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Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change

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Abstract

The expression in females of ornaments thought to be the target of sexual selection in males is a long-standing puzzle. Two main hypotheses are proposed to account for the existence of conspicuous ornaments in both sexes (mutual ornamentation): genetic correlation between the sexes and sexual selection on females as well as males. We examined the pattern of ornament gains and losses in 240 species of dragon lizards (Agamidae) in order to elucidate the relative contribution of these two factors in the evolution of mutual ornamentation. In addition, we tested whether the type of shelter used by lizards to avoid predators predicts the evolutionary loss or constraint of ornament expression. We found evidence that the origin of female ornaments is broadly consistent with the predictions of the genetic correlation hypothesis. Ornaments appear congruently in both sexes with some lineages subsequently evolving male biased sexual dimorphism, apparently through the process of natural selection for reduced ornamentation in females. Nevertheless, ornaments have also frequently evolved in both sexes independently. This suggests that genetic correlations are potentially weak for several lineages and sexual selection on females is responsible for at least some evolutionary change in this group. Unexpectedly, we found that the evolutionary loss of some ornaments is concentrated more in males than females and this trend cannot be fully explained by our measures of natural selection.

Introduction

Males of many animals use exaggerated physical features, or ornaments, as sexual advertisements or signals during aggressive encounters. Such ornaments include the spectacular plumage of many birds (e.g. Andersson *et al.*, 2002) and the elongated tail filaments and dark vertical bars exhibited by many fishes (e.g. Basolo, 1990,1991; Moretz & Morris, 2003). The origin of such elaborate ornamentation is a topic of long-standing interest to biologists. Sexual selection (Darwin, 1874) is widely believed to be the driving force behind the evolution of most extravagant male traits. Yet, structures assumed to be exclusively selected for in males are also frequently observed in females (reviewed in Amundsen, 2000b). The prevailing view is that sexual selection acts on males to produce male biased sexual dimorphism. The widespread occurrence of ornamentation in both sexes is therefore puzzling, but surprisingly few studies have examined this phenomenon. Furthermore, traditional emphasis has been on explaining the evolutionary gain of ornamental traits targeted by sexual selection in males. However, a growing number of studies are showing that many sexually selected traits are often lost more times than they have evolved (reviewed in Wiens, 2001). This trend is taxonomically widespread (e.g. insects – Emlen *et al.*, 2005; fish – Basolo, 1996; amphibians – Emerson, 1996; lizards – Wiens, 1999; Quinn & Hews, 2000; birds – Ödeen & Björklund, 2003; de Kort & Ten Cate, 2004) but remains largely unexplained (Wiens, 2001).

Two main hypotheses are proposed to account for the existence of conspicuous ornaments in both sexes: genetic correlation between the sexes (e.g. Lande, 1980) and/or sexual selection on females as well as

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males (e.g. Amundsen, 2000a,b). Darwin realized that many of the structures he postulated to have evolved as a consequence of sexual selection on males were also expressed in females. He explained this phenomenon through a process of 'inheritance' in which traits selected for in males become 'transferred' to females (Darwin, 1874, pp. 236). Lande (1980; Lande & Arnold, 1985) formalized this idea with a mathematical model that explained how a genetic correlation between the sexes might lead to traits selected for only in males to also appear in females. Depending on the strength of this correlation, a trait initially expressed in both sexes could eventually become restricted to one sex through natural selection. Natural selection will favour reduced ornamentation if the production or maintenance of conspicuous ornaments is energetically costly (e.g. Basolo & Alcaraz, 2003) and/or increases the risk of predation (e.g. Wallace, 1889; Stuart-Fox *et al.*, 2003; see also Langerhans *et al.*, 2005). While the strength of sexual selection is enough to override the influence of natural selection on males, this cost will select against the expression of ornaments in females and ultimately result in the evolution of sexual dimorphism. The genetic correlation hypothesis predicts an evolutionary gain in ornamentation in both sexes simultaneously, followed by an eventual loss of ornamentation in females.

Alternatively, female ornamentation may itself be the product of sexual selection (West-Eberhard, 1983; Amundsen, 2000a,b). Frequent intrasexual disputes over territories and other resources among members of both sexes have been documented in a variety of taxa (e.g. fish – Forsgren *et al.*, 2004; lizards – Martins, 1993; birds – Langmore, 1998; Heinsohn *et al.*, 2005; Siefferman & Hill, 2005). Because the sexes share the vast majority of their genome, intrasexual selection will presumably favour the evolution of similar ornamental traits in both males and females, particularly in the presence of genetic correlations (Amundsen, 2000a). Male mate choice is another mechanism by which ornamentation might evolve in females and may even promote female biased sexual dimorphism (Amundsen, 2000a; Griggio *et al.*, 2005). The mutual sexual selection hypothesis predicts an evolutionary gain and subsequent retention of ornamentation in both sexes. Most importantly, the historical appearance of ornaments in males and females does not necessarily have to occur in concert. For example, sexual selection might initially produce male-biased sexual dimorphism followed by mutual ornamentation when homologous traits are sexually selected in females.

Here, we examine macroevolutionary patterns of ornament gain and loss within the family Agamidae (dragon lizards) from across the 'old' world (Africa, Asia and Australo-Papuan region) in order to elucidate the relative contribution of genetic correlation and sexual selection on mutual ornamentation. Sexual ornaments in these and many other lizards include gular sacs, nape/dorsal crests, fleshy spines/horns and rostral appendages (Fig. 1) that are extended or exaggerated through posturing during territorial disputes and may also provide cues during mate choice (Darwin, 1874; Carpenter & Ferguson, 1977; Greer, 1989; Shine, 1990; Manthey & Schuster, 1996; Watkins, 1998; Schulte *et al.*, 2002; Townsend & Larson, 2002; Osborne, 2005). In a previous study (Stuart-Fox & Ord, 2004), we found dragon species that possessed many ornaments are also highly sexually dimorphic in head size, the latter characteristic typically reflecting the intensity of sexual selection experienced by species (e.g. male-male competition often selects for males with larger body or head size – Andersson, 1994). However, dragons living in open habitats, where there is an expected increase in predation pressure, are significantly less likely to evolve ornaments, and this trend seems to be more pronounced in females than males (Stuart-Fox & Ord, 2004). Natural selection appears to have constrained the evolution of ornamentation in dragon lizards although the precise mechanism is unknown. We hypothesized that the types of shelters used by species occupying open vs. closed habitats may exert selection on dragon ornamentation (Stuart-Fox & Ord, 2004). Specifically, species occupying open habitats tend to flee into dense ground vegetation, rock crevices or burrows as their primary escape mechanism whereas closed forest species tend to hide behind tree trunks or branches. Species occupying open habitats should therefore be less likely to evolve protruding ornaments. We test this hypothesis by examining the influence of shelter type on the evolution of ornamentation. Our goal was to determine whether natural selection (via shelter type) explains ornament loss, especially in females as predicted by the genetic correlation hypothesis.

Few attempts have been made to examine the macroevolutionary origins of sexual dimorphism in sexually selected traits (Dunn *et al.*, 2001; Wiens, 2001; Ödeen & Björklund, 2003; Emlen *et al.*, 2005), especially with respect to the relative contribution of genetic correlation and mutual sexual selection on the presence of ornaments in both sexes (Amundsen, 2000b; Wiens, 2001). In addition, the influence of natural selection on the pattern of gains and losses of sexually selected traits remains largely unexplored within a comparative framework. In this study, we use data on ornamentation in males and females for 240 species of dragon lizard to reveal historical patterns of ornament gain and loss. First, we determine if dragons are derived from sexually monomorphic or dimorphic ancestors and whether evolutionary loss in ornamentation differs between the sexes. Second, we test whether natural selection – specifically, the type of shelter used by lizards to avoid predators – predicts the loss, or constrains the evolution, of exaggerated ornaments and whether the influence of natural selection differs by sex.

Methods

Data collection

We compiled a database on agamid ornamentation and shelter type by examining museum specimens and reviewing published literature (see Stuart-Fox & Owens, 2003 for details). Seven different ornament types were observed for specimens representing 240 species and 65% of all recognized agamid lizards globally (Macey *et al.*, 2000; Appendix S1). These ornament types were: rostral appendage, supra-ocular spines/ridges, nape crest/spines, gular sac, dorsal crest/spines, tail crest/spines and enlarged cheeks (e.g. Fig. 1). Physical features unlikely to result from sexual selection were not scored. For example, the Australian thorny devil, *Moloch horridus*, has an impressive array of fleshy body spines not included in our analyses because they putatively function in crypsis and predator avoidance.

The variety of ornaments across the Agamidae family is quite extraordinary, which complicates attempts to trace their evolutionary origins. Some physical features can be reasonably interpreted as convergent or homologous across species (e.g. gular sacs), while others are structurally quite different making classification more difficult (e.g. some rostral appendages – Fig. 1b, d). Rather than attempt to delineate ornaments by subjective interpretations of appearance (e.g. are a few, large dorsal spines in one species homologous to many, smaller dorsal spines in another species?), we instead grouped structures into 'ornament types'. Doing so will tend to underestimate the number of gains and losses reconstructed for some ornaments (e.g. nape crests and nape spines). Our results should therefore be considered conservative.

Information on shelter type was also obtained for 180 species using published sources (Appendix S1). Shelter type was defined as the refuge reported to be used by a species to avoid a potential predation threat. Four general

