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Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae)

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Lizards of the family Eublepharidae exhibit interspecific diversity in body size, sexual size dimorphism (SSD), head size dimorphism (HSD), occurrence of male combat, and presence of male precloacal pores. Hence, they offer an opportunity for testing hypotheses for the evolution and maintenance of sexual dimorphism. Historical analysis of male agonistic behaviour indicates that territoriality is ancestral in eublepharid geckos. Within Eublepharidae, male combat disappeared twice. In keeping with predictions from sexual selection theory, both events were associated with parallel loss of male-biased HSD and ventral scent glands. Eublepharids therefore provide new evidence that male-biased dimorphic heads are weapons used in aggressive encounters and that the ventral glands probably function in territory marking rather than in intersexual communication. Male-biased SSD is a plesiomorphic characteristic and was affected by at least three inversions. Shifts in SSD and male combat were not historically correlated. Therefore, other factors than male rivalry appear responsible for SSD inversions. Eublepharids demonstrate the full scope of Rensch's rule (small species tend to be female-larger, larger species male-larger). Most plausibly, SSD pattern hence seems to reflect body size variation. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **76**, 303–314.

ADDITIONAL KEYWORDS: aggression – epidermal glands – *Eublepharis* – head size – sexual selection – size dimorphism.

INTRODUCTION

Sexual dimorphism (SD), defined as a phenotypic difference between males and females of a species, is a common phenomenon in animals including reptiles (Darwin, 1871; Andersson, 1994). Despite great theoretical effort (e.g. Slatkin, 1984; Shine, 1988, 1989; Hedrick & Temeles, 1989; Kozlowski, 1989; Reeve & Fairbairn, 2001), there is still controversy as to what conditions promote SD and from which mechanism it has evolved.

The most prevalent explanation for the origin and maintenance of SD in reptiles is still Darwin's original sexual selection theory. It predicts a correlation between gains/losses of sexually selected traits and major forms of competition among males (Wiens, 2001). Males should be the larger sex (Shine, 1978, 1994; Berry & Shine, 1980) and they should exaggerate organs related to rivalry success (weapons) and/or territory advertisement in lineages exhibiting male–male aggression. In lizards, heads are typically used as weapons in combats. Taxonomically widespread male-biased head size dimorphism (HSD) therefore probably reflects that head size apparently determines the outcome of direct physical aggressive encounters (Carothers, 1984; Vitt & Cooper, 1985; Vial & Stewart, 1989; Anderson & Vitt, 1990; Hews, 1990; Mouton & Wyk, 1993). Lizards also engage in a number of threat displays without physical combat or risk of injury, such as push-up displays or chemical signals (Martins, 1994). Many lizards (both iguanian and scleroglossan) exhibit sexually dimorphic ventral glands producing waxy secretions. Their precise significance remains unclear. However, they probably function as chemical signals in territory advertisement (Duvall, 1979; Alberts, 1991). Consequently, if the function of the waxy secretion in threat displays

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*Corresponding author. E-mail: lukkrat@email.cz is correct, the reduction in male territoriality should be associated with a loss of these ventral glands.

Not so intuitively, the variable that has been repeatedly reported to affect sexual size dimorphism (SSD) in animals is body size itself. Females tend to be larger than males in small species, males larger than females in large species (Colwell, 2000). This general trend commonly known as 'Rensch's rule' has been found many times in various taxa (reviewed in Fairbairn, 1990, 1997; Abouheif & Fairbairn, 1997; Colwell, 2000). Although the functional and adaptive consequences of this empirical allometry for SSD remains unclear (Fairbairn, 1997), we feel that every comparative study of SD should encompass investigation of SSD scaling to body size as it might strongly influence the observed pattern.

Phylogenetic analysis of both SD and possible explanatory characters (e.g. male–male aggression, body size) within a single lineage exhibiting substantial variation in all these characters is a powerful tool for testing hypotheses explaining SD. Regrettably, because of widespread phylogenetic conservatism, lineages in which closely related taxa differ significantly in salient traits are scarce among reptiles (Shine & Fitzgerald, 1995). The present study provides documentation of variation in traits of interest in eublepharid geckos. The family Eublepharidae is a monophyletic assemblage, sister group of all other gekkotan lizards (Kluge, 1987). The phylogenetic relationships among the eublepharid species are well-corroborated (phylogeny based on morphology Kluge, 1975; Grismer, 1983, 1988, 1991; Grismer, Viets & Boyle, 1999; molecular approach Ota *et al*., 1999). There is considerable variation in body size within this family – the largest species *Eublepharis angramainyu* Anderson & Leviton, 1966 is more than 20 times heavier than the smallest *Coleonyx brevis* Stejneger, 1893. Male contests have been reported as regular behaviour in some eublepharid species, while the evidence concerning male-male aggression is still equivocal or lacking in others (Greenberg, 1943; Dial, 1978; Benefield, Gimpe & Olsen, 1981; Viets *et al*., 1994). Males of most species possess conspicuous precloacal pores and frequently mark substrates with the secretions of these scent glands (Brandstaetter, 1992; Kratochvíl, pers. observ.), but pores are completely missing in *Holodactylus* and some *Goniurosaurus* species (Grismer, 1988; Grismer *et al*., 1999). All eublepharids except *Aeluroscalabotes felinus* (Günther, 1864), the only arboreal form (Inger & Greenberg, 1966) share similar ecology – they are nocturnal and terrestrial (Grismer, 1988). Moreover, the general biology of this group is well understood as *E. macularius* Blyth, 1854 is one of the most extensively studied lizards (recent reviews in Crews, Sakata & Rhen, 1996; Crews, 1998; Crews *et al.*, 1998).

Our objective was to review original and published data on SSD, HSD, precloacal glands presence and male combat occurrence in eublepharids. Next, we used members of this family as a study system to analyse the mechanisms underlying variation in sexually dimorphic traits. We performed historical analysis (*sensu* McLennan, 1991; Dial & Grismer, 1992) of character changes and explored how behavioural and morphological traits have been associated within this family. We were specifically interested in the possible role played by male–male combat and body size variation in the evolution of dimorphism in this group.

MATERIAL AND METHODS

We studied 958 captive individuals belonging to the following nine eublepharid species (number of individuals examined are given in parentheses): *Coleonyx brevis* (62), *C. elegans* Gray, 1845 (119), *C. mitratus* (Peters, 1845) (62), *C. variegatus* (Baird, 1858) (30), *Eublepharis angramainyu* (15), *E. macularius* (317), *Goniurosaurus luii* Grismer, Viets & Boyle, 1999 (39), *G. kuroiwae* (Namiye, 1912) (12), *Hemitheconyx caudicinctus* (Duméril, 1851) (170) and *Holodactylus africanus* Boettger, 1893 (132). All the individuals came from breeding stocks, except for *H. africanus* (from unknown locality in Tanzania), *E. angramainyu* (collected by the authors and their coworkers in Iran and Syria) and 10 individuals of *C. elegans* (from Mexico), 16 *C. variegatus* (from Arizona) and 63 *H. caudicinctus* (from Ghana). For each individual, we recorded the sex according to external characters, snout–vent length (SVL), head length (HL, from the anterior edge of tympanum to the tip of snout) and head width (HW, in the widest point of head).

Controversy still exists, whether ratios or residuals should be used to estimate SD (cf. Ranta, Laurila & Elmberg, 1994; Zamudio, 1998; Smith, 1999). For reasons recently discussed in detail in Smith (1999), we decided to employ Lovich–Gibbons revised two-step ratio (Lovich & Gibbons, 1992):

(1) if $M \geq F$, dimorphism = M/F
(2) if $F \geq M$, dimorphism = $2 - F/M$

where M, F are the measures of male and female traits, respectively, (i.e. estimation of SVL or head size in our case).

THE CHARACTERS

Sexual size dimorphism

Estimation of SSD is highly sensitive to individual growth trajectories of the study animals (e.g. Powell & Russell, 1985; Madsen & Shine, 1993; St. Clair, 1998; Brown *et al*., 1999; for reviews see Stamps, 1993;

Stamps & Krishnan, 1997). To evaluate the growth mode of eublepharids, we examined the growth curves of both sexes of four species (*E. macularius*, *C. brevis*, *C. elegans*, *C. mitratus*). This sample includes one species with temperature-dependent sex determination (*E. m.*) and two species with genotypic sex determination (*C. m.*, *C. b.*) (Viets *et al.*, 1993; Bragg, Fawcett & Bragg, 2000). As far as we know, the mechanism of sex determination in *C. elegans* has not been examined. The environmental effects on growth in reptiles have been well documented (e.g. Ferguson & Talent, 1993; Madsen & Shine, 1993; Niewiarowski & Roosenburg, 1993; Sinervo & Adolph, 1994), including in a study of *E. macularius* (Autumn & DeNardo, 1995). Therefore, we measured growth under standardized conditions. Experimental individuals were kept in cages 30 × 30 × 30 cm with shelters and substrate (wet peat-moss or sand according to preferred humidity). They were placed in a centrally heated room with temperature between 25 and 27°C (near the preferred body temperature in eublepharids (Dial & Grismer, 1992) and a 12:12 light/dark cycle. Water and food (vitaminized crickets and mealworms) were provided *ad libitum*. Animals were regularly measured from hatching up to the age of approximately 2 years in intervals of 1 or 2 months. The growth was evidently asymptotic, so the two asymptotic growth models were fitted to pooled data of the species and sex in question: the logistic-by-length model (Schoener & Schoener, 1978; Powell & Russell, 1985) $\mathrm{SVL} = (a^3/(1 + b\mathrm{e}^{-\mathrm{r}*\mathrm{t}})^{1/3}$ and the von Bertalanffy model (St. Clair, 1998) $\mathrm{SVL} = \mathrm{a}(1 - \mathrm{e}^{-\mathrm{k}(t-t_0)})$, where e is the base of the natural logarithm, t is age (in days), a is the asymptotic SVL (in mm), k is the rate of approach to asymptotic SVL, r is the characteristic growth rate, t_0 is the hypothetical time at length zero, and b is the function of the length at birth. The logistic model explained a larger fraction of the variance (Table 1), so we used this model to estimate the asymptotic SVL.

Unfortunately, growth curves were not available for all studied species. Therefore, we had to search for another simple statistics well estimating the asymptotic size. Maximum SVL has been repeatedly used for this purpose (Stamps & Andrews, 1992), but it clearly overestimates asymptotic body size and is highly sensitive to unbalanced sex ratio. Alternatively, the use of percentiles has been recommended both for theoretical and empirical reasons (cf. Brown *et al.*, 1999). We found that 90-percentiles of SVL (Table 2, computed from overall samples of given species and sex, pseudoreplications excluded) fit well the asymptotic values computed by the logistic model. There was a strong correlation ($n = 8$, $r = 0.990$, $P < 0.00001$) between these two estimates. Hence, we feel confident to use 90-percentile as an appropriate evaluation of body size. However, use of maximum SVL instead of 90-percentile values did not change the results; thus we report only the latter analyses. Wherever possible, we added published data on SVL in species least represented (*E. angramainyu, G. kuroiwae*) or lacking (*C. reticulatus* Davis & Dixon, 1958) in our material.

Head size dimorphism

In order to lessen the number of analyses and reduce the variance, we expressed head size as a single variable (HS), the geometric mean of HL and HW. Data were natural log-transformed before analysis. To avoid individuals in transitional allometry between juvenile and adult, only those reaching at least 70% of maximum SVL were included into HSD analysis. Analysis of covariance (ANCOVA) in which sex was given as factor and SVL as a covariate was introduced to compare HS between the sexes of the same species. Back-transformed values of the adjusted means were used to determinate HSD indexes (Lovich–Gibbons ratios, see above). This procedure was substantiated by the absence of significant ($P > 0.05$ in each of

Table 1. Growth curves characteristics for males, resp. females for four species of eublepharid geckos

			Asymptotic SVL (mm), R^2	
Species	Sex	Number of pseudoreplicates (individuals)	logistic model	von Bertalanffy model
E. macularius	males	48 (13)	124.79, 97.0	128.40, 96.5
	females	238 (51)	113.12, 89.6	117.50, 88.5
C. mitratus	males	65 (18)	74.38, 95.2	76.96, 93.0
	females	75 (19)	72.86, 93.6	74.84, 92.7
C. elegans	males	46 (12)	80.43, 92.6	82.70, 89.8
	females	48 (12)	78.90, 87.7	81.37, 86.0
C. brevis	males	16 (6)	46.21, 92.5	47.46, 92.7
	females	14 (5)	51.27, 91.5	53.55, 92.6

Table 2. Sex specific data for snout–vent length and SSD indexes (Lovich–Gibbons ratios) for 11 eublepharid species

Species	*n* males, females	Max. SVL (mm) males, females	90-percentile of SVL (mm) males, females	SSD index
E. macularius	72, 126	137.8, 128.7	125.1, 121.7	1.03
C. mitratus	24, 32	96.1, 86.8	88.7, 79.7	1.11
H. caudicinctus	65, 99	144.5, 128.4	138.7, 121.7	1.14
C. elegans	52, 34	107.7, 91.2	86.6, 82.2	1.05
C. brevis	29, 26	62.0, 66.6	55.5, 59.7	0.92
C. variegatus	18, 11	66.6, 69.0	63.9, 68.9	0.92
H. africanus	63, 68	73.5, 78.6	69.9, 74.7	0.93
*G. kuroiwae**	197, 196	96.0, 100.0	92.0, 96.0	0.96
E. angramainyu†	9, 8	170.0, 156.4	170.0, 156.4	1.09
G. luii	17, 22	117.15, 122.8	113.2, 117.6	0.96
C. reticulatus‡	9, 6	94.0, 91.0	94.0, 91.0	1.03

*Data from Tanaka & Nishihira (1989). †Data added from Baloutch & Thireau (1986); Anderson (1999). ‡Data from Seifert & Murphy (1972); Seifert, Rainwater & Kasper (1973); Easterla & Reynolds (1975).

studied species) differences between the sexes in slopes of allometric relationships.

Male combats

To assess the existence of male–male aggressiveness, we performed simple behavioural experiments. We added a second nonfamiliar sexually mature male (intruder) to the cage with a single, resident male and recorded the occurrence of the combat. Resident males were kept in isolation for at least 1 week before each trial. Owing to geckos' nocturnality and cryptic way of life, all the trials were carried out in the evening hours in dim light. Each trial started after gentle removal of the shelter and lasted 10 min or was interrupted in the moment of attack. Only vigorous, healthy and regularly feeding animals were included in the experiments. Numbers of tested residents were as follows: 20 males of *E. macularius*, four males of *E. angramainyu*, nine males of *H. caudicinctus*, 16 males of *C. elegans*, 14 males of *C. mitratus*, eight males of *C. brevis*, eight males of *C. variegatus* and six males of *H. africanus*. In the case of the last mentioned species the experiments were repeated several times and the results were verified by the observation of groups of recently imported individuals ($n \approx 60$) when taking their measurements.

PHYLOGENY OF EUBLEPHARIDAE

Phylogenetic relationships within the eublepharid clade have been repeatedly studied. We combined numerous morphological and physiological features from the works of Kluge (1975) and Grismer and his coworkers (Grismer, 1983, 1988, 1991; Dial & Grismer, 1992; Grismer *et al.*, 1999) and molecular data (12S rRNA and 16S rRNA gene sequences) of Ota *et al.* (1999) to compute a total evidence tree. *Gekko gecko* (Linnaeus, 1758), a member of the sister family Gekkonidae, was used as the outgroup. Altogether, we obtained 428 informative characters. Phylogenetic analysis was performed employing maximum-parsimony method (heuristic search) using PAUP*4.0, ver. b2a (Swofford, 1998). Bootstrap search performed 1000 pseudoreplicates. To test for congruence between molecular and nonmolecular data, we used the method proposed by Wiens (1998). Mitochondrial rDNA sequences and the nonmolecular characters (mostly morphological) were analysed separately, and support for individual clades was evaluated by bootstrapping. The position of *Aeluroscalabote felinus* differs between these two datasets. Ota *et al.* (1999) debated discrepancies between molecular and morphological data in more details. The tree from the combined data was taken to be the best approximation of phylogeny. The resulting cladogram (Fig. 1) was quite robust, half the nodes received 90% or greater bootstrap support and all but two of the 19 nodes received greater than 50% bootstrap support. However, the position of *A. felinus* should be taken with caution. The cladogram was nearly congruent with previously published phylogenetic hypothesis. The main exception was the position of the genus *Goniurosaurus* as a sister clade of the genus *Coleonyx*. *Goniurosaurus* has previously been proposed as the sister group of the *Eublepharis* +(*Hemitheconyx*+*Holodactylus*) clade (Grismer, 1988; Dial & Grismer, 1992).

However, the altered topology does not affect our results (not shown) and former reconstruction of body size evolution and precloacal pores presence. According to previous analysis (Grismer, 1988; Grismer *et al.*, 1999), ancestral large body size (SVL > 97 mm) and presence of glands is the most parsimonious solution

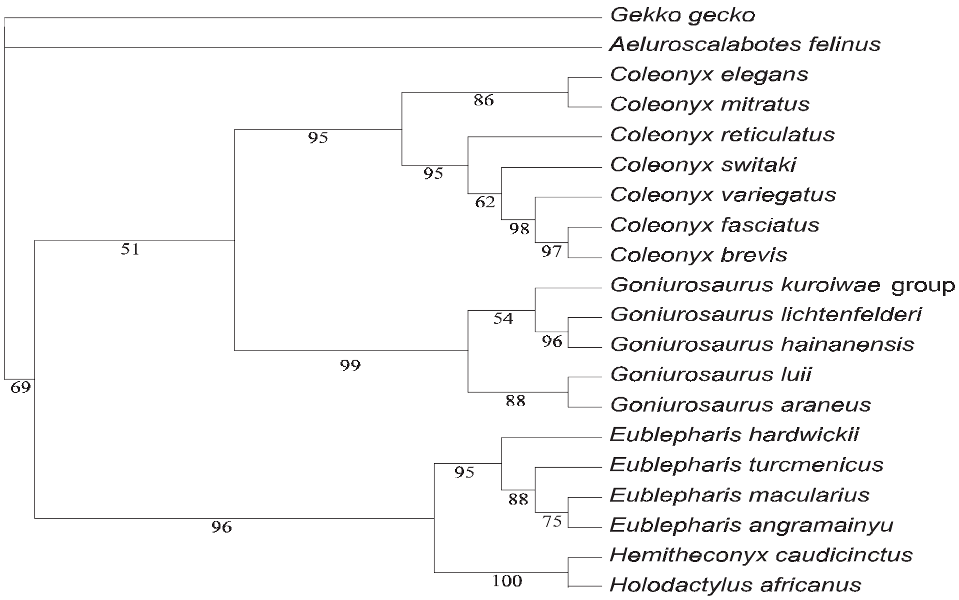

Figure 1. Total evidence tree for Eublepharidae with bootstrap supports.

for the eublepharid geckos. Small size of *Holodactylus*, *Coleonyx* and *Goniurosaurus lichtenfelderi-hainanensis-kuroiwae* clade and the absence of secretory glands in *H. africanus* and *G. kuroiwae* group were considered to be derived. Within the genus *Coleonyx*, there was an additional reduction of body size in the ancestor of the *variegatus-brevis-fasciatus* clade (Grismer, 1988).

The computed cladogram was used to carry out historical analysis of changes in studied characters, and to analyse relationships between SSD, HSD and body size using independent contrast analysis (Felsenstein, 1985). We generated the independent contrasts of log(male body size), log(female body size), log(SSD index) and log(HSD index) by the software COMPARE ver. 4.4 program (Martins, 2001). All branch lengths were set to 1. We used this branch lengths because a diagnostic of Garland, Harvey & Ives (1992) revealed that the contrasts were appropriately standardized. To test the consistency with Rensch's rule, we computed the slope (β) of allometry in the contrasts of log(female body size) on the contrasts of log(male body size) in major axis regression (model 2). A slope less than unity indicates conformity (Abouheif & Fairbairn, 1997). All correlations and regressions using contrasts were computed through the origin.

RESULTS

MORPHOLOGICAL TRAITS

Sexual size dimorphism

Studied species differ in their SSD, both female-biased and male-biased size-dimorphism occurs within eublepharid clade (Table 2). The male-biased species are *C. elegans*, *C. mitratus*, *E. macularius* and *H. caudicinctus*. Although only limited data are available in *C. reticulatus* and *E. angramainyu*, we could tentatively include them into male-biased species. On the other hand, females are the larger sex in *C. brevis*, *C. variegatus*, *H. africanus, G. luii* and *G. kuroiwae*.

Head size dimorphism

We adopted one-factor ANCOVA with sex as a factor and SVL as a covariate to test intersexual differences in size-adjusted head size (Table 3). Males have significantly (all $P < 0.05$) larger heads than conspecific females in *E. macularius*, *H. caudicinctus, G. luii* and in all the four studied species of the genus *Coleonyx*. Although sample sizes were small in *E. angramainyu,* this species exhibits the same pattern, its HSD being only marginally insignificant ($P = 0.06$ for two-tailed test, i.e. 0.03 for less conservative one-tailed test). In spite of the large sample, the sexes of *H. africanus* are not dimorphic in the relative head size. ANCOVA proved female-biased HSD in *G. kuroiwae*.

MALE–MALE COMBAT

All species except *H. africanus* exhibited male combat in our experimental trials. Usually, aggression (biting) between tested males occurred and trials were interrupted prior to the 10-min limit. Combat between males of *H. africanus* has never been recorded. Tanaka & Nishihira (1987, 1989) did not observed male–male combats during their extensive field study of *G.*

Table 3. Results from ANCOVAs of head size of the nine eublepharid species with respect to sex. All the interactions between the factor (sex) and the covariate (SVL) were insignificant ($P > 0.05$). HSD indexes are Lovich–Gibbons ratios of back-transformed adjusted means

Species	d.f.	*P*	*F*	Adjusted means (m, f)	HSD index
E. angramainyu	1, 9	0.065	4.37	32.38, 31.68	1.02
E. macularius	1, 86	<0.0001	21.85	24.86, 24.03	1.04
C. mitratus	1, 48	<0.0001	39.44	16.00, 15.18	1.05
H. caudicinctus	1, 125	<0.0001	31.62	25.40, 24.54	1.04
C. elegans	1, 83	<0.001	13.62	14.48, 14.06	1.03
C. brevis	1, 19	<0.01	7.97	10.67, 10.25	1.04
C. variegatus	1, 26	<0.0001	42.37	12.31, 11.58	1.06
H. africanus	1, 122	0.165	1.95	15.68, 15.84	0.99
G. luii	1, 29	<0.01	10.26	24.51, 23.68	1.04
G. kuroiwae	1, 9	0.044	5.44	17.73, 18.26	0.97

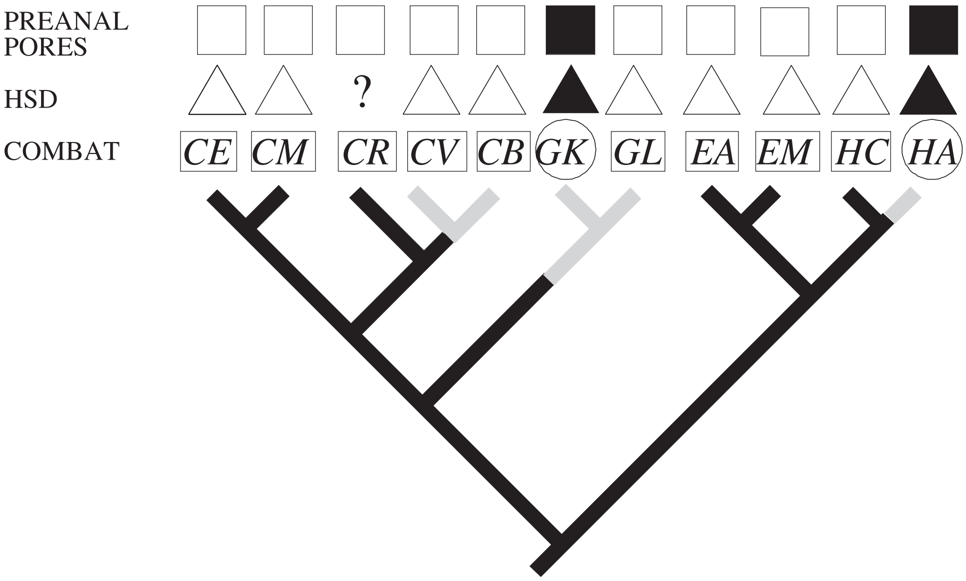

Figure 2. Historical analysis of character states in Eublepharidae. Black lines show male-larger species, grey lines female-larger species. Species shorts are in rectangles in species with antagonistic males, in circles in peaceful species. Open triangles represent male-biased HSD, solid triangles represent the lack of HSD. Open squares stand for the presence of preanal pores in males, their missing is indicated by black solid squares. Abbreviations: CE, *Coleonyx elegans*; CM, *C. mitratus*, CR, *C. reticulates*; CV, *C. variegates*; CB, *C. brevis*; GK, *Goniurosaurus kuroiwae*; GL, *G. luii*; EA, *Eublepharis angramainyu*; EM, *E. macularius*; HC, *Hemitheconyx caudicinctus*; HA, *Holodactylus africanus.*

kuroiwae, and consequently we consider this species nonaggressive as well. In contrast, male–male aggression was also reported in another two eublepharid species: *C. reticulatus* (Dial, 1978) and *G. luii* (Sotorník, pers. comm.).

Pattern of character changes

Character states (SSD, HSD, Combat) when plotted onto the cladogram (only species for which there is information regarding the characters concerned were included) indicate the following parsimonious reconstruction (Fig. 2): male-biased SSD, male-biased HSD, presence of male-male combat and preanal pores are ancestral (plesiomorphic) states:

(1) Five female-biased species were produced by three events: in the ancestor of *H. africanus*, in the ancestor of *Goniurosaurus* clade, and the ancestor of *C. variegates*–*C. brevis* clade;

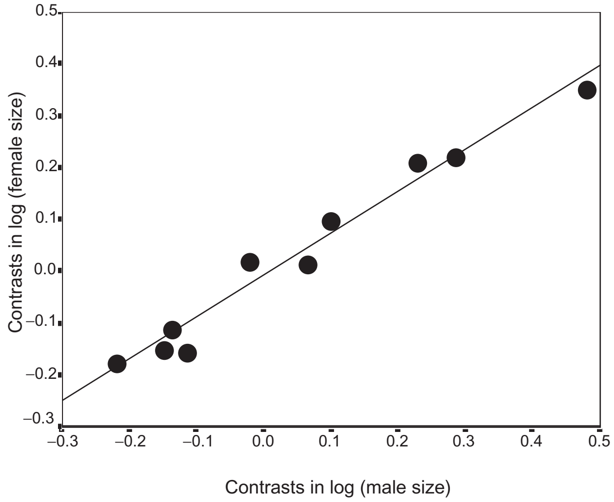

Figure 3. Contrasts in female size (SVL) vs. contrasts in male size for eublepharid geckos. Line is the major axis fitted to these data. Its slope is significantly less then 1, and thus shows the consistency with Rensch's rule.

(2) Male-male combats;
(3) Male-biased HSD; as well as
(4) Preanal pores disappeared twice, in the ancestor of *H. africanus* and the ancestor of *G. kuroiