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Size constraints and the evolution of display complexity: why do large lizards have simple displays?

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Social, environmental, and perceptual factors have been suggested to account for the evolution of visual signal diversity in lizards. Previous investigations have inferred that signal complexity may also be related to body size. In this study, we use three complementary comparative analyses to investigate whether body size has influenced macroevolutionary trends in display modifier repertoire size for 110 species of iguanian lizards. We found evidence that signal complexity, as measured by repertoire size, is negatively associated with body size. However, this relationship was not strictly linear. Rather, body size seems to impose a threshold on signal evolution. Specifically, the evolution of large repertoire size appears to be less likely above a particular size threshold, which results in large-bodied lizards having a significantly lower probability of evolving elaborate displays. This relationship may reflect the influence of body size on resource use and the emergent social dynamics it promotes. Large lizards tend to be herbivorous and typically do not defend foraging patches. Consistent with this hypothesis is the previously reported finding of a similar size threshold dividing herbivorous from insectivorous lizards. We suggest to fully understand the evolutionary processes acting on communicative systems, it is important that we identify both the selective forces involved and the nature of their influence. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **76**, 145–161.

ADDITIONAL KEYWORDS: body size – evolution – lizard – signal complexity – the comparative method – visual communication.

INTRODUCTION

The remarkable variety of communicative signals that have captivated biologists since Darwin (1872) result from the interaction of numerous selective forces. Communicative complexity is known to have evolved in response to intersexual selection (Andersson, 1994), intrasexual selection (Ord, Blumstein & Evans, 2001), properties of the signal environment (Endler, 1992), perceptual biases (Ryan & Rand, 1993), predation risk (Stoddard, 1999), and social complexity (Blumstein & Armitage, 1997).

Body size is also an important determinant of signal design. For example, size may constrain the lowest frequency at which vocalizations can be produced (Clutton-Brock & Albon, 1979; Ryan & Brenowitz, 1985; Gouzoules & Gouzoules, 1990; Hauser, 1993) and influence the ability of receivers to locate the source of acoustic signals (Bradbury & Vehrencamp, 1998). Similarly, body size may affect the size, type, and transmission distance of static and dynamic visual cues (Bradbury & Vehrencamp, 1998). The morphology of a sender will determine the maximum size of an ornament, and therefore the area over which it can be perceived. In turn, the resolving power of receiver visual systems is also body-size dependent with smaller animals typically possessing poorer spatial resolution through size constraints on eye morphology (Kirschfeld, 1976).

Agamid and iguanid lizards have an extraordinary diversity of visual signals. Social communication in these animals is conducted primarily through discrete and sequentially predictable motor patterns centred on a core display of push-ups and head-nods. These visual signals are important in territorial acquisi-

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tion/defence (Trivers, 1976; Carpenter, 1978) and mate selection (Jenssen, 1970a; Crews, 1975a,b). Signal complexity, or the repertoire of components used in displays, varies across species and can be quantified by the number of 'modifiers' accompanying a display (Jenssen, 1977). Modifiers may include: dewlap extensions/throat engorging, tail movements, arm waving, crest raising, body compression/inflation, back arching, body raising/tilting and changes in body colour.

We expect body size to influence modifier use during lizard visual displays for two reasons. First, Jenssen (1978) predicted that large-bodied anoline species, which typically roam over large territories (Turner, Jennrich & Weintraub, 1969; Christian & Waldschmidt, 1984), will subsequently conduct signal exchanges over relatively long distances. He therefore suggested that there would be little evolutionary incentive to evolve anything other than a basic display repertoire, and that this repertoire would most likely be limited to conspicuous components for maximizing signal detection by a distant receiver. Second, sexual size dimorphism (hereafter SSD) in lizards is related to body size (Stamps, 1983; Andersson, 1994; McCoy, Fox & Baird, 1994). While in most vertebrates, SSD increases with body size (Andersson, 1994), this pattern does not appear to exist in iguanian lizards and, may in fact, be reversed (Stamps, 1983; Andersson, 1994; McCoy *et al.*, 1994). We have found previously that display repertoire size in lizards is positively associated with SSD and suggest that this is explained by differences in male–male competitive intensity, which is reflected by SSD, influencing the evolution of signal complexity for improved opponent assessment (Ord *et al.*, 2001). As smaller species are typically more size dimorphic, this would therefore predict the evolution of more elaborate signals in smaller species, while larger-bodied species, which presumably experience reduced levels of male–male competition, would have limited selection for large display repertoires.

We investigated whether variation in signal complexity was associated with changes in body size in two ways. First, we tested for a continuous relationship or whether gradual decreases in body size were correlated with gradual increases in modifier use. Second, we searched for evidence of a 'threshold effect' whereby once a particular size has been reached, the evolution of an elaborate display becomes significantly less likely.

MATERIAL AND METHODS

THE DATA

We first examined all available published accounts of signal behaviour and body size for iguanian lizards (156 sources, 133 species). From this larger dataset (T. J. Ord, unpubl. data), the subset of accounts providing complete information on both signal complexity, as quantified by modifier repertoire size, and body size was identified (Tables 1 and 125 sources, 110 species).

One inherent problem in comparing communicative systems across a diverse range of species is obtaining an appropriate and reliable index of signal variation that can be adequately standardized across species. Visual displays in agamid and iguanid lizards almost invariably include the stereotyped head and body movements commonly termed 'head-nod' or 'push-up' displays. Subtle variation does exist within these displays (e.g. differences in display rate, speed, amplitude, etc.) and there are several species for which this variation has been quantified. However, we found that this information could not be incorporated into our display complexity index because of methodological differences among published accounts. Also, these core displays (head-nod and/or push-up) may vary within a species. For example, some anoline lizards are reported to have up to five different core display types, each varying in structure and social context (Hover & Jenssen, 1976; Jenssen & Rothblum, 1977). Thus, it was impractical to obtain a single value for each species based upon core display characteristics.

We focused instead on 'display modifiers', which are postures or movements that accompany and elaborate core displays (Jenssen, 1977). Modifier use varies across species and accounts for a considerable proportion of signal diversity. In addition, information on modifier repertoire size could be readily collated from the literature, and standardized across species. This allowed us to include a large, and taxonomically diverse, range of species in our analyses. While the presence of specific modifiers may be influenced by social context in some species, many are employed consistently across all types of display interaction. We therefore used the number of modifiers accompanying core displays to quantify a form of signal complexity (see also Ord *et al.*, 2001).

Modifiers scored included: back arching, arm waving, body compression/inflation, body raising, body tilting, eye 'orbing', changes in body colouration, lip smacking, crest raising, tail displays, throat displays (dewlap extensions, gorging of the throat, etc.), and tongue protrusions. To be conservative, and to acknowledge the presence/absence of core displays, three species (Table 1) that were reported not to possess a core display were scored as having a repertoire size of 0, irrespective of the presence of any modifiers (one species was observed to possess a throat display, while others had a tail display). Some modifiers are unique to species or species groups. However,

Table 1. Sources consulted for species data

Species	Repertoire size	Body size (mm SVL)	Diet[a]	References[b]
Agama agama	4	128	non-herbivore	1
Amblyrhynchus cristatus	5	318	herbivore	2–4
Amphibolurus muricatus	2	125	non-herbivore	5–8
Anolis acutus	2	66	non-herbivore	9,10
A. aeneus	5	60	non-herbivore	11–18
A. auratus	3	51	non-herbivore	10,19–21
A. bonairensis	6	75	n.d.	18,22
A. brevirostris	1	51	n.d.	23
A. carolinensis	8	64	non-herbivore	10,24–37
A. carpenteri	5	41	n.d.	10,38
A. caudalis	3	51	n.d.	23
A. cooki	6	65	non-herbivore	39
A. cristatellus	6	70	non-herbivore	9,10,39
A. cupreus	5	55	non-herbivore	10,38
A. cybotes	4	81	non-herbivore	40–44
A. distichus	2	50	non-herbivore	10,44
A. equestris	4	166	non-herbivore	29,45
A. evermanni	6	70	non-herbivore	39
A. extremus	5	83	n.d.	18,22
A. grahami	4	63	non-herbivore	34
A. griseus	5	127	n.d.	18,22
A. gundlachi	6	70	non-herbivore	10,39,46
A. humilis	5	38	non-herbivore	10,38
A. intermedius	5	54	n.d.	10,38
A. limifrons	5	40	non-herbivore	10,38,47,48
A. lineatopus	5	70	non-herbivore	10,49
A. luciae	5	85	non-herbivore	18,46
A. marcanoi	5	65	non-herbivore	40–42
A. monensis	6	60	non-herbivore	39
A. nebulosus	5	42	non-herbivore	10,50–53
A. opalinus	8	48	non-herbivore	10,54,55
A. pentaprion	5	75	n.d.	38
A. richardii	5	125	n.d.	18,22
A. roquet	6	80	non-herbivore	18,46
A. sagrei	6	55	non-herbivore	10,25,30,34,37,43
A. sericeus	5	50	n.d.	10,38
A. townsendi	5	45	n.d.	38,56,57
A. trinitatis	6	72	non-herbivore	17,18,46
A. tropidolepis	5	59	n.d.	10,38
A. valencienni[c]	0	85	non-herbivore	58
Brachylophus fasciatus	3	250	herbivore	4,46,59,60
Callisaurus draconoides	5	93	non-herbivore	46,61
Chalarodon madagascariensis	5	87	non-herbivore	62
Chamaelinorops barbouri	2	41	non-herbivore	63
Conolophus subcristatus	6	400	herbivore	4,64
Cophosaurus texanus	5	70	non-herbivore	61
Crotaphytus collaris	4	110	non-herbivore	46,60,65–67
Ctenophorus decresii	5	90	non-herbivore	68
C. fionni	5	96	non-herbivore	6,68
C. fordi	1	53	non-herbivore	6,69–72
C. maculosus	4	69	non-herbivore	6,73
C. nuchalis	5	90	non-herbivore	5,8
C. pictus	2	66	non-herbivore	74
C. vadnappa	5	90	non-herbivore	68
Ctenosaura clarki	2	150	n.d.	4,65,75

Table 1. *Continued*

Species	Repertoire size	Body size (mm SVL)	Diet[a]	References[b]
C. quiquecarinata	0	200	non-herbivore	4,46
C. similis	1	302	herbivore	4,76
Cyclura carinata	5	267	herbivore	4,77,78
C. collei	0	428	n.d.	77,79
C. cornuta	2	355	herbivore	4,77,80
C. cychlura	3	411	n.d.	4,77,79
C. nubila	1	745	herbivore	4,60,77,79,81
C. ricordi	0	355	herbivore	77,80
C. rileyi	0	306	n.d.	4,77,79
Dipsosaurus dorsalis	3	144	herbivore	4,82–84
Gambelia sila	4	97	non-herbivore	85,86
G. wislizenii	3	102	non-herbivore	85–87 17887
Holbrookia lacerata	5	60	non-herbivore	61
H. maculata	5	60	non-herbivore	61
H. propinqua	5	54	non-herbivore	61,88–91
Iguana iguana	7	360	herbivore	4,92–95
Lophognathus temporalis	1	130	non-herbivore	6,8,96
Microlophus albemarlensis	4	104	non-herbivore	60,97
M. bivittatus	4	63	non-herbivore	60,97
M. delanonis	4	129	non-herbivore	60,97
M. duncanensis	4	85	non-herbivore	60,97
M. grayii	4	69	non-herbivore	60,97
M. habelii	4	84	non-herbivore	60,97
M. pacificus	4	84	non-herbivore	60,97
Petrosaurus mearnsi	2	99	non-herbivore	98–100
Phrynocephalus arabicus[c]	0	58	n.d.	101
P. maculatus[c]	0	62	non-herbivore	102,103
Phrynosoma cornutum	0	120	non-herbivore	46,104
P. coronatum	0	107	non-herbivore	46,104
P. douglassii	0	67	non-herbivore	46,104
P. modestum	0	71	non-herbivore	46,104
P. platyrhinos	0	87	non-herbivore	46,104
P. solare	0	113	non-herbivore	46,104
Pogona barbata	6	250	non-herbivore	5,6,29,105,106
Sauromalus obesus	4	164	herbivore	4,107
Sceloporus dugesii	2	88	n.d.	108,109
S. graciosus	4	57	non-herbivore	110–113
S. jarrovii	4	97	non-herbivore	46,108,109,114
S. magister	2	140	non-herbivore	46,109,115
S. merriami	4	58	non-herbivore	109,116,117
S. mucronatus	2	101	n.d.	108,109
S. occidentalis	2	70	non-herbivore	100,118–120
S. ornatus	2	73	n.d.	108,109
S. poinsetti	2	120	non-herbivore	46,108,109
S. torquatus	2	141	n.d.	108
S. un.d.ulatus	3	83	non-herbivore	43,112,113,121–123
Uma exsul	7	100	non-herbivore	124,125
U. inornata	6	113	non-herbivore	100,126
U. notata	6	113	non-herbivore	100,126
U. paraphygas	7	86	n.d.	124,125
U. scoparia	6	113	non-herbivore	100,126
Urosaurus graciosus	2	60	non-herbivore	46,98,99
U. microscutatus	0	40	non-herbivore	46,99
U. ornatus	2	53	non-herbivore	99,117,127–133
Uta stansburiana	4	54	non-herbivore	46,98,99,134–136

Table 1. *Continued*

[a] n.d., no data.

[b] 1, Harris (1964); 2, Carpenter (1966b); 3, Schmidt (1935); 4, Carpenter (1982); 5, Carpenter, Badham & Kimble (1970); 6, Greer (1989); 7, Groom (1973); 8, Wilson & Knowles (1988); 9, Philibosian (1975); 10, Andrews (1979); 11, Stamps & Barlow (1973); 12, Stamps (1978); 13, Stamps & Crews (1976); 14, Stamps (1976); 15, Stamps (1973); 16, Stamps & Krishnan (1994); 17, Gorman (1969); 18, Gorman (1968); 19, Fleishman (1988a); 20, Fleishman (1992); 21, Fleishman (1988b); 22, Roughgarden (1995); 23, Jenssen & Gladson (1984); 24, Cooper (1977); 25, Tokarz & Beck (1987); 26, Jenssen, Greenberg & Hovde (1995); 27, Evans (1935); 28, McMann (1993); 29, Bels (1992); 30, Evans (1938a); 31, Greenberg & Noble (1944); 32, Crews (1975b); 33, Greenberg (1977); 34, Macedonia & Stamps (1994); 35, Ruby (1984); 36, Decourcy & Jenssen (1994); 37, Evans (1938b); 38, Echelle *et al*. (1971); 39, Ortiz & Jenssen (1982); 40, Losos (1985a); 41, Losos (1985b); 42, Macedonia, Evans & Losos (1994); 43, Noble & Teale (1930); 44, Jenssen (1983); 45, Font & Kramer (1989); 46, Rogner (1997); 47, Jenssen & Hover (1976); 48, Hover & Jenssen (1976); 49, Rand (1967); 50, Jenssen (1970a); 51, Jenssen (1971); 52, Jenssen (1970b); 53, Lister & Aguayo (1992); 54, Jenssen (1979a); 55, Jenssen (1979b); 56, Jenssen & Rothblum (1977); 57, Carpenter (1965); 58, Hicks & Trivers (1983); 59, Greenberg & Jenssen (1982); 60, Ackerman (1998); 61, Clarke (1965); 62, Blanc & Carpenter (1969); 63, Jenssen & Feely (1991); 64, Carpenter (1969); 65, Yedlin & Ferguson (1973); 66, Fitch (1956); 67, Greenberg (1945); 68, Gibbons (1979); 69, Webber (1981); 70, Cogger (1978); 71, Tsellarius & Tsellarius (1997); 72, Cogger (1996); 73, Mitchell (1973); 74, Mayhew (1963); 75, Carpenter (1977); 76, Henderson (1973); 77, Martins & J. Lamont 1998; 78, Iverson (1979); 79, Schwartz & Carey (1977); 80, Carey (1975); 81, Buide (1951); 82, Carpenter (1961a); 83, Norris (1953); 84, Parker (1972); 85, Montanucci (1965); 86, Tollestrup (1983); 87, Montanucci (1967); 88, Mason & Adkins (1976); 89, Cooper (1985); 90, Cooper & Guillette (1991); 91, Cooper (1988); 92, Dugan (1982); 93, Distel & J. Veazey (1982); 94, Lazell (1973); 95, Swanson (1950); 96, Blamires (1998); 97, Carpenter (1966a); 98, Carpenter (1962); 99, Purdue & Carpenter (1972b); 100, Stebbins (1966); 101, Ross (1995); 102, Ross (1989); 103, Nikol'skii (1963); 104, Lynn (1965); 105, Brattstrom (1971); 106, Lee & Badham (1963); 107, Nagy (1973); 108, Hunsaker (1962); 109, Martins (1993a); 110, Martins (1991); 111, Martins (1993b); 112, Ferguson (1971); 113, Ferguson (1973); 114, Ruby (1977); 115, Vitt *et al*. (1974); 116, Carpenter (1961b); 117, Milstead (1970); 118, Tarr (1982); 119, Fitch (1940); 120, Purdue & Carpenter (1972a); 121, Cooper & N. Burns (1987); 122, Rothblum &Jenssen (1978); 123, Roggenbuck & Jenssen (1986); 124, Carpenter (1967); 125, de Queiroz (1989); 126, Carpenter (1963); 127, Carpenter & Grubitz (1961); 128, Mahrt (1998); 129, Thompson & Moore (1992); 130, Carpenter & Grubitz (1960); 131, Zucker (1987); 132, Deslippe *et al*. (1990); 133, M'Closkey, Deslippe & Szpak (1990); 134, Ferguson (1970a); 135, Ferguson (1966); 136, Ferguson (1970b).

[c] Species not possessing core displays.

our aim was to quantify repertoire size to obtain an index of signal complexity across species. Thus, we did not compare individual modifiers to assess more subtle differences or similarities in structure with those of other species.