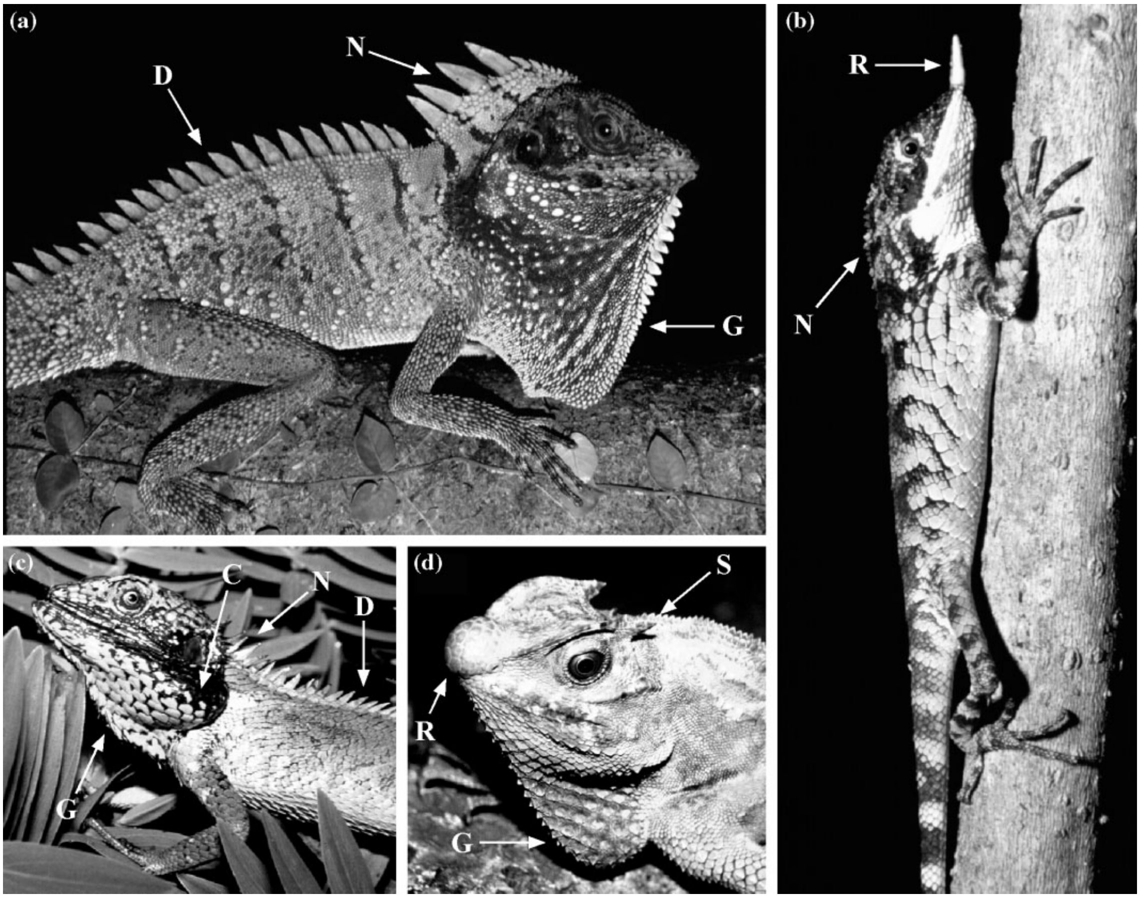


Fig. 1 Agamid ornaments: (a) *Hypsilurus dilophus*, Papua New Guinea, possessing gular pouch (G), nape (N) and dorsal (D) crest/spines; (b) *Ceratophora stoddarti*, Sri Lanka, possessing rostral (R) ornament and nape crest/spines; (c) *Calotes nigrilabris*, Sri Lanka, possessing enlarged cheeks (C), gular pouch, nape and dorsal crest/spines; and (d) *Lyriocephalus scutatus*, Sri Lanka, showing rostral ornament, gular pouch, and supra-ocular (S) spines/ridges. Photos by DSF.

shelter types were found in the literature: rock crevices, soil burrows or 'sand-shimmying' (species that hide by burying themselves in loose sand), ground vegetation (species reported to run under or into small bushes or grass clumps), and trees/shrubs (species that climb onto or hide behind trunks or branches of trees and large shrubs). These are not mutually exclusive, with some species using more than one shelter type (e.g. the Australian painted dragon, *Ctenophorus pictus*, uses both burrows and ground vegetation). For several riparian lizards, the primary escape response is to leap into water (e.g. the Asian sailfin lizards, *Hydrosaurus* spp., and the Australian eastern water dragon, *Physignathus lesuerii*). These species were scored as zero for all four shelter-types.

Comparative analyses

A composite phylogenetic tree was created from several sources as no single phylogeny included all species of interest (see Stuart-Fox & Ord, 2004). The majority of species were positioned using the MtDNA-based phylogenies presented in Schulte *et al.* (2002, 2003) and Macey *et al.* (2000). To resolve relationships within *Phyrnocephalus* and *Draco*, we used Pang *et al.* (2003) and McGuire & Heang (2001), respectively. *Gonocephalus grandis*, *Gonocephalus chameleontinus*, and *Agama hispida* were placed following Moody's (1980) morphological hypothesis. Species not represented in any phylogeny were left as polytomies within their respective genera and resolved randomly across 1000 alternative trees using MACCLADE V3.08A (Maddison & Maddison, 1992, 1999). These randomly resolved trees were then used to examine general patterns of ornament evolution in both ancestor state reconstructions (e.g. Wiens, 1999) and regression analyses (e.g. Losos, 1994; Martins, 1996; Stamps *et al.*, 1997). We assumed branch lengths to be of equal length because branch length information was not available for most of the species investigated. Species synonyms were checked using the EMBL reptile database (http://www.embl-heidelberg.de/~uetz/LivingReptiles.html).

We began our investigation by mapping evolutionary transitions between ornament monomorphism and dimorphism through ancestor state reconstructs using linear parsimony (Swofford & Maddison, 1987; as implemented in MacClade). Species were scored as zero when an ornament type was absent in both sexes, one if present in both sexes, two when present only in males (male biased dimorphism). There were no cases where ornaments were present only in females (female biased dimorphism). Although ornaments present in both sexes may be larger in males, we were primarily interested in the presence or absence of mutual ornamentation. For simplicity, we use the term 'dimorphism' to refer to cases in which the ornament is present only in males (not simply larger in males).

