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
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A griseus5121n.d.18,22A gundlachi670non-herbivore10,39,46A humilis538non-herbivore10,38A intermedius554n.d.10,38A limifrons540non-herbivore10,49A lineatopus570non-herbivore10,49A lineatopus570non-herbivore10,49A luciae585non-herbivore10,49A marcanoi565non-herbivore10,50-53A opalinus848non-herbivore10,54,55A pentaprion575n.d.18,22A roquet680non-herbivore10,25,30,34,37,43A segrei655non-herbivore10,25,30,34,37,43A segreicus555n.d.18,46A tropidolepis545n.d.10,38A valencienni ^e 085non-herbivore17,18,46A valencienni ^e 085non-herbivore4,65,9,60Callisaurus draconoides593non-herbivore4,64Copolophus usbcristatus6400herbivore4,64Copolophus usbcristatus690non-herbivore6,68Chanadoto madagascariensis590non-herbivore6,68Conolophus usbcristatus690non-herbivore6,68Conolophus usbcristatus590non-herbivore6,68 <td>A. granami</td> <td>4 F</td> <td>63 197</td> <td>non-nerbivore</td> <td>34</td>	A. granami	4 F	63 197	non-nerbivore	34
A gundacht670non-herbivore $10,39,46$ A humilis538non-herbivore $10,38,47,48$ A linetrmedius554n.d. $10,38,47,48$ A linetappus570non-herbivore $10,49$ A luciae585non-herbivore $10,49$ A luciae565non-herbivore $10,49$ A monensis660non-herbivore 39 A mothousus542non-herbivore $10,50-53$ A nebulosus542non-herbivore $10,54,55$ A coguinus848non-herbivore $10,54,55$ A repart680non-herbivore $18,46$ A sagrei655non-herbivore $10,25,30,34,37,43$ A sagrei655non-herbivore $10,38$ A traintatis672non-herbivore $10,38$ A traintatis672non-herbivore $10,38$ A traintatis672non-herbivore 58 Brachylophus fasciatus3250herbivore $46,61$ Chalaeodon madagascariensis587non-herbivore 68 Chalarodon madagascariensis596non-herbivore 68 Chalarodon madagascariensis590non-herbivore 68 C forni596non-herbivore 68 C fordi153non-herbivore $6,69-72$ Chalasotas590non-her	A. griseus	0 C	127	n.a.	18,22
A. intermedius 5 56 1001-Herrivore 10,35 A. limitfrons 5 54 n.d. 10,38 A. limitfrons 5 40 non-herbivore 10,38,47,48 A. lineatopus 5 70 non-herbivore 10,49 A. luciae 5 85 non-herbivore 40-42 A. marcanoi 5 65 non-herbivore 39 A. nebulosus 5 42 non-herbivore 10,54,55 A. nebulosus 5 125 n.d. 18,22 A. richardii 5 125 n.d. 18,22 A. roquet 6 80 non-herbivore 10,25,30,34,37,43 A. sericeus 5 50 n.d. 10,38 A. townsendi 5 59 n.d. 10,38 A. valenciennič 0 85 non-herbivore 10,38 A. valenciennič 0 85 non-herbivore 10,38 A. tropidolepis 5 59 n.d. 10,38 A. valenciennič 0 85	A. gundlachi	6 E	70	non-nerbivore	10,39,46
A. Intermeditus 5 34 n.a. 10,35 A. limitrons 5 40 non-herbivore 10,38,47,48 A. lineiatopus 5 70 non-herbivore 10,49 A. luciae 5 65 non-herbivore 40–42 A. monensis 6 60 non-herbivore 40–42 A. monensis 5 42 non-herbivore 10,50–53 A. pentaprion 5 75 n.d. 38 A. roquet 6 80 non-herbivore 10,54,55 A. pentaprion 5 75 n.d. 18,46 A. sagrei 6 55 non-herbivore 10,25,30,34,37,43 A. sagrei 6 55 non-herbivore 10,38 A. troinitatis 6 72 non-herbivore 17,18,46 A. tropidolepis 5 59 n.d. 10,38 A. valencienni [*] 0 85 93 non-herbivore 4,64,59,60 Chalarodon madagascariensis 5 70 non-herbivore 62 Chanaeli	A. humilis	0 F	38	non-nerpivore	10,38
A. limetrons540Inon-herbivore $10,36,47,48$ A. lineatopus570non-herbivore $10,36,47,48$ A. lineatopus570non-herbivore $10,50-53$ A. monensis660non-herbivore $40-42$ A. nebulosus542non-herbivore $10,50-53$ A. opalinus848non-herbivore $10,54,55$ A. opalinus848non-herbivore $10,54,55$ A. richardii5125n.d. $18,22$ A. roquet680non-herbivore $10,25,30,34,37,43$ A. sericeus550n.d. $10,38$ A. tounsendi545n.d. $38,56,57$ A. trinitatis672non-herbivore $17,18,46$ A. valencienti*085non-herbivore 58 Brachylophus fasciatus3250herbivore $46,61$ Chalardon madagascariensis587non-herbivore 62 Chanaelinorops barbouri241non-herbivore 63 Conolophus subcristatus6400herbivore $4,64$ Cophosaurus texanus590non-herbivore $6,68-67$ C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $6,69-72$ C. maculosus590non-herbivore $6,68-67$ C. fordi153non-herbivore $6,69-72$ C. maculosus <td>A. Intermedius</td> <td>0 F</td> <td>54</td> <td>n.a.</td> <td>10,38</td>	A. Intermedius	0 F	54	n.a.	10,38
A. Luciac510Internivore $10,49$ A. luciac585non-herbivore $18,46$ A. marcanoi565non-herbivore 39 A. monensis660non-herbivore $10,50-53$ A. opalinus848non-herbivore $10,50-53$ A. opalinus848non-herbivore $10,54,55$ A. pentaprion575n.d. $18,22$ A. rougut680non-herbivore $10,25,30,34,37,43$ A. sagrei655non-herbivore $10,25,30,34,37,43$ A. sericeus550n.d. $10,38$ A. trinitatis672non-herbivore $17,18,46$ A. trinitatis672non-herbivore $14,6,56,57$ A. trinitatis672non-herbivore $44,6,59,60$ Callisaurus draconoides593non-herbivore $46,61$ Charaeclinorio085non-herbivore $46,61$ Charaeclinorops barboari241non-herbivore 62 Charaeclinorops barboari241non-herbivore 66 Conolophus subcristatus590non-herbivore $66,68$ C. fonni596non-herbivore $6,69-72$ C. maculosus469non-herbivore $6,69-73$ C. nuchalis590non-herbivore $6,68$ C. forni15390non-herbivore $6,68$ C. patalas	A. limentary	Э Е	40	non-nerbivore	10,38,47,48
A. $lactade565non-herbivore10,40A. marcanoi565non-herbivore10,50-53A. monensis660non-herbivore10,54,55A. opalinus848non-herbivore10,54,55A. pentaprion575n.d.38A. richardii5125n.d.18,22A. roquet680non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,38A. townsendi545n.d.38,56,57A. troyidolepis559n.d.10,38A. valenciennie085non-herbivore46,69,60Caliasurus draconoides593non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,66Cophosaurus texanus570non-herbivore61Crotaphytus collaris410non-herbivore63C. fordi153non-herbivore68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herb$	A. Incino	0 F	70 of	non-nerbivore	10,49
A. matranol5651001-herbivore40-42A. monensis660non-herbivore39A. nebulosus542non-herbivore10,50-53A. opalinus848non-herbivore10,54,55A. pentaprion575n.d.38A. richardii5125n.d.18,22A. roquet680non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,25,30,34,37,43A. sericeus550n.d.10,38A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valencienni ^c 085non-herbivore46,61Callisaurus draconoides593non-herbivore62Chalarodon madagascariensis587non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus590non-herbivore61Crotaphytus collaris4110non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi1 <td< td=""><td>A. tucide</td><td>0 F</td><td>60 65</td><td>non-nerbivore</td><td>10,40</td></td<>	A. tucide	0 F	60 65	non-nerbivore	10,40
A. mehnensis000Interfactorie55A. nebulosus542non-herbivore10,50–53A. opalinus848non-herbivore10,54,55A. pentaprion575n.d.38A. richardii5125n.d.18,22A. roquet680non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,25,30,34,37,43A. sericeus550n.d.10,38A. townsendi545n.d.38,56,57A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valenciennic085non-herbivore58Brachylophus fasciatus3250herbivore46,61Chalarodon madagascariensis587non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore46,64Cophosurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore6,68C. fordi153non-herbivore6,68C. fordi15390non-herbivore6,68C. fordi15390non-herbivore6,68C. fordi15390non-herbivore6,69–72C. maculosus469non-herbivore74 <td>A. mananaia</td> <td>0 6</td> <td>60</td> <td>non-herbivore</td> <td>40-42</td>	A. mananaia	0 6	60	non-herbivore	40-42
A. nearborns542Indifference $10,50-53$ A. opalinus848non-herbivore $10,54,55$ A. opalinus575n.d.38A. richardii5125n.d. $18,22$ A. roquet680non-herbivore $10,25,30,34,37,43$ A. sagrei655non-herbivore $10,25,30,34,37,43$ A. sericcus550n.d. $10,38$ A. townsendi545n.d. $38,56,57$ A. tropidolepis559n.d. $10,38$ A. valencientic085non-herbivore 58 Brachylophus fasciatus3250herbivore $46,61$ Chalarodon madagascariensis593non-herbivore 63 Conolophus subcristatus6400herbivore 64 Cophosaurus texanus570non-herbivore 66 C. fionni596non-herbivore 668 C. forni590non-herbivore 668 C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $5,8$ C. pictus266non-herbivore $5,8$ C. pictus266non-herbivore $6,8$ C. pictus266non-herbivore $6,8$ C. vadnappa590non-herbivore $6,8$	A. monensis	5	49	non horbiyoro	10 50 53
A. opatitus543Indicient brower10,5,5,55A. pentaprion575n.d.38A. richardii5125n.d.18,22A. roquet680non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,28,30,34,37,43A. sagrei655non-herbivore10,28,30,34,37,43A. sagrei672non-herbivore17,18,46A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valencienni ^c 085non-herbivore4,66,10Callisaurus draconoides593non-herbivore46,61Chalarodon madagascariensis570non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fordi153non-herbivore68C. fordi153non-herbivore6,69C. maculosus469non-herbivore6,69C. nuchalis590non-herbivore6,73C. nuchalis590non-herbivore6,8C. pictus266non-herbivore68C. pictus260non-herbivore68 <td>A. medulosus</td> <td>0</td> <td>42</td> <td>non horbiyoro</td> <td>10,50-55</td>	A. medulosus	0	42	non horbiyoro	10,50-55
In pendprix510Int.60A. richardii5125n.d.18,22A. roquet680non-herbivore10,25,30,34,37,43A. sagrei655non-herbivore10,25,30,34,37,43A. sericeus550n.d.10,38A. townsendi545n.d.38,56,57A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valencienni*085non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore63Crotaphytus collaris4110non-herbivore68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,68C. fordi153non-herbivore6,69-72C. maculosus469non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68C. pictus266non-herbivore68C. pictus2150n.d.4,65,75	A nentanrion	5	75	n d	38
A. roquet680non-herbivore18,46A. sagrei655non-herbivore10,25,30,34,37,43A. sericeus550n.d.10,38A. townsendi545n.d.38,56,57A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valenciennic085non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fonni596non-herbivore6,69–72C. maculosus469non-herbivore5,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore68C. pictus266non-herbivore68C. vadnappa590non-herbivore6,8C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa	A richardii	5	195	n d	18.99
A. roquet66060Initial Harmer10,40A. sagrei655non-herbivore10,25,30,34,37,43A. sericeus550n.d.10,38A. townsendi545n.d.38,56,57A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valenciennic085non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore46,61Chalarodon madagascariensis587non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fionni596non-herbivore6,68C. fordi153non-herbivore6,69-72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore6,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	A roquet	6	80	non-horbiyoro	18.46
A. sericeus 5 50 n.d. 10,38 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. valenciennic 0 85 non-herbivore 4,46,59,60 Callisaurus draconoides 5 93 non-herbivore 62 Chaardon madagascariensis 5 87 non-herbivore 62 Chaardon madagascariensis 5 87 non-herbivore 63 Conolophus subcristatus 6 400 herbivore 4,64 Cophosaurus texanus 5 70 non-herbivore 68 C. fionni 5 90 non-herbivore 6,68 C. fionni 5 96 non-herbivore 6,69–72 C. maculosus 4 69 non-herbivore 6,73 C. nuchalis 5 90 non-herbivore 5,8 C. pictus	A sagrei	6	55	non-herbivore	10,25 30 34 37 43
A. townedi5601.1.115,00A. townedi545n.d.38,56,57A. trinitatis672non-herbivore17,18,46A. tropidolepis559n.d.10,38A. valencienni"085non-herbivore4,46,59,60Callisaurus draconoides593non-herbivore46,61Chalarodon madagascariensis587non-herbivore62Chanaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fionni596non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore5,8C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore68C. tenosaura clarki2150n.d.4,65,75	A sericeus	5	50	n d	10.38
A. trinitation510Ind. $60,0,01$ A. troitation672non-herbivore17,18,46A. troitation559n.d.10,38A. valencienni ^e 085non-herbivore58Brachylophus fasciatus3250herbivore4,46,59,60Callisaurus draconoides593non-herbivore62Chanaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fionni596non-herbivore6,68C. fordi153non-herbivore6,69–72C. maculosus469non-herbivore5,8C. pictus266non-herbivore5,8C. pictus266non-herbivore68C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590non-herbivore68C. vadnappa590 <td>A townsendi</td> <td>5</td> <td>45</td> <td>n d</td> <td>38 56 57</td>	A townsendi	5	45	n d	38 56 57
A. tropidolepis559n.d.10,38A. tropidolepis559n.d.10,38A. valenciennic085non-herbivore $4,46,59,60$ Brachylophus fasciatus3250herbivore $4,46,59,60$ Callisaurus draconoides593non-herbivore $6,61$ Chalarodon madagascariensis587non-herbivore 62 Chamaelinorops barbouri241non-herbivore 63 Conolophus subcristatus6400herbivore $4,64$ Cophosaurus texanus570non-herbivore 61 Crotaphytus collaris4110non-herbivore 68 C. fionni596non-herbivore $6,68$ C. fordi153non-herbivore $6,73$ C. nuchalis590non-herbivore $5,8$ C. pictus266non-herbivore 74 C. vadnappa590non-herbivore 68 C. pictus266non-herbivore 68 C. pictus266non-herbivore 68 C. vadnappa590non-herbivore 68 C. vadnappa590non-herbivore 68 Ctenosaura clarki2150n.d. $4,65,75$	A trinitatis	6	72	non-herbivore	17 18 46
A. valencientic085non-herbivore58A. valencientic085non-herbivore $4,46,59,60$ Callisaurus fasciatus3250herbivore $4,46,59,60$ Callisaurus draconoides593non-herbivore $46,61$ Chalarodon madagascariensis587non-herbivore 62 Chamaelinorops barbouri241non-herbivore 63 Conolophus subcristatus6400herbivore $4,64$ Cophosaurus texanus570non-herbivore 61 Crotaphytus collaris4110non-herbivore 68 C. fionni596non-herbivore $6,68$ C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $5,8$ C. pictus266non-herbivore 74 C. vadnappa590non-herbivore 68 Ctenosaura clarki2150n.d. $4,65,75$	A. tropidolenis	5	59	n.d.	10.38
Brachylophus fasciatus3250herbivore $4,46,59,60$ Callisaurus draconoides593non-herbivore $46,61$ Chalarodon madagascariensis587non-herbivore 62 Chamaelinorops barbouri241non-herbivore 63 Conolophus subcristatus6400herbivore $4,64$ Cophosaurus texanus570non-herbivore 61 Crotaphytus collaris4110non-herbivore 68 C. fionni590non-herbivore $6,68$ C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $5,8$ C. nuchalis590non-herbivore $6,73$ C. nuchalis590non-herbivore $6,73$ C. vadnappa590non-herbivore $6,88$ C. pictus266non-herbivore $6,88$ C. vadnappa590non-herbivore $6,73$	A. $valencienni^c$	0	85	non-herbivore	58
Callisaurus draconoides593non-herbivore46,61Chalarodon madagascariensis587non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fionni590non-herbivore6,68C. fordi153non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore6,73C. pictus266non-herbivore68C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore6,73C. tenosaura clarki2150n.d.4,65,75	Brachvlophus fasciatus	3	250	herbivore	4.46.59.60
Chalarodon madagascariensis587non-herbivore62Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore68C. fionni590non-herbivore68C. fionni596non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore6,88C. pictus266non-herbivore6,88C. vadnappa590non-herbivore6,73C. vadnappa590non-herbivore6,88C. tenosaura clarki2150n.d.4,65,75	Callisaurus draconoides	5	93	non-herbivore	46.61
Chamaelinorops barbouri241non-herbivore63Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore46,60,65–67Ctenophorus decresii590non-herbivore68C. fionni596non-herbivore6,68C. fordi153non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68	Chalarodon madagascariensis	5	87	non-herbivore	62
Conolophus subcristatus6400herbivore4,64Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore46,60,65–67Ctenophorus decresii590non-herbivore68C. fionni596non-herbivore6,68C. fordi153non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	Chamaelinorops barbouri	2	41	non-herbivore	63
Cophosaurus texanus570non-herbivore61Crotaphytus collaris4110non-herbivore $46,60,65-67$ Ctenophorus decresii590non-herbivore 68 C. fionni596non-herbivore $6,68$ C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $6,73$ C. nuchalis590non-herbivore $5,8$ C. pictus266non-herbivore 74 C. vadnappa590non-herbivore 68	Conolophus subcristatus	6	400	herbivore	4,64
C is the formula for the formula fo	Cophosaurus texanus	5	70	non-herbivore	61
Ctenoporus decresii590non-herbivore68C. fionni596non-herbivore6,68C. fordi153non-herbivore6,69–72C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	Crotaphytus collaris	4	110	non-herbivore	46,60,65-67
C. fonni596non-herbivore $6,68$ C. fordi153non-herbivore $6,69-72$ C. maculosus469non-herbivore $6,73$ C. nuchalis590non-herbivore $5,8$ C. pictus266non-herbivore 74 C. vadnappa590non-herbivore 68 Ctenosaura clarki2150n.d. $4,65,75$	Ctenophorus decresii	5	90	non-herbivore	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	C. fionni	5	96	non-herbivore	6,68
C. maculosus469non-herbivore6,73C. nuchalis590non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	C. fordi	1	53	non-herbivore	6,69–72
C. nuchalis590non-herbivore5,8C. pictus266non-herbivore74C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	C. maculosus	4	69	non-herbivore	6,73
C. pictus 2 66 non-herbivore 74 C. vadnappa 5 90 non-herbivore 68 Ctenosaura clarki 2 150 n.d. 4,65,75	C. nuchalis	5	90	non-herbivore	5,8
C. vadnappa590non-herbivore68Ctenosaura clarki2150n.d.4,65,75	C. pictus	2	66	non-herbivore	74
Ctenosaura clarki 2 150 n.d. 4,65,75	C. vadnappa	5	90	non-herbivore	68
	Ctenosaura clarki	2	150	n.d.	4,65,75

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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

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Table 1. Continued

^an.d., no data.

^b1, 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). ^cSpecies 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 nonindependence 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 Winguist & 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.

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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 reper-



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

toire 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.

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 bodysize 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 bodysize 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

Body-size range (mm SVL)	Polytomies unresolved		Fully bifurcating tree	
	$\overline{F_{\scriptscriptstyle 87}}$	P^{a}	$\overline{F_{108}}$	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

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

 size quartiles

^aNS, not significant (P > 0.10).



Figure 3. Means \pm 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 84mm 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

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

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)

^aTotal 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.

^bNS, 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 smallbodied 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 $\leq 84 \text{ mm}$ SVL (snout-vent length; 50th percentile cutoff) reconstructed assuming parsimony. Species are represented by numerals (see Fig. 1). Data were obtained from a variety of sources (Table 1). \blacksquare = trait present, \Box = trait absent, \Box = equivocal reconstruction. Large repertoire size was assumed to be absent following outgroup analysis at the ancestral node (see Ord *et al.*, 2001).

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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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REFERENCES

Ackerman DV. 1998. The biology of reptilies. Neptune, NJ: TFH Publications.

- Adest GA. 1977. Genetic relationships in the genus Uma (Iguanidae). Copeia 1977: 47–52.
- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press.
- Andrews RM. 1979. Evolution of life histories: a comparison of Anolis lizards from matched island and mainland habitats. Breviora 454: 1–51.
- **Bels VL. 1992.** Functional analysis of the ritualized behavioural motor pattern in lizards: evolution of behaviour and the concept of ritualization. *Zoologische Jahrebuecher Anatomy* **122:** 141–159.
- Bennett AF. 1982. The energetics of reptilian activity. In: Gans C, ed. *Biology of the reptilia*. London: Academic Press, 155–199.
- Benton MJ. 1999. The history of life: large databases in paleontology. In: Harper DAT, ed. *Numerical paleontology*. Chichester: John Wiley & Sons, 249–283.
- **Blamires SJ. 1998.** Circumduction and head bobbing in the agamid lizard *Lophognathus temporalis*. *Herpetofauna* **28**: 51–52.
- Blanc CP, Carpenter CC. 1969. Studies on the Iguanidae of Madagascar. III. Social and reproductive behavior of *Chalarodon madagascariensis*. Journal of Herpetology 3: 125–134.
- Blumstein DT, Armitage KB. 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist* 150: 179–200.
- Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland, MA: Sinauer Associates.
- Brattstrom BH. 1971. Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. Copeia 1971: 484–497.
- **Buide MS. 1951.** Observation on habits of the Cuban Iguana. *Herpetologica* **7:** 124.
- **Burnell KL, Hedges SB. 1990.** Relationships of West Indian *Anolis* (Sauria: Iguanidae): an approach using slow-evolving protein loci. *Caribbean Journal of Science* **26:** 7–30.
- Carey WM. 1975. The rock iguana, Cyclura pinguis, on Anegada, British Virgin Islands, with notes on Cyclura ricordi and Cyclura cornuta on Hispaniola. Bulletin of the Florida State Museum, Biological Sciences 19: 189–234.
- Carpenter CC. 1961a. Patterns of social behavior in the desert iguana, *Dipsosaurus dorsalis*. Copeia 1961: 396–405.
- **Carpenter CC. 1961b.** Patterns of social behaviour of Merriam's canyon lizard (*Sceloporus m. merriami –* Iguanidae). *Southwestern Naturalist* **6:** 138–148.
- Carpenter CC. 1962. A comparison of the patterns of display of Urosaurus, Uta, and Streptosaurus. Herpetologica 18: 145-152.
- Carpenter CC. 1963. Patterns of behavior in three forms of the fringe-toed lizards (Uma – Iguanidae). Copeia 1963: 406–412.
- Carpenter CC. 1965. The display of the Cocos island anole. *Herpetologica* 21: 256–260.
- Carpenter CC. 1966a. Comparative behaviour of the Galapagos lava lizards Tropidurus. In: Bowman R, ed. The Galapagos proceedings of the Galapagos International

Scientific Project. Berkeley, CA: University of California Press, 269–273.