We acknowledge the possibility that, in some cases, the original sources from which we obtained repertoire size information may have underestimated the number of modifiers used. This may have happened if only part of the display repertoire was observed and/or if the focus of the investigator(s) was on other aspects of behaviour. This potential inaccuracy might increase the apparent variation in repertoire size, but there is no reason to expect such errors to be systematically associated with the other factors of interest. The effect will hence be to reduce the likelihood of detecting a significant relationship (see Benton, 1999; Nunn & Barton, 2001).

Snout-vent length (SVL) was used as a measure of body size. Where possible, as our predictions regarding signal use and body size are based primarily on male–male display interactions, maximum male SVL was favoured. However, in species that were reported to have no significant difference between the sexes, or when male data were unavailable, the maximum species SVL was used.

COMPARATIVE ANALYSES

We used three methods to test whether modifier repertoire size is associated with body size: regression analysis using unmanipulated or 'raw' species data; standardized phylogenetic independent contrast analysis (Purvis & Rambaut, 1995); and the concentrated-changes test using ancestor-trait reconstructions (Maddison, 1990). Raw and contrast regression analyses were used to test for a linear relationship, while analysis of variance on contrast data and concentrated-changes analyses were used to test for a threshold effect between modifier use and body size.

PHYLOGENY

Independent contrasts and ancestor trait reconstructions require phylogenetic information. No single phylogenetic hypothesis is available for all species of interest, and different species groups have been analysed to varying degrees of detail. In some cases, there were several conflicting phylogenetic hypotheses available. We 'ranked' each hypothesis and favoured those based on combined data over purely molecular or morphological data. If hypotheses were still equally ranked, we preferred trees constructed using parsimony, then those with the fewest number of polytomies, and finally those more recent in publication. Species synonyms were checked using the 'EMBL Reptile Database' (http://www.embl-heidelberg.de/~uetz/livingreptiles.html).

Using these criteria, we compiled information from 18 sources to construct a composite tree (Fig. 1). Agamidae: genera positions follow Macey *et al*. (2000) with species within the genus *Ctenophorus* based on A. E. Greer (unpubl. data). Iguanidae: subfamilies are based on Schulte *et al.*'s (1998) most resolved hypothesis. Anoles and *Chamaelinorops* were inferred from Jackman *et al*. (1999) with additional species being positioned from other sources: *Anolis auratus, A. cupreus, A. nebulosus* (Stamps, Losos & Andrews, 1997); *A. caudalis, A. cybotes, A. opalinus* (Burnell & Hedges, 1990); *A. cooki, A. evermanni, A. gundlachi, A. monensis (*Roughgarden & Pacala, 1989); *A. bonairensis, A. extremus, A. griseus, A. richardii, A. roquet, A. trinitatis* (Yang, Soule & Gorman, 1974; Roughgarden & Pacala, 1989); *A. carpenteri, A. intermedius, A. sericeus, A. townsendi, A. tropidolepis* (Echelle, Echelle & Fitch, 1971); *A. pentaprion* (Echelle *et al*., 1971; Guyer & Savage, 1992). Crotaphytinae and genera level positions for Phrynosomatinae are taken from Schulte *et al*. (1998) and Reeder & Wiens (1996). Species positions were from several sources: *Phrynosoma* (Garland, 1994); *Sceloporus* (Wiens & Reeder, 1997) with *S. mucronatus* by Mindellm, Sites & Graur (1989); *Uma* (Adest, 1977); *Urosaurus* (Reeder & Wiens, 1996). Iguaninae are based on Sites *et al*. (1996) and on Wiens & Hollingsworth (2000) combined morphological and molecular hypothesis, with *Ctenosaura* and *Cyclura* positioned by de Queiroz (1987) and Martins & Lamont (1998), respectively. No hypotheses for *Holbrookia* or *Microlophus* were found.

INDEPENDENT CONTRAST ANALYSIS ON CONTINUOUS DATA

We calculated standardized independent contrasts (Felsenstein, 1985) for repertoire size and $\log_{10}$(SVL) using the program CAIC v.2.6.2 (http://www.bio.ic.ac.uk/evolve/software/caic/index.html; see also Purvis & Rambaut, 1995), which were then used in regression analyses. Independent contrasts are a common way to control for phylogenetic non-independence of species comparative data in statistical tests (Harvey & Pagel, 1991). While the CAIC program can calculate contrasts from trees possessing polytomies (where the precise phylogenetic relationship between species is unknown), to be consistent with the phylogenetic hypothesis used in the concentrated-changes test (see below), we also conducted additional analyses by randomly resolving polytomies using MacClade software v.3.08a (Maddison & Maddison, 1992, 1999). As branch length data were only available for some species pairs, branch lengths were set equal to include the maximum number of species in our analysis. We selected the 'Crunch' algorithm for contrast analysis, and regressed subsequent data through the origin as required by the method (Purvis & Rambaut, 1995).

INDEPENDENT CONTRAST ANALYSIS ON BODY SIZE CATEGORIES

In addition to calculating contrasts from continuous data, we split body-size data into quartiles to form four broad body-size ranges (0–60, 61–84, 85–120, 121–745 mm SVL). Splitting at the quartiles ensured that size categories were not biased by a preconceived notion of how body size was likely to influence the evolution of repertoire size. Following Dunn, Whittingham & Pitcher (2001), we scored each using categorical dummy variables (see also Winquist & Lemon, 1994; Martin, 1995) and analysed these using the 'Crunch' algorithm in CAIC. Contrasts for each dummy variable were then multiplied with corresponding contrasts for repertoire size. This allowed us to calculate a mean repertoire size for each body size quartile while controlling for possible phylogenetic non-independence. Analysis of variance and *F*-test comparisons were then used to test for differences across size categories.

CONCENTRATED-CHANGES TESTS AND ANCESTOR TRAIT RECONSTRUCTIONS

In order to identify a possible threshold, we used Maddison's (1990) concentrated-changes test to determine whether the evolution of a specified body size range precedes or occurs simultaneously with that of signal complexity. This method requires dichotomous data. We created frequency distributions of both traits. The median value was used to split repertoire size into two discrete variables. Species with more than the median number of display modifiers (4; range: 0–8) were scored as having large repertoires, while those with as many or fewer than this value were scored as having small repertoires. In contrast, body-size data were divided sequentially at the 30th, 40th, 50th, 60th and 70th percentiles (65, 70, 84, 90, 108 mm SVL, respectively). Those species smaller than or equal to a

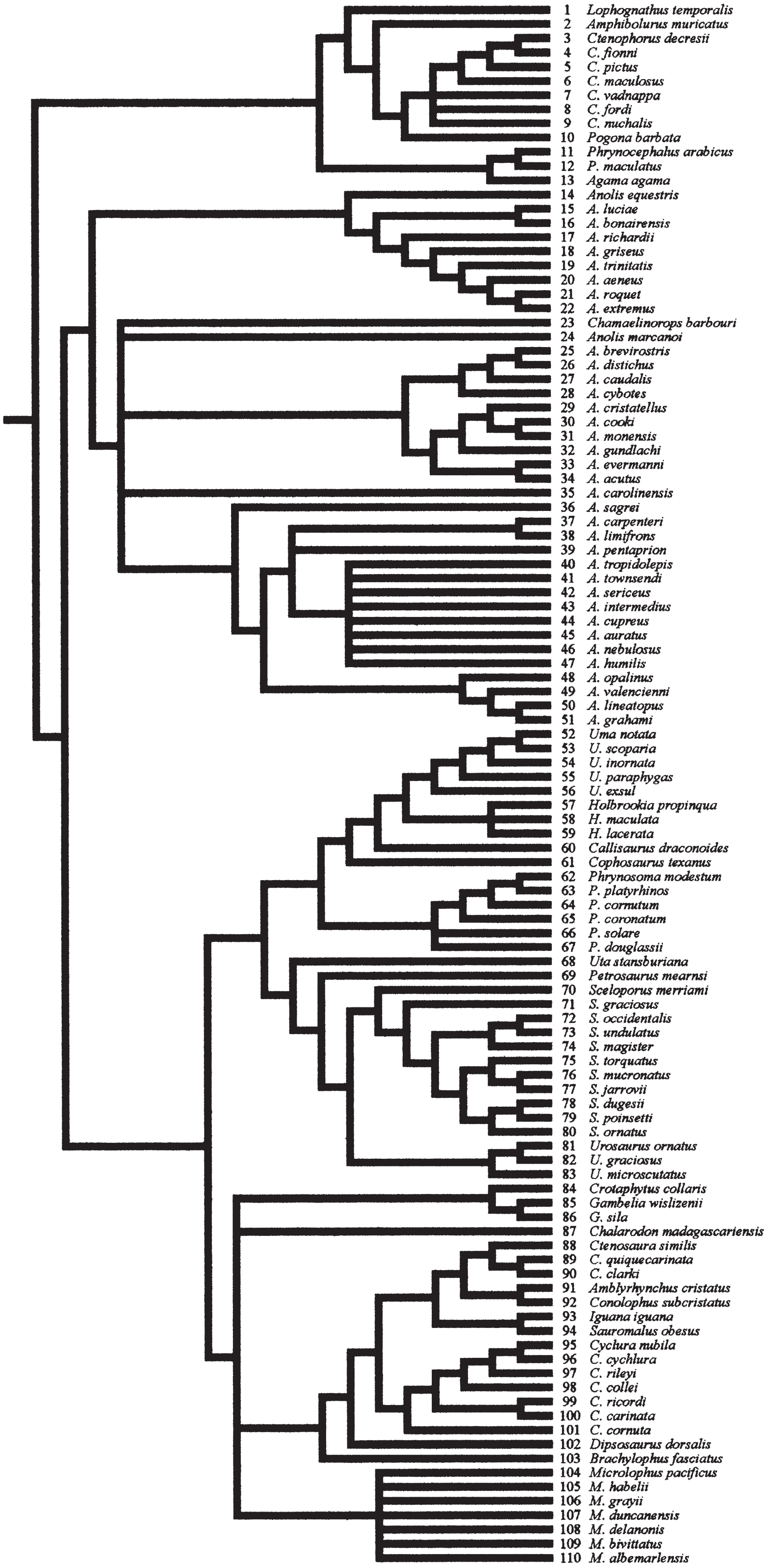

Figure 1. The phylogenetic hypothesis used to calculate independent contrasts and reconstruct ancestor states for concentrated-changes analyses. Polytomies are left unresolved. See text for sources.

percentile boundary were grouped together. This allowed us to create several alternative size ranges to provide a more detailed test of our 'threshold' hypothesis than splitting data at the quartiles, as in contrast analyses.

In order to reconstruct ancestor states for use in the concentrated-changes test we employed the same phylogenetic hypothesis used in contrast analyses. However, the test can only be applied to a fully bifurcating tree. Thus, we randomly resolved polytomies and used the phylogenetic program MacClade v.3.08a (Maddison & Maddison, 1992, 1999) to reconstruct ancestor states assuming parsimony. Equivocal resolutions, where two equally parsimonious trait reconstructions are possible, were resolved using both the available algorithms provided by the program: ACCTRAN (which accelerates changes toward the root) and DELTRAN (which delays changes away from the root).

The concentrated-changes test has low statistical power and is therefore likely to be conservative (Lorch & Eadie, 1999). Following Ortolani & Caro (1996) and suggestions by Lorch & Eadie (1999), we considered associations with $P < 0.05$ as highly significant, while P-values falling between 0.05 and 0.10 were considered as marginally significant (Ord *et al.*, 2001; T.J. Ord, D.T. Blumstein & C.S. Evans, unpubl. data). The large number of species investigated prevented us from calculating an exact probability; we therefore report P-values calculated using a simulation algorithm (Maddison & Maddison, 1992) with 10 000 replicates. This method has been shown to provide consistent results with that of exact P-value calculations (Maddison, 1990).

RESULTS

LINEAR RELATIONSHIP TESTS

There was a significant negative correlation between modifier repertoire size and SVL in a regression of raw species data (d.f. = 109, $R = 0.19$, one-tailed $P = 0.022$; Fig. 2). However, there was no relationship in a series of contrast analyses where we regressed body size on repertoire size (polytomies unresolved: d.f. = 88, $R = 0.08$, one-tailed $P = 0.235$; fully bifurcating tree: d.f. = 109, $R = 0.10$, one-tailed $P = 0.162$).

INDEPENDENT CONTRAST ANALYSIS ON BODY SIZE CATEGORIES

There was no significant difference in contrasts for mean repertoire size across body size categories split at the quartiles (ANOVA, polytomies unresolved: $F_{3,348} = 0.57$, $P = 0.633$; fully bifurcating tree: $F_{3,432} = 0.58$, $P = 0.626$). However, variance in repertoire size at smaller body sizes did increase significantly (Table 2; Fig. 3). This suggests that body size constrains (or is coupled with factors that limit) the evolution of elaborate repertoires in large bodied lizards, while it apparently has little influence on the evolution of display behaviour in smaller bodied lizards.

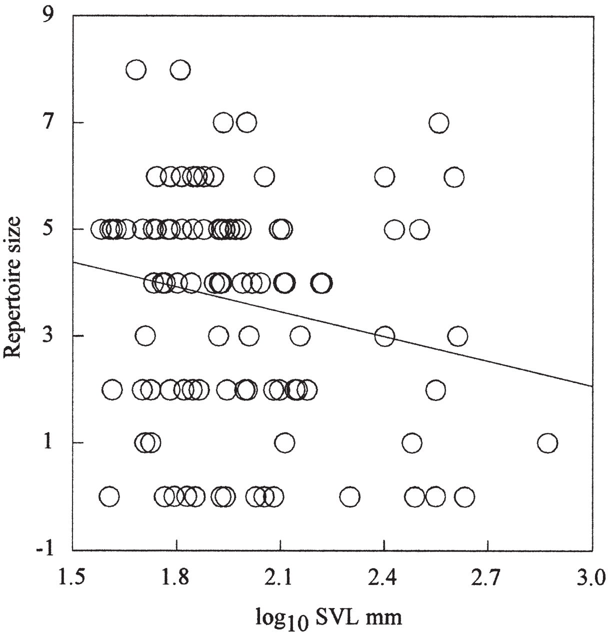

Figure 2. The relationship between repertoire size and body size for 110 iguanian lizards. Data were obtained from a variety of sources (Table 1).

CONCENTRATED-CHANGES TESTS AND ANCESTOR TRAIT RECONSTRUCTIONS

All but two ancestor trait reconstructions had evolutionary gains for large repertoire size in regions of the phylogenetic tree possessing each body size range (Table 3a). For these body-size ranges, we used the concentrated-changes analysis to test for significant historical associations between repertoire size and body size. We found that gains in large repertoire size occurred more often than expected by chance on branches of the phylogenetic tree possessing a body-size range of 0–70 and 0–84 mm SVL (Table 3a; Fig. 4). Only one or two of the total 10 or 11 potential gains in large repertoire size were associated with each body-size range (Table 3a) suggesting a large effect size. Nonetheless, our results provide evidence that species above a particular size threshold – likely to be somewhere between 70 and 84 mm SVL – are significantly less likely to evolve large repertoires. This suggests

Table 2. F-test comparisons of variance in repertoire size contrasts between body size quartiles

Body-size range (mm SVL)	Polytomies unresolved		Fully bifurcating tree	
	F_{87}	P^a	F_{108}	P^a
0–60 vs. 61–84	1.53	NS	1.28	NS
0–60 vs. 85–120	1.34	NS	1.68	0.007
0–60 vs. 121–745	3.43	<0.0001	5.41	<0.0001
61–84 vs. 85–120	0.88	NS	1.31	NS
61–84 vs. 121–745	2.26	0.0002	4.22	<0.0001
85–120 vs. 121–745	2.57	<0.0001	3.22	<0.0001

[a] NS, not significant ($P > 0.10$).

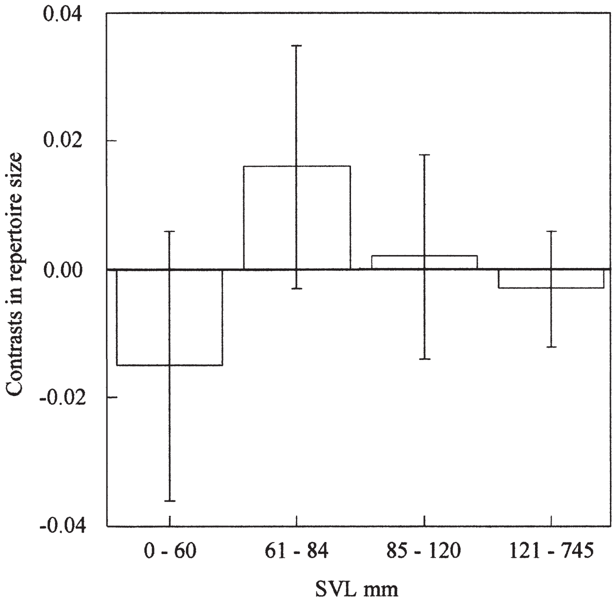

Figure 3. Means ± SE for phylogenetically independent contrasts of repertoire size across four body size quartiles in iguanian lizards calculated from a fully bifurcating tree. The expected size threshold constraining the evolution of elaborate repertoires in large-body lizards occurs between 70 and 84 mm SVL (see Table 3a). Positive values on the y-axis illustrate increases in repertoire size within a size category while negative values indicate decreases in repertoire size. The average represents the magnitude of these trends. Thus, a large positive value demonstrates a strong trend for increased repertoire size with size.

that other, unrelated, evolutionary forces are acting on signal design below the influence of body size.

In order to minimize the possible influence of a herbivorous diet on this size threshold (see discussion), we conducted an additional series of tests that included only species that were known to be insectivores/ carnivores (Table 1). In doing so, we would expect the presence of a size threshold to be weaker or lacking, assuming large-bodied herbivores, that do not typically defend resources, are accounting for small repertoire sizes in large-bodied species. Results were ambiguous and dependent on ancestor reconstruction (Table 3b). Specifically, a size threshold between 70 and 84 mm SVL was still detected using DELTRAN, but not ACCTRAN reconstructions. As a result, there is some support that excluding herbivores reduced or eliminated the presence of a size threshold on repertoire size.

DISCUSSION

We found little evidence to support the prediction that the evolution of signal complexity, as measured by modifier repertoire size, followed a consistent and continuous pattern of increase with corresponding decreases in body size in iguanian lizards. Instead, body size appears to convey a threshold effect on signal complexity by reducing the likelihood of large display repertoires evolving in large-bodied species. However, below this boundary, the selective pressure associated with body size becomes relaxed and species have a greater potential to evolve more elaborate displays.

We expected that body size would be negatively associated with repertoire size for two reasons. First, home range size tends to increase with body size in lizards (Turner *et al*., 1969; Christian & Waldschmidt, 1984) and thus signal exchanges are likely to be conducted over increasingly greater distances in larger-bodied species. Signal transmission over large distances suffer from degradation constraints (Endler, 1992) that may limit displays to those components most readily perceivable. Jenssen (1978) hypothesized

Table 3. The correlated evolution of repertoire size and body size in iguanian lizards when no distinction on diet is made (a) and for non-herbivorous species only (b)

Body-size range	Reconstruction	No. of gains & losses[a]	P[b]
(a) ALL SPECIES			
≤30th percentile (0–65 mm SVL)	ACCTRAN	G10L7/G0	n/a
	DELTRAN	G11L6/G0	n/a
≤40th percentile (0–70 mm SVL)	ACCTRAN	G10L7/G2	0.089
	DELTRAN	G11L6/G1	0.028
≤50th percentile (0–84 mm SVL)	ACCTRAN	G10L7/G2	0.039
	DELTRAN	G11L6/G1	0.010
≤60th percentile (0–90 mm SVL)	ACCTRAN	G10L7/G6	NS
	DELTRAN	G11L6/G7	NS
≤70th percentile (0–108 mm SVL)	ACCTRAN	G10L7/G6	NS
	DELTRAN	G11L6/G7	NS
(b) NON-HERBIVORES			
≤30th percentile (0–65 mm SVL)	ACCTRAN	G7L7/G0	n/a
	DELTRAN	G8L6/G0	n/a
≤40th percentile (0–70 mm SVL)	ACCTRAN	G7L7/G2	NS
	DELTRAN	G8L6/G1	0.087
≤50th percentile (0–84 mm SVL)	ACCTRAN	G7L7/G2	NS
	DELTRAN	G8L6/G1	0.050
≤60th percentile (0–90 mm SVL)	ACCTRAN	G7L7/G6	NS
	DELTRAN	G8L6/G7	NS
≤70th percentile (0–108 mm SVL)	ACCTRAN	G7L7/G6	NS
	DELTRAN	G8L6/G7	NS

[a] Total number of gains (G) and losses (L) in large repertoire size against number of gains (G) in large repertoire size on branches also possessing the specified body-size range.

[b] NS, not significant ($P > 0.10$); n/a, not applicable as no gains were reconstructed in regions of the tree possessing the specified body-size range.

that large-bodied lizards with relatively large territories should therefore be expected to evolve only basic display repertoires; a prediction that was also supported by our previous finding that modifier use is negatively correlated with home range size (T.J. Ord, D.T. Blumstein & C.S. Evans, unpubl. data). Second, there is a tendency for male-biased SSD to be negatively correlated with overall body size in some lizards (Stamps, 1983; McCoy *et al.*, 1994). In a previous study, we found modifier repertoire size increases with SSD (Ord *et al.*, 2001). As a consequence, modifier use is also expected to be negatively correlated with body size.

However, our results reveal a more complex interaction occurring between body size and signal complexity than would be expected initially through associations with SSD and home range size. A more precise interpretation of the relationship is that body size influences repertoire complexity above a certain ‘threshold’. Specifically, at larger body sizes, an elaborate repertoire is less likely to evolve. In contrast, below this threshold, the apparent affect of body size becomes relaxed and other, possibly unrelated, selective forces may then influence the evolution of signal complexity (e.g. Ord *et al.*, 2001; unpubl. data). This interpretation is consistent with the finding that repertoire size varies significantly more in small-bodied species indicating that body-size effects are probably not as important in signal design in these animals as they are in larger lizards.