To compare the relative frequency of evolutionary change in the sexes more closely, we also reconstructed the presence (1) or absence (0) of ornament types for males and females separately. All ancestor state analyses were conducted with data entered into MacClade as 'unordered' and mapped onto phylogenies with the assumption that gains and losses in character states were equally likely (e.g. Wiens, 1999; de Kort & Ten Cate, 2004).

Next, we tested whether the type of shelter used by an animal could reliably predict differences in the number of ornaments exhibited by species. Specifically, we wanted to know whether the use of rock crevices and/or burrowing behaviour (i.e. hiding in soil burrows or sand-shimmying) has constrained the evolution of ornaments and whether this trend is differentiated by sex. The total number of ornaments possessed by each sex was tallied and entered into a Phylogenetic General Least Squares (PGLS) regression model (Martins & Hansen, 1997) with shelter type represented by four dichotomous independent variables (i.e. rock crevices, burrows/sand-shimmying, ground vegetation and trees/shrubs). We then followed the technique outlined by Martins (1994) to construct 95% confidence intervals around regression slopes to identify those shelter types correlated with ornament number. As applied here, PGLS uses maximum likelihood to calculate an α parameter that measures the extent phenotypic variation across taxa can be explained by phylogeny and subsequently controls for this effect in the regression model. If α is manually set to 0, results are identical to Felsenstein (1985)'s independent contrasts (FIC), while forcing α to be very large (e.g. 15.50+) produces results that essentially ignore phylogeny all together (TIPS). When PGLS is allowed to estimate α, this parameter can be interpreted as the extent trait data are phylogenetically conservative, or the product of rapid evolutionary change (Martins & Hansen, 1997). All regression analyses were conducted in COMPARE V4.6 (Martins, 2004).

Results

Ornament diversity

Of the 240 species included in our study, 70% of species have at least one ornament, with the most common feature being a nape crest or spines (Table 1). Possessing a gular sac and dorsal crest or spines was also widespread, while the rarest ornament type was a rostral appendage. Highly ornamented species exhibiting four or more ornaments are taxonomically diverse, distributed across 32 species and 13 genera. The most spectacularly ornamented dragons topping our list come from Asia, specifically the Sri Lankan snout agama (*Harpesaurus thescelorhinos*), Indonesian/New Guinea forest dragons (*Hypsilusus dilophus, Hypsilusus nigrigularis*; Fig. 1), Sri Lankan lyre-headed agama (*Lyriocephalus scutatus*; Fig. 1)

Table 1 Frequency of ornament occurrence in dragon lizards of the world.

	Number of species	Number of genera
Included in study	240	49
Ornaments scored		
Rostral appendages	11 (4.6%)	4
In males	11	
In females	7	
In both sexes	7	
Supra-ocular spines/ridges	14 (5.8%)	8
In males	14	
In females	13	
In both sexes	13	
Nape crest/spines	128 (53.3%)	37
In males	128	
In females	112	
In both sexes	112	
Gular sac	87 (36.3%)	23
In males	87	
In females	73	
In both sexes	73	
Dorsal crest/spines	74 (30.8%)	21
In males	74	
In females	66	
In both sexes	66	
Tail crest/spines	41 (17.1%)	13
In males	41	
In females	29	
In both sexes	29	
Enlarged cheeks	43 (17.9%)	18
In males	43	
In females	n/a	
In both sexes	n/a	

Values in brackets are the proportions of ornamented species relative to the total number of species included in the study. The number of species with ornaments present in males, females and shared across the sexes are given.

and the Indian Anaimalai spiny lizard (*Salea anamallayana*).

Origins of dimorphism

For almost all features, ancestor state reconstructions reveal ornament evolution has typically occurred simultaneously in both sexes (no ornament → both sexes ornamented; Fig. 2). The only exception is enlarged cheeks, an attribute that can only be readily distinguished by its appearance in males relative to females (i.e. presence of this trait in females or in both sexes was not scored). Ornament dimorphism has subsequently evolved in many lineages following an evolutionary loss in females (present in both sexes → present in males only (dimorphism); Fig. 2). Nevertheless, the reverse is also true in some lineages: dimorphism has occurred quite frequently as a consequence of evolutionary gains in males only (no ornament → dimorphism), which in several instances has been followed by ornament evolution in females (dimorphism → both sexes ornamented; Fig. 2).

Consider the evolution of a gular sac (Fig. 2), which has experienced between 10 and 76 evolutionary transitions in state depending on how polytomies are resolved (mean over 1000 alternative trees = 36.5). Approximately 49% of these shifts have occurred from no gular sac to presence in both sexes, with females then losing a gular sac to produce male-biased dimorphism 8% of the time. More commonly, the trait is retained in both sexes in extant taxa, or disappears in a lineage following the simultaneous loss of gular sacs in both sexes (13% of total changes). The origin of male-biased dimorphism is probably more accurately described by an evolutionary gain of a gular sac exclusively in males (19% of the evolutionary transitions). Females might then evolve a gular sac (to produce mutual ornamentation), but this accounts for only 7% of changes. This complex history of evolutionary transitions between no ornamentation, mutual ornamentation and dimorphism has been repeated in dragons for most ornament types we examined.

Gains and losses in ornamentation

Trait reconstructions also indicate that similar forms of ornamentation have evolved independently on multiple occasions throughout the history of agamids. This is particularly clear from examination of ornament evolution in males and females separately (Fig. 3). For example, the distribution of rostral appendages in extant species can be explained by at least two, but possibly as many as five, independent evolutionarily origins (mean = 3 in males, 4 in females; Fig. 3; see also Schulte *et al.*, 2002). More strikingly, gular sacs have evolved on 9–29 separate occasions (mean = 15 in males, 23 in females) and this recurrent convergence may be the rule, rather than the exception, for most ornament types (Fig. 3).

Evolutionary losses in ornamentation are also apparently widespread. Nape crest/spines have experienced the largest number of evolutionarily reversals, with ancestor state reconstructions estimating these features have been lost somewhere between 11 and 30 times in males (mean: 21) and 10–26 times in females (mean 19; Fig. 3). Interestingly, gular sacs and dorsal crest/spines also exhibit a high number of evolutionary losses, but this pattern is largely restricted to males, suggesting these ornaments are more readily lost in males than females.

Natural selection on ornament evolution

In regression analyses that ignore phylogeny, the total number of ornaments possessed by males was negatively associated with burrowing behaviour and the use of ground vegetation (TIPS, Fig. 4a). This trend was also found for females, but in addition female ornaments were negatively associated with crevices (TIPS, Fig. 4b).

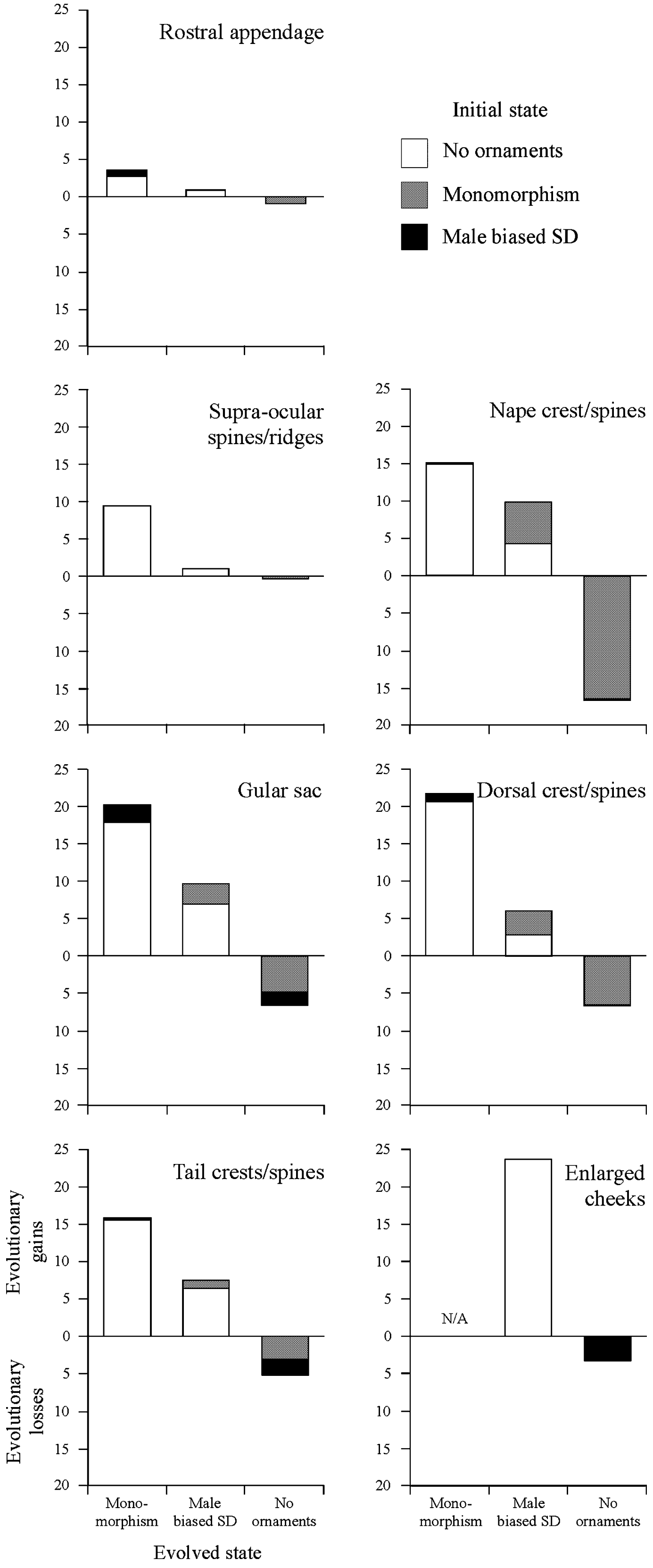
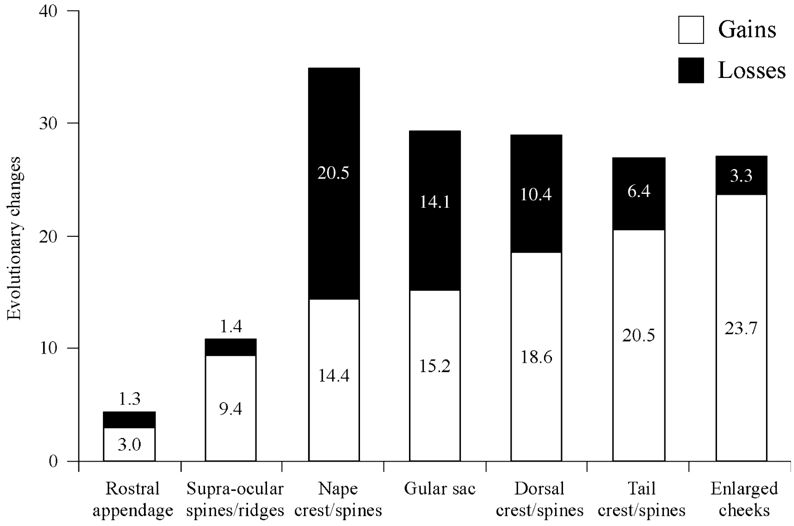


Fig. 2 The evolution of agamid ornamentation. Trait changes were reconstructed by parsimony using MacClade v3.08a (Maddison & Maddison, 1992, 1999), with polytomies randomized across 1000 alternative resolutions. Enlarged cheeks represent the degree of male cheek ornamentation relative to females. For brevity, 'monomorphism' is used to refer to presence of the ornament in both sexes although the trait may be larger in males. For almost all traits, ornaments typically evolve in both sexes simultaneously (i.e. no ornamentation → presence in both sexes; see text for details). Nevertheless, direct transitions to male biased dimorphism have also been common, as a consequence of ornament evolution exclusively in males (i.e. no ornaments → male biased dimorphism).

(a) Male ornamentation



(b) Female ornamentation

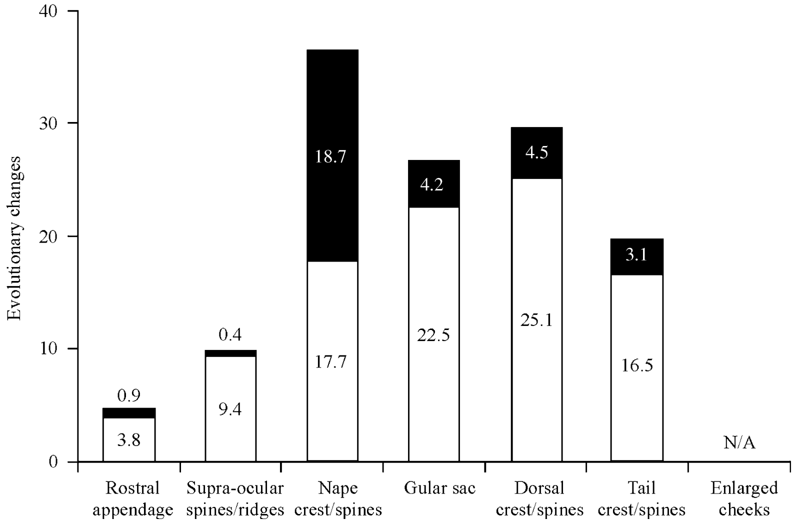


Fig. 3 Evolutionary change in (a) male and (b) female ornamentation in agamid lizards. Values indicate the mean number of gains and subsequent losses of a trait calculated from 1000 alternative resolutions of a polytomous phylogeny. Reconstructions show similar ornaments have evolved following multiple independent evolution events, but also a surprisingly large number of evolutionary losses.

At the other extreme, multiple regression analyses using independent contrasts (FIC) found similar evidence for a negative association between male ornament number and burrowing behaviour, both with a polytomous phylogeny (burrows/sand-shimmy, 95% CI: $-1.84 < B < -0.08$) and for the majority of trees in which polytomies were randomly resolved (95% CI less than 0 = 752 of 1000 trees; FIC, Fig. 4a). In most cases, however, regression slopes for male ornamentation and the use of ground vegetation could not be considered reliably different from zero (polytomous tree: 95% CI: $-1.73 < B < 0.15$; polytomies randomized: 95% CI less than 0 = 90 of 1000 trees, FIC, Fig. 4a). Female ornamentation also tended to be negatively associated with burrowing behaviour using independent contrasts and a polytomous phylogeny (burrows/sand-shimmy, 95% CI: $-1.51 < B < -0.03$) and, to some extent, when polytomies were randomly resolved (461 of 1000 trees; FIC, Fig. 4b). The use of ground vegetation was rarely correlated with female ornamentation (polytomous tree: 95% CI: $-1.14 < B < 0.34$; polytomies randomized: 95% CI less than 0 = 42 of 1000 trees, FIC, Fig. 4a).

When PGLS was allowed to estimate α and partition out the effects of phylogeny more reliably, the total number of ornaments possessed by both males and females was consistently, negatively associated with burrowing behaviour. This was true whether polytomies were left unresolved (males: $-2.04 < B < -0.28$; females: $-1.71 < B < -0.19$) or randomized (males: 1000 of 1000 trees; females: 995 of 1000 trees;

