationship provides additional support for our hypothesis that intrasexual selection is one factor driving signal evolution; historical increases in signal complexity have occurred in regions of high pre-existing SSD.

4. DISCUSSION

We used two complementary comparative methods in order to reveal a relationship between signal structure and SSD. The results demonstrate that the size of lizard display repertoires is positively associated with male-biased SSD and that the evolution of SSD has generally preceded or occurred simultaneously with that of large repertoires. Since variation in SSD most probably reflects the level of intrasexual selection (see § 1), we conclude that male–male competition has been an important factor in the evolution of complex visual signals.

Intersexual selection, which usually acts through female mate choice, is commonly invoked in explaining the evolution and design of animal signals (Andersson 1994). In contrast, the effects of intrasexual selection are assumed to be largely restricted to the evolution of weapons, such as horns and spines, and of large male body size. Male–male contests have rarely been considered a significant influence on signal design (although see Krebs *et al.* 1978; Morris & Ryan 1996; Borgia & Coleman 2000).

To the authors' knowledge, our comparative analyses provide the first evidence that the evolution of large display repertoires is associated with SSD. This implies that complex visual signals confer fitness benefits under conditions of high male–male competition in agamids and iguanids. Male lizards of these families defend territories that overlap several female home ranges (Stamps 1983). Border disputes are mediated by signal exchanges that may escalate in intensity and vigour as the distance between rivals decreases and boundaries are progressively infringed (Hover & Jenssen 1976). If participants are evenly matched in size and condition such contests may degenerate into physical combat (Stamps & Krishnan 1994a). As the costs associated with escalated fighting increase, we expect the evolution of signals that permit assessment of opponents and, thus, reduce the risk of injury (Dawkins & Krebs 1978).

The relationship between snout–vent length and dominance in lizards (Stamps & Krishnan 1994b) may have influenced the evolution of display modifiers that increase apparent size (e.g. lateral compression). However, static cues based upon body size provide information about condition integrated over relatively long time-periods. In contrast, dynamic and energetically costly displays, such as those of lizards (Bennett *et al.* 1981; Marler & Moore 1988), reveal moment-to-moment variation in condition and may better predict the outcome of subsequent aggressive interactions (e.g. Clutton-Brock & Albon 1979).

The evolution of honest signals (Zahavi 1977) should be favoured whenever males compete vigorously and the

risk of injury is high. Complex signal repertoires potentially provide more information about fighting ability. We suggest that high levels of male–male competition may be consistently associated with large repertoire size in systems characterized by strong reproductive skew and/or polygamy.

We made the explicit assumption that SSD is the product of intrasexual selection. Alternative explanations based on ecological differences between the sexes are unlikely (Stamps 1983; Vitt 1983; Carothers 1984; Vitt & Cooper 1985; Perry 1996; Johnston 1997; Stamps *et al.* 1997; Wikelski & Trillmich 1997). In contrast, evidence for the origin of SSD through sexual selection is compelling (Trivers 1976; Schoener & Schoener 1980; Stamps 1983; Vitt 1983; Carothers 1984; Vitt & Cooper 1985; Anderson & Vitt 1990; Hews 1990; Perry 1996; Baird *et al.* 1997; Johnston 1997; Stamps *et al.* 1997; Wikelski & Trillmich 1997). Although many authors have concluded that SSD most probably reflects intrasexual selection in lizards (Stamps 1983; Andrews 1985; Tokarz 1995, 1998; Baird *et al.* 1997; Johnston 1997; Jenssen & Nunez 1998), we cannot rule out the possibility that female preference may be acting on male size and signal evolution in some species (Evans 1938a,b; Greenberg & Noble 1944; Jenssen 1970a; Trivers 1972, 1976; Crews 1975; Sigmund 1983; Cooper & Vitt 1993). For example, the correlation between male size and resource acquisition may have favoured female preference for larger males (Cooper & Vitt 1993). Alternatively, where the resource-acquiring attributes of a male are revealed to a female through his ability to compete with other males, male–male competition could evolve through female mate choice (Trivers 1976). In each of these scenarios, the presence of female preference would reinforce the direct effects of intrasexual selection on the evolution of SSD and, thus, indirectly promote the evolution of signal complexity for improved opponent assessment when male–male competition is high.

Many factors play a role in the evolution of communicative systems, and their effects are not mutually exclusive. In order to understand fully the historical processes responsible for signal diversity, we must integrate information about all possible selective forces. Intrasexual selection has rarely been implicated as a major influence on signal design. Our results implicate male–male competition as a significant factor in increasing display complexity in lizards. We suggest that intrasexual selection should be added to the list of social, environmental and perceptual factors that account for signal variation.

We thank P. Harlow for sharing unpublished SSD data, J. B. Losos, E. P. Martins and J. J. Wiens for advice on Iguanidae phylogeny and comments on our phylogenetic selection criteria, S. Hocknull for advice on Agamidae phylogeny, A. E. Greer for sharing unpublished phylogenetic hypotheses, C. L. Nunn for advice on CCT methodology and L. Evans, J. J. Wiens and one anonymous reviewer for constructive comments on a previous version of the manuscript. We are also indebted to the staff of the Macquarie University library for tracking down and obtaining many of the sources used in this study. T.J.O. was supported by a Macquarie University Postgraduate Award, the Macquarie University Postgraduate Research Fund, the Australian Geographic Society, a Sigma Xi grant-in-aid of research, and Rufunsa Technology Services. D.T.B. was funded by an Australian Research Council postdoctoral fellowship and C.S.E.

by an Australian Research Council grant. This research was conducted as partial fulfilment of a doctoral thesis for T.J.O. at Macquarie University.

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