A potential, though unlikely, hypothesis accounting

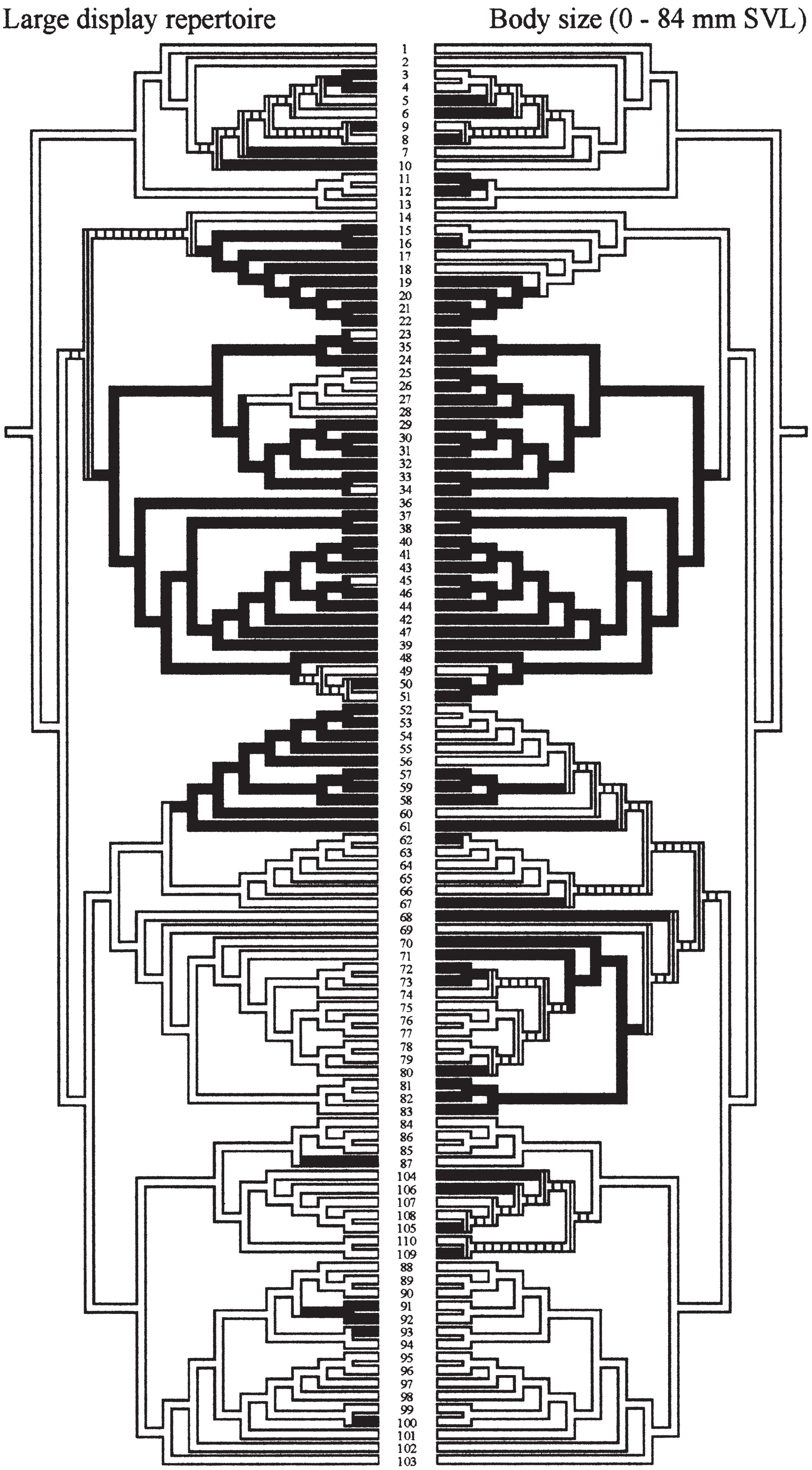

Figure 4. The evolution of large display repertoires and body size ≤84 mm SVL (snout–vent length; 50th percentile cut-off) reconstructed assuming parsimony. Species are represented by numerals (see Fig. 1). Data were obtained from a variety of sources (Table 1). ■ = trait present, □ = trait absent, ◫ = equivocal reconstruction. Large repertoire size was assumed to be absent following outgroup analysis at the ancestral node (see Ord *et al.*, 2001).

for this unusual body-size effect on signal evolution is that it reflects the mass-specific metabolic cost associated with activity, which tends to increase with body size in lizards (Bennett, 1982). We might therefore expect energetic costs to constrain the evolution of elaborate displays in large lizards (Purdue & Carpenter, 1972a; Carpenter, 1982). Whether this would manifest itself through a threshold effect is not clear, as the relationship between cost and activity tends to be relatively linear (Bennett, 1982). In addition, this explanation would be sufficient only in accounting for reductions in *dynamic* display components. However, not all display modifiers making up lizard signal repertoires are dynamic. Thus, larger species could still evolve complex repertoires based on static modifiers alone, which are presumably less energetically costly, if there was a selective advantage to do so.

An alternative, and more likely, explanation is that signal variation reflects differing resource-utilization strategies and the social dynamics they promote. Body-size-dependent energetic requirements influence the type of food resources animals may effectively exploit. Smaller lizards can be supported on an insectivorous diet, but larger species, with their higher metabolic costs, have typically switched to a diet of plant material requiring less energy to harvest (Sokol, 1967; Pough, 1973). For many herbivorous lizards, the availability of food resources can fluctuate dramatically in space and time (see Stamps, 1983, and references therein). The difficulty in defending these food resources economically is believed to have limited the evolution of territoriality and promoted instead non-aggressive aggregations for exploiting clumped resources (Stamps, 1977, 1983). This lack of aggressiveness in large-bodied herbivorous lizards may have eliminated the selective advantage for having complex signals to mediate territorial disputes. Indeed, we have demonstrated previously that non-herbivores are significantly more likely to evolve large display repertoires than herbivores (T.J. Ord, D.T. Blumstein & C.S. Evans, unpubl. data).

This hypothesis would suggest the existence of a corresponding body-size threshold acting on the evolution of a herbivorous diet in iguanian lizards. Two reviews of lizard diets provide some support for this prediction. Pough (1973) found that larger iguanian lizards were herbivorous above a similar threshold [110 mm SVL; approximated from body weight data using Pough's (1973) fig. 1]. Similarly, Schluter (1984) found that the proportion of plant material that iguanid lizards incorporate into their diet increases dramatically from 10% to 80% over a body-size range of just 90–110 mm SVL (his fig. 3). Both thresholds are remarkably similar to what also appears to be affecting the evolution of modifier use. While we have previously tested dietary influences on modifier repertoire size in an earlier study (Ord *et al*. unpubl. data), if a herbivorous diet is influencing the evolution of a size threshold, then excluding herbivorous species from the analyses would, in theory, eliminate the presence of a threshold effect on repertoire size. On conducting such analyses, there is partial support for this prediction (Table 3b). However, we suggest that a direct test of repertoire size and resource defensibility will be necessary to determine whether body size limits the evolution of elaborate signals as a secondary consequence of social characteristics typically associated with being large and herbivorous.

While a body-size threshold on the evolution of signal complexity may be unique to the idiosyncrasies of iguanian energetic requirements, the possibility remains that similar body-size influences may exist in other reptilian and non-reptilian communicative systems. We have identified that body size may influence the presence of visual displays in iguanian lizards by reducing the likelihood of signals evolving at relatively large body sizes. The most interesting and revealing finding of this study is the nature by which this interaction between size and signal design appears to occur. It demonstrates the importance of identifying both the selective forces involved, and the nature through which these forces work, in order to fully understand the evolutionary processes that have led to the extraordinary diversity of animal signals.

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