- **Carpenter CC. 1966b.** The marine iguana of the Galapagos islands, its behavior and ecology. *Proceedings of the California Academy of Sciences* **34:** 329–376.
- Carpenter CC. 1967. Display patterns of the Mexican iguanid lizards of the genus *Uma*. *Herpetologica* 23: 285–293.
- Carpenter CC. 1969. Behavioral and ecological notes on the Galapagos land iguanas. *Herpetologica* 25: 155–164.
- Carpenter CC. 1977. The display of *Enyaliosaurus clarki* (Iguanidae: Lacertilia). *Copeia* 1977: 754–758.
- Carpenter CC. 1978. Ritualistic social behaviors in lizards. In: Greenberg N, Maclean PD, eds. *Behavior and neurology* of lizards. Washington, DC: National Institute of Mental Health. 253–267.
- Carpenter CC. 1982. The aggressive displays of iguanine lizards. In: Burghardt GM, Rand AS, eds. *Iguanas of the* world: their behavior, ecology and conservation. New Jersey: Noyes, 215–231.
- Carpenter CC, Badham JA, Kimble B. 1970. Behavior patterns of three species of *Amphibolurus* (Agamidae). *Copeia* 1970: 497–505.
- Carpenter CC, Grubitz GG. 1960. Dominance shifts in the tree lizard (Urosaurus ornatus – Iguanidae). Southwestern Naturalist 5: 123–128.
- Carpenter CC, Grubitz GG. 1961. Time-motion study of a lizard. *Ecology* 42: 199–200.
- Christian KA, Waldschmidt S. 1984. The relationship between lizard home range and body size: a reanalysis of the data. *Herpetologica* 40: 68–75.
- Clarke RF. 1965. An ethological study of the iguanid lizard genera Callisaurus, Cophosaurus, and Holbrookia. Emporia State Research Studies 13: 1–66.
- Clutton-Brock TH, Albon SD. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145–169.
- Cogger HG. 1978. Reproductive cycles, fat body cycles and socio-sexual behaviour in the mallee dragon, *Amphibolurus* fordi (Lacertilia: Agamidae). Australian Journal of Zoology 26: 653–672.
- **Cogger HG. 1996.** *Reptiles and amphibians of Australia*. Port Melbourne: Reed Books.
- Cooper WE Jr. 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, Anolis carolinensis. Copeia 1977: 721–735.
- **Cooper WE Jr. 1985.** Female residency and courtship intensity in a territorial lizard, *Holbrookia propinqua*. *Amphibia-Reptilia* **6:** 63–69.
- Cooper WE Jr. 1988. Aggressive behaviour and courtship rejection in brightly and plainly coloured female keeled earless lizards *Holbrookia propingua*. *Ethology* 77: 265–278.
- Cooper WE Jr, Burns N. 1987. Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. *Animal Behaviour* 35: 526–532.
- Cooper WE Jr, Guillette LJ. 1991. Observations on activity, display behaviour, coloration and androgen levels in the keeled earless lizard, *Holbrookia propinqua*. *Amphibia*-*Reptilia* 12: 57–66.

- Crews D. 1975a. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis* carolinensis. Animal Behaviour 23: 349–356.
- Crews D. 1975b. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. *Herpetologica* 31: 37–47.
- **Darwin C. 1872.** The expression of the emotions in man and the animals. London: Murray.
- **Decourcy KR, Jenssen TA. 1994.** Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Animal Behaviour* **47:** 251–262.
- Deslippe RJ, M'Closkey RT, Dajczak SP, Szpak CP. 1990. A quantitative study of the social behavior of tree lizards, Urosaurus ornatus. Journal of Herpetology 24: 337–341.
- **Distel H, Veazey J. 1982.** The behavioral inventory of the green iguana, *Iguana Iguana*. In: Burghardt GM, Rand AS, eds. *Iguanas of the world*. New Jersey: Noyes, 252–270.
- **Dugan B. 1982.** A field study of the headbob displays of male green iguanas *Iguana iguana*: variation in form and context. *Animal Behaviour* **30**: 327–338.
- **Dunn PO, Whittingham LA, Pitcher TE. 2001.** Mating systems, sperm competition and the evolution of sexual dimorphism in birds. *Evolution* **55:** 161–175.
- Echelle AA, Echelle AF, Fitch HS. 1971. A comparative analysis of aggressive display in nine species of Costa Rican *Anolis. Herpetologica* 27: 271–288.
- Endler JA. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist supplement 139: S125– S153.
- Evans LT. 1935. Winter mating and fighting behavior of Anolis carolinensis as induced by pituitary injections. Copeia 1935: 3-6.
- Evans LT. 1938a. Courtship behaviour and sexual selection of Anolis. Journal of Comparative Psychology 26: 475– 492.
- Evans LT. 1938b. Cuban field studies on territoriality of the lizard, Anolis sagrei. Journal of Comparative Psychology 35: 97–123.
- Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1–15.
- Ferguson GW. 1966. Releasers of courtship and territorial behaviour in the side blotched lizard Uta stansburiana. Animal Behaviour 14: 89–92.
- Ferguson GW. 1970a. Mating behaviour of the side-blotched lizards of the genus Uta (Sauria: Iguandidae). Animal Behaviour 18: 65-72.
- Ferguson GW. 1970b. Variation and evolution of the push-up displays of the side-blotched lizard genus *Uta* (Iguanidae). *Systematic Zoology* 19: 79–101.
- Ferguson GW. 1971. Observations on the behavior and interactions of two sympatric Sceloporus. Utah. American Midland Naturalist 86: 190–196.
- Ferguson GW. 1973. Character displacement of the push-up displays of two partially-sympatric species of spiny lizards, *Sceloporus* (Sauria: Iguanidae). *Herpetologica* 29: 281–284.

- Fitch HS. 1940. A field study of the growth and behavior of the fence lizard. University of California Publications in Zoology 44: 151–172.
- Fitch HS. 1956. An ecological study of the collared lizard Crotaphytus collaris. University of Kansas Publications, Museum of Natural History 8: 213–274.
- Fleishman LJ. 1988a. Sensory influences on physical design of a visual display. Animal Behaviour 36: 1420–1424.
- Fleishman LJ. 1988b. The social behavior of Anolis auratus, a grass anole from Panama. Herpetology 22: 13–23.
- Fleishman LJ. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist* 139: S36–S61.
- Font EF, Kramer M. 1989. A multivariate clustering approach to display repertoire analysis: headbobbing in *Anolis equestris. Amphibia-Reptilia* 10: 331–344.
- Garland T Jr. 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt LJ, Pianka ER, eds. *Lizard ecology: historical* and experimental perspectives. Princeton, NJ: Princeton University Press, 248–249.
- Gibbons JR. 1979. The hind leg pushup display of the Amphibolurus decresii species complex (Lacertilia: Agamidae). Copeia 1979: 29-40.
- **Gorman GC. 1968.** The relationships of *Anolis* of the Roquet species group (Sauria: Iguanidae) III. Comparative study of display behavior. *Breviora* **284:** 1–31.
- **Gorman GC. 1969.** Intermediate territorial display of a hybrid *Anolis* lizard (Sauria: Iguanidae). *Zeitschrift für Tierpsychologie* **26:** 390–393.
- Gouzoules H, Gouzoules S. 1990. Body size effects on the acoustic structure of pigtail Macaque (Macaca nemestrina) screams. Ethology 85: 324–334.
- Greenberg B. 1945. Notes on the social behavior of the collared lizard. *Copeia* 1945: 225–230.
- Greenberg N. 1977. A neuroethological study of display behavior in the lizard Anolis carolinensis (Reptilia, Lacertilia, Iguanidae). American Zoologist 17: 191–201.
- Greenberg N, Jenssen TA. 1982. Displays of captive banded iguanas, Brachylophus fasciatus. In: Burghardt GM, Rand AS, eds. Iguanas of the world: their behavior, ecology and conservation. New Jersey: Noyes, 231–251.
- Greenberg B, Noble GK. 1944. Social behavior of the American chameleon Anolis carolinensis (Voigt). Physiological Zoology 17: 392–439.
- Greer AE. 1989. The biology and evolution of Australian lizards. Chipping Norton: Surrey Beatty & Sons.
- Groom S. 1973. Further notes on the jacky lizard, Amphibolurus muricatus, in captivity. Herpetofauna 6: 6.
- Guyer C, Savage JM. 1992. Anole systematics revisited. Systematic Biology 41: 89–110.
- Harris VA. 1964. The life of the rainbow lizard. London: Hutchinson.
- Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. New York: Oxford University Press.
- Hauser MD. 1993. The evolution of nonhuman primate vocal-

izations: effects of phylogeny, body weight and social context. *American Naturalist* **142:** 528–542.

- Henderson RW. 1973. Ethoecological observations of Ctenosaura similis (Sauria: Iguanidae) in British Honduras. Journal of Herpetology 7: 27–33.
- Hicks RA, Trivers RL. 1983. The social behavior of Anolis valencienni. In: Rhodin AGJ, Miyata K, eds. Advances in herpetology and evolutionary biology. Cambridge, MA: Museum of Comparative Zoology, 570–595.
- Hover EL, Jenssen TA. 1976. Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria, Iguanidae). *Behaviour* 58: 173–191.
- Hunsaker D. 1962. Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. *Evolution* 16: 62–74.
- **Iverson JB. 1979.** Behavior and ecology of the rock iguana Cyclura carinata. Bulletin of the Florida State Museum, Biological Sciences **24:** 1–358.
- Jackman TR, Larson A, de Queiroz K, Losos JB. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Systematic Biology* **48**: 254–285.
- Jenssen TA. 1970a. The ethoecology of Anolis nebulosus (Sauria, Iguanidae). Journal of Herpetology 4: 1–38.
- Jenssen TA. 1970b. Female response to filmed displays of Anolis nebulosus (Sauria, Iguanidae). Animal Behaviour 18: 640–647.
- Jenssen TA. 1971. Display analysis of Anolis nebulosus (Sauria, Iguanidae). Copeia 1971: 197–209.
- Jenssen TA. 1977. Evolution of anoline lizard display behavior. American Zoologist 17: 203–215.
- Jenssen TA. 1978. Display diversity in anoline lizards and problems in interpretation. In: Greenberg N, Maclean PD, eds. *Behavior and neurology of lizards*. Washington, DC: National Institute of Mental Health, 269–285.
- Jenssen TA. 1979a. Display behaviour of male Anolis opalinus (Sauria, Iguanidae): a case of weak display stereotypy. Animal Behaviour 27: 173–184.
- Jenssen TA. 1979b. Display modifiers of Anolis opalinus (Lacertilia: Iguanidae). Herpetologica 35: 21–30.
- Jenssen TA. 1983. Display behavior of two Haitian lizards, Anolis cybotes and Anolis distichus. In: Rhodin AGJ, Miyata K, eds. Advances in herpetology and evolutionary biology. Cambridge, MA: Museum of Comparative Zoology, 552-569.
- Jenssen TA, Feely CF. 1991. Social behavior of the male anoline lizard *Chamaelinorops barbouri*, with comparison to *Anolis. Journal of Herpetology* 25: 454–462.
- Jenssen TA, Gladson NL. 1984. A comparative display analysis of the Anolis brevirostris complex in Haiti. Journal of Herpetology 18: 217–230.
- Jenssen TA, Greenberg N, Hovde KA. 1995. Behavioural profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* 9: 41–662.
- Jenssen TA, Hover EL. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behaviour* 57: 227–240.
- Jenssen TA, Rothblum LM. 1977. Display repertoire analy-

sis of Anolis townsendi (Sauria: Iguanidae) from Cocos Island. Copeia **1977:** 103–109.

- Kirschfeld K. 1976. The resolution of lens and compound eyes. In: Zethler F, Weiler R, eds. *Neural principles in vision*. Berlin: Springer, 354–370.
- Lazell JD. 1973. The lizard genus *Iguana* in the lesser Antilles. *Bulletin of the Museum of Comparative Zoology* 145: 1–28.
- Lee AK, Badham JA. 1963. Body temperature, activity, and behavior of the agamid lizard, *Amphibolurus barbatus*. *Copeia* 1963: 387–394.
- Lister BC, Aguayo AG. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* 61: 717–733.
- Lorch PD, Eadie JA. 1999. Power of the concentrated changes test for correlated evolution. Systematic Biology 48: 170–191.
- Losos JB. 1985a. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. *Copeia* 1985: 905–910.
- Losos JB. 1985b. Male aggressive behavior in a pair of sympatric sibling species. *Breviora* 484: 1–30.
- Lynn RT. 1965. A comparative study of display behavior in *Phrynosoma* (Iguanidae). Southwestern Naturalist 10: 25–30.
- M'Closkey RT, Deslippe RJ, Szpak CP. 1990. Tree lizard distribution and mating system: the influence of habitat and food resources. *Canadian Journal of Zoology* 68: 2083–2089.
- Macedonia JM, Evans CS, Losos JB. 1994. Male Anolis lizards discriminate video-recorded conspecific and heterospecific displays. Animal Behaviour 47: 1220–1223.
- Macedonia JM, Stamps JA. 1994. Species recognition in Anolis grahami (Sauria, Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. Ethology 98: 246–264.
- Macey JR, Schulte JA, Larson A, Ananjeva NB, Wang Y, Pethiyagoda R, Rastegar-Pouyani N, Papenfuss TJ. 2000. Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology 49: 233–256.
- Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44: 539–557.
- **Maddison WP, Maddison DR. 1992.** *MacClade: analysis of phylogeny and character evolution.* Sunderland: Sinauer.
- Maddison WP, Maddison DR. 1999. MacClade Upgrade, v.3.08a. Available free from:
- http://phylogeny.arizona.edu/macclade/macclade.html.
- Mahrt LA. 1998. Territorial establishment and maintenance by female tree lizards, Urosaurus ornatus. Journal of Herpetology 32: 176–182.
- Martin TE. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.
- Martins EP. 1991. Individual and sex differences in the use
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of the push-up display by the sagebrush lizard, *Sceloporus* graciosus. Animal Behaviour **41**: 403–416.

- Martins EP. 1993a. A comparative study of the evolution of Sceloporus push-up displays. American Naturalist 142: 994-1018.
- Martins EP. 1993b. Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Animal Behaviour* 45: 25–36.
- Martins EP, Lamont J. 1998. Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas. *Animal Behaviour* 55: 1685–1706.
- Mason P, Adkins EK. 1976. Hormones and social behaviour in the lizard, Anolis carolinensis. Hormones and Behaviour 7: 75–86.
- Mayhew WW. 1963. Observations on captive Amphibolurus pictus: an Australian agamid lizard. Herpetologica 19: 81–88.
- McCoy JK, Fox SF, Baird TA. 1994. Geographic variation in sexual dimorphism in the collared lizard, *Crotaphytus* collaris (Sauria: Crotaphytidae). Southwestern Naturalist 39: 328–335.
- McMann S. 1993. Contextual signalling and the structure of dyadic encounters in Anolis carolinensis. Animal Behaviour 46: 657–668.
- Milstead WW. 1970. Late summer behavior of the lizards Sceloporus merriami and Urosaurus ornatus in the field. Herpetologica 26: 343–354.
- Mindell DP, Sites JW, Graur D. 1989. Speciational evolution: a phylogenetic test with allozymes in *Sceloporus* (Reptilia). *Cladistics* 5: 49–61.
- Mitchell FJ. 1973. Studies on the ecology of the agamid lizard Amphibolurus maculosus (Mitchell). Transactions of the Royal Society of South Australia 97: 47–76.
- Montanucci RR. 1965. Observations on the San Joaquin leopard lizard, *Crotaphytus wislizenii silus* (Stejneger). *Herpetologica* 21: 270–283.
- Montanucci RR. 1967. Further studies on leopard lizards, Crotaphytus wislizenii. Herpetologica 23: 119–126.
- Nagy KA. 1973. Behavior, diet and reproduction in a desert lizard, Sauromalus obesus. Copeia 1973: 93–102.
- Nikol'skii AM. 1963. Reptiles, Vol. 1: Chelonia and Sauria. Jerusalem: Israel Program for Scientific Translations.
- Noble GK, Teale HK. 1930. The courtship of some iguanid and teiid lizards. *Copeia* 1930: 54–56.
- Norris KS. 1953. The ecology of the desert iguana Dipsosaurus dorsalis. Ecology 34: 265–287.
- Nunn CL, Barton RA. 2001. Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology* 10: 81–98.
- Ord TJ, Blumstein DT, Evans CS. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London, Series B* 268: 737–744.
- Ortiz PR, Jenssen TA. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. Zeitschrift für Tierpsychologie **60**: 227–238.
- **Ortolani A, Caro TM. 1996.** The adaptive significance of color patterns in carnivores: phylogenetic tests of classic hypotheses. In: Gittleman JL, ed. *Carnivore behavior*,

ecology and evolution. London: Cornell University Press, 132–188.

- Parker WS. 1972. Notes on Dipsosaurus dorsalis in Arizona. Herpetologica 28: 226–229.
- Philibosian R. 1975. Territorial behavior and population regulation in the lizards, Anolis acutus and A. cristatellus. Copeia 1975: 428–443.
- Pough FH. 1973. Lizard energetics and diet. *Ecology* 54: 837–844.
- **Purdue JR, Carpenter CC. 1972a.** A comparative study of the body movements of displaying males of the lizard genus *Sceloporus* (Iguanidae). *Behaviour* **41:** 68–81.
- Purdue JR, Carpenter CC. 1972b. A comparative study of the display motion in the iguanid genera Sceloporus, Uta, and Urosaurus. Herpetologica 28: 137–141.
- Purvis A, Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applied Bioscience* 11: 247–251.
- de Queiroz K. 1987. Phylogenetic systematics of Iguanine lizards: a comparative osteological study. University of California Publications in Zoology 118: 1–203.
- de Queiroz K. 1989. Morphological and biochemical evolution in the sand lizards. PhD thesis, University of California, Berkeley.
- Rand AS. 1967. Ecology and social organization in the iguanid lizard Anolis lineatopus. Proceedings of the United States National Museum 122: 1–77.
- Reeder TW, Wiens JJ. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. *Herpetologica Monographs* 10: 43–84.
- Roggenbuck ME, Jenssen TA. 1986. The ontogeny of display behaviour in *Sceloporus undulatus* (Sauria: Iguanidae). *Ethology* 71: 153–165.

Rogner M. 1997. Lizards. Malabar: Krieger.

- **Ross W. 1989.** Notes on ecology and behaviour with special reference to tail signalling in *Phrynocephalus maculatus* (Reptilia: Agamidae). *Fauna of Saudi Arabia* **10:** 417–422.
- Ross W. 1995. Tail signalling in populations of *Phrynocephalus arabicus* (Anderson, 1894) (Reptilia: Agamidae). *Reptilia* 11: 63–71.
- Rothblum L, Jenssen TA. 1978. Display repertoire analysis of *Sceloporus undulatus hyacinthinus* (Sauria: Iguanidae) from South-Western Virginia. *Animal Behaviour* 26: 130– 137.
- **Roughgarden J. 1995.** Anolis lizards of the caribbean: ecology, evolution and plate tectonics. New York: Oxford University Press.
- Roughgarden J, Pacala S. 1989. Taxon cycle among Anolis lizard populations: review of evidence. In: Otte D, Endler JA, eds. Speciation and its consequences. Sunderland, MA: Sinauer Associates, 403–432.
- Ruby DE. 1977. The function of shudder displays in the lizard Sceloporus jarrovi. Copeia 1977: 110–114.
- Ruby DE. 1984. Male breeding success and differential access to females in Anolis carolinensis. Herpetologica 40: 272– 280.
- Ryan MJ, Rand AS. 1993. Sexual selection and signal evolu-

tion: the ghost of biases past. *Philosophical Transactions of* the Royal Society of London, Series B **B340**: 187–195.

- Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* 126: 87–100.
- Schluter D. 1984. Body size, prey size and herbivory in the Galapagos lava lizard *Tropidurus*. Oikos 43: 291–300.
- Schmidt KP. 1935. Notes on the breeding behavior of lizards. Zoological Series of the Field Museum of Natural History 20: 71–76.
- Schulte JA, Macey JR, Larson A, Papenfuss TJ. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family Iguanidae. *Molecular Phylogenetics and Evolution* 10: 367–376.
- Schwartz A, Carey M. 1977. Systematics and evolution in the West Indian iguanid genus Cyclura. Studies on the Fauna of Curacao and Other Caribbean Islands 173: 1–97.
- Sites JW, Davis SK, Guerra T, Iverson JB, Snell HL. 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: a case study in the living iguanas (Squamata, Iguanidae). *Molecular Biology and Evolution* 13: 1087–1105.
- Sokol OM. 1967. Herbivory in lizards. Evolution 21: 192–194.
- Stamps JA. 1973. Displays and social organization in female Anolis aeneus. Copeia 2: 264–272.
- Stamps JA. 1976. Rainfall, activity and social behaviour in the lizard, Anolis aeneus. Animal Behaviour 24: 603–608.
- Stamps JA. 1977. Social behavior and spacing patterns in lizards. In: Gans C, Twinkle DW, eds. *Biology of the reptilia*. New York: Academic Press, 265–334.
- Stamps JA. 1978. A field study of the ontogeny of social behaviour in the lizard Anolis aeneus. Behaviour 66: 1–31.
- Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW, eds. *Lizard ecology: studies of a model organism*. Cambridge, MA: Harvard University Press, 169–204.
- Stamps JA, Barlow GW. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour* 47: 67–94.
- Stamps JA, Crews DP. 1976. Seasonal changes in reproduction and social behavior in the lizard *Anolis aeneus*. Copeia 3: 467–476.
- Stamps JA, Krishnan VV. 1994. Territory acquisition in lizards. I. First encounters. Animal Behaviour 47: 1375– 1385.
- Stamps JA, Losos JB, Andrews RM. 1997. A comparative study of population density and sexual size dimorphism in lizards. *American Naturalist* 149: 64–90.
- Stebbins RC. 1966. A field guide to western reptiles and amphibians. Boston, MA: Houghton Mifflin.
- **Stoddard PK. 1999.** Predation enhances complexity in the evolution of electric fish signals. *Nature* **400**: 254–256.

- Swanson PL. 1950. The iguana iguana iguana (L). Herpetologica 6: 187–193.
- Tarr RS. 1982. Species typical display behaviour following stimulation of the reptilian striatum. *Physiology and Behaviour* 29: 615–620.
- Thompson CW, Moore MC. 1992. Behavioural and hormonal correlates of alternative reproductive strategies in a polygynous lizard: tests of the relative plasticity and challenge hypotheses. *Hormones and Behaviour* 26: 568– 585.
- Tokarz RR, Beck JW. 1987. Behaviour of the suspected lizard competitors Anolis sagrei and Anolis carolinensis: an experimental test for behaviour interference. Animal Behaviour 35: 722–734.
- **Tollestrup K. 1983.** The social behaviour of two species of closely related leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. Zeitschrift für Tierpsychologie **62**: 307–320.
- Trivers RL. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30: 253–269.
- Tsellarius AY, Tsellarius EY. 1997. Behaviour of Varanus griseus during encounters with conspecifics. Asiatic Herpetological Research 7: 108–130.
- Turner FB, Jennrich RI, Weintraub JD. 1969. Home ranges and body size of lizards. *Ecology* 50: 1076–1081.
- Vitt LJ, Congdon JD, Hulse AC, Platz JE. 1974. Territorial aggressive encounters and tail breaks in the lizard Sceloporus magister. Copeia 1974: 990–993.
- Webber P. 1981. To spy on a desert skink. Australian Natural History 19: 270–275.
- Wiens JJ, Hollingsworth BD. 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. *Systematic Biology* 49: 143–159.
- Wiens JJ, Reeder TW. 1997. Phylogeny of the spiny lizards Sceloporus based on molecular and morphological evidence. Herpetological Monographs 11: 1–44.
- Wilson SK, Knowles DG. 1988. Australia's reptiles. Sydney: Collins Books.
- Winquist T, Lemon RE. 1994. Sexual selection and exaggerated male tail length in birds. American Naturalist 143: 95–116.
- Yang SY, Soule M, Gorman GC. 1974. Anolis lizards of the eastern Caribbean: a case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the Roquet group. Systematic Zoology 23: 387–399.
- Yedlin IN, Ferguson GW. 1973. Variations in aggressiveness of free-living male and female collared lizards, *Crotaphytus* collaris. Herpetologica 29: 268–275.
- Zucker N. 1987. Behavior and movement patterns of the tree lizard Urosaurus ornatus (Sauria: Iguanidae) in semi-natural enclosures. Southwestern Naturalist 32: 321– 333.