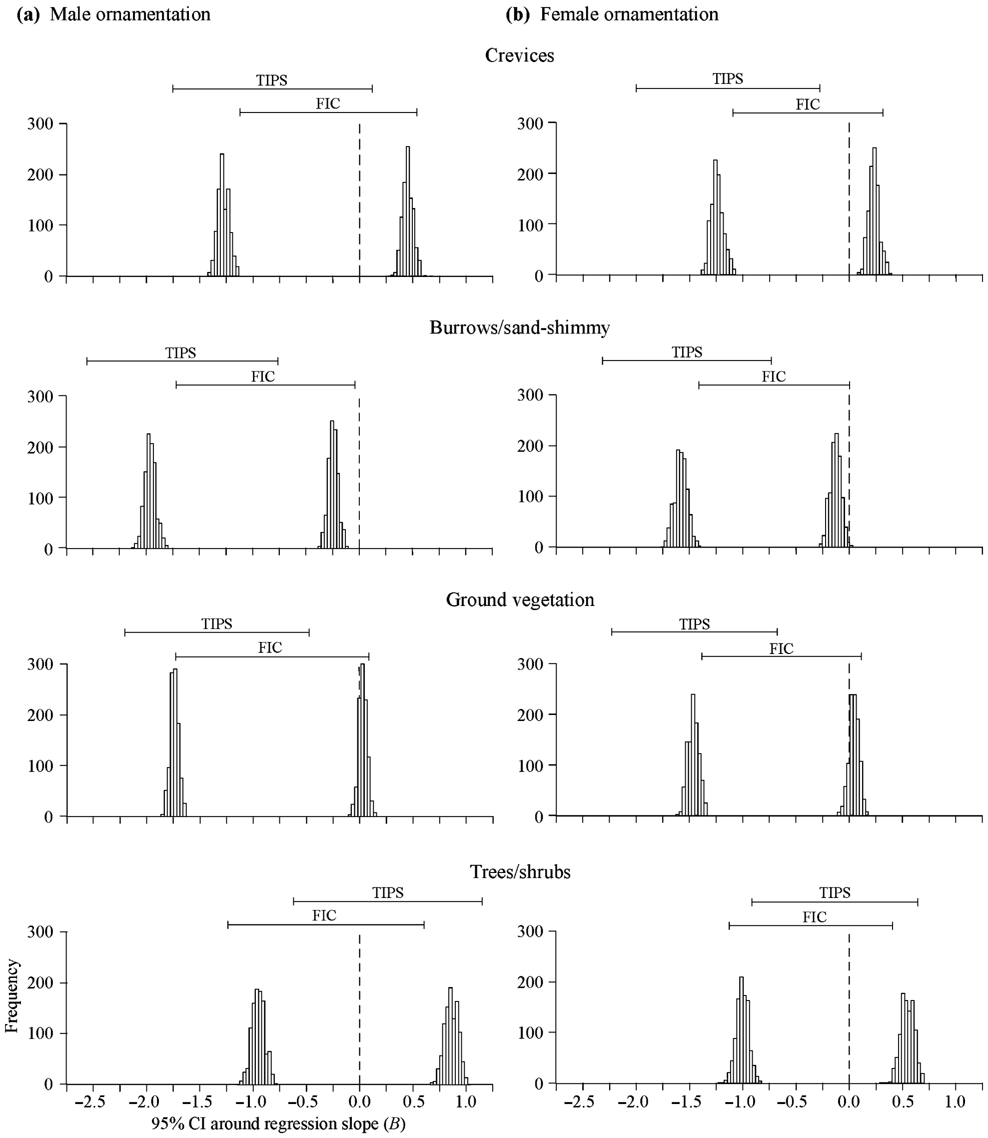


Fig. 4 Shelter type and the evolution of ornamentation in (a) males and (b) females. Frequency distributions represent 95% confidence intervals (CI) around regression slopes from Phylogenetic General Least Squares (PGLS) multiple regression models (n = 180 species). Data was calculated across 1000 alternative resolutions of a polytomous phylogeny. CIs from regression models using phylogenetically uncorrected data (TIPS) and the mean across 1000 trees for Felsenstein (1985)'s Independent Contrasts (FIC) are presented for comparison. A shelter type consisting of burrows and/or 'sand-shimmying' appears to have constrained or promoted the evolutionary loss of multiple ornaments in both sexes (i.e. PGLS CIs for the majority of phylogenetic resolutions fall to the left of zero, indicating a negative regression slope that can be considered reliably different from zero).

Fig. 4). Again, ornamentation was generally not negatively correlated with ground vegetation for either males (polytomous tree: 95% CI: $-1.33 < B < 0.43$; polytomies randomized: 95% CI less than 0 = 139 of 1000) or females (polytomous tree: 95% CI: $-1.32 < B < 0.20$; polytomies randomized: 95% CI less than 0 = 183 of 1000 trees).

As estimated here, PGLS α summarizes the degree of phylogenetic signal for ornamentation and shelter use collectively (i.e. a single estimate is calculated for the regression model as a whole). However, values are quite high, particularly for males (mean ± SE for 1000 trees with polytomies randomized: males = 5.27 ± 0.01; females = 3.86 ± 0.01), suggesting a moderate degree of evolutionary lability in ornamentation. This corresponds well with the large number of evolutionary shifts calculated for most ornaments in trait reconstructions (previous section).

Discussion

The pattern of gains and losses of ornamentation and ornament dimorphism in dragon lizards indicates a role for both genetic correlation and sexual selection on females. In support of the genetic correlation hypothesis, in the majority of cases, both sexes evolve ornaments congruently, with some lineages becoming sexually dimorphic following a subsequent evolutionary loss in females. Contrary to this general trend, however, our results also indicate that some ornaments have originated exclusively in males. In a small proportion of these lineages, mutual ornamentation evolves after the secondary appearance of the trait in females. These cases support the mutual sexual selection hypothesis as the independent evolution of ornaments in each sex is expected to occur when genetic correlations are weak and sexual selection acts on females as well as males.

Although few studies have investigated the macroevolutionary patterns of sexual monomorphism and dimorphism in sexually selected traits, available evidence is similarly mixed. Comparative evidence for the genetic correlation hypothesis has been found in mammals (Wright, 1993) and insects (Baker & Wilkinson, 2001). Sexual dimorphism of canine teeth in mammals (Wright, 1993) and eye span in stalk-eyed flies (Baker & Wilkinson, 2001) both evolved from monomorphic ancestors as a consequence of subsequent trait reduction in females. In contrast, historical reconstructions of dichromatism in birds (Irwin, 1994; Price & Birch, 1996; Burns, 1998) and lizards (Wiens, 1999) reveal monomorphism evolves more frequently from dimorphism, suggesting that genetic correlation does not constrain the evolution of dimorphism and that female ornaments are the product of direct sexual selection.

Quantitative estimates of genetic correlation between the sexes are rarely calculated for sexually selected traits (e.g. Chenoweth & Blows, 2003) and have not been reported for lizards. However, experimental evidence for sexual selection on females is available for many taxa, including lizards. Male mate choice has been reported for some lizards (Orrell & Jenssen, 2002), including dragons (LeBas & Marshall, 2000). However, female lizards have been frequently found to defend territories using visual signals (e.g. Stamps, 1973, 1977; Martins, 1993; Baird & Sloan, 2003; Comendant *et al.*, 2003). This suggests that female–female competition is the more likely mechanism for the secondary gain of female ornamentation rather than male mate choice.

Most often, however, female ornaments are secondarily lost and we found some evidence that ornament loss is driven by the type of shelter used by species to avoid predators. Lizards relying on soil burrows and/or burying themselves in sand either lose or are less likely to evolve protruding ornaments. Such predation-induced natural selection is consistent with our previous finding that species occupying more open habitats, where predation risk is expected to be higher, are significantly less likely to evolve (or retain) conspicuous colouration or ornamentation than lizards found in closed environments (Stuart-Fox & Ord, 2004). Furthermore, habitat openness explains more interspecific variance in female ornamentation than males, suggesting that the influence of natural selection is potentially more pronounced for females (Stuart-Fox & Ord, 2004). Thus, consistent with the genetic correlation hypothesis, ornament dimorphism in agamid lizards has probably evolved most often through natural selection driven loss of female ornamentation from mutually ornamented ancestors.

The genetic correlation hypothesis predicts that females should exhibit the majority of evolutionary losses (c.f. Lande, 1980). However, we found that males have typically experienced more evolutionary losses than females for several ornament types. The loss of male sexually selected traits is a surprisingly widespread, and still largely unexplained, phenomenon (e.g. Ödeen & Björklund, 2003; de Kort & Ten Cate, 2004; see Wiens, 2001 for review). There are several hypotheses that might account for the loss of male ornaments in agamids. The risk of predation associated with possessing conspicuous morphology might have facilitated trait loss in male lizards (Wiens, 1999; Stuart-Fox & Ord, 2004). Dragons with fewer ornaments are typically found in environments expected to be associated with increased predation pressure, however, this trend seems to be more apparent in females than males (Stuart-Fox & Ord, 2004). The type of shelter used by species to escape predators appears to have prompted the loss (and/or constrained the evolution) of ornaments, but the strength of this relationship is generally consistent across both sexes.

Another explanation for loss of male ornamentation is that a historical shift in the direction of sexual selection may have occurred (e.g. Iwasa & Pomiankowski, 1995) because of ecological shifts, changes in female preferences, or demographic processes. For example, a drastic reduction in population size might lead to a preferred male phenotype becoming extremely rare, resulting in females becoming less choosy due to greater mate searching costs. Female mate preferences may subsequently shift following recovery from a population bottleneck. This process has been suggested to account for the loss of complex song and subsequent gain of elaborate plumage in peacock-pheasants (Ödeen & Björklund, 2003). Similar founder effects and/or genetic drift might explain why some male dragons no longer possess particular types of ornamentation. The loss of exaggerated traits used in opponent assessment would also be expected in species where territoriality is reduced due to ecological shifts or specialization. For example, the ant-specialist, iguanid horn lizards (*Phrynosoma* spp.) do not defend territories (Zamudio, 1998), have lost the ancestral throat colouration typical of their close relatives

(Wiens, 1999) and retain only a rudimentary head-bob sequence (Lynn, 1965). Whether changes in the dynamics of natural selection, sexual selection and genetic effects explain the loss of ornaments in males remains to be tested, but offer promising avenues for future research. Furthermore, identifying the developmental basis of ornament expression (e.g. hormonal) may provide the mechanism by which evolutionary loss occurs (Owens & Short, 1995).

While sexual selection drives the evolution of exaggerated male traits in many systems (Andersson, 1994), it is unlikely selection will be restricted to males or work in isolation of other extrinsic and intrinsic factors (Lande, 1980; Lande & Arnold, 1985; Hedrick & Temeles, 1989; Owens & Short, 1995; Amundsen, 2000a,b). This point is illustrated by the evolution of ornaments in dragon lizards. In these animals, the phylogenetic distribution of ornaments reflects a complex history of genetic correlation, sexual selection (on both sexes), and predation induced evolutionary loss. Our study highlights the utility of adopting a macroevolutionary approach for understanding mechanisms influencing the expression of secondary sexual traits and the evolution of sexual dimorphism.

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Supplementary material

The following supplementary material is available for this article online:

Appendix S1. Dragon ornamentation and reported shelter type.

This material is available as part of the online article from http://www.blackwell-synergy.com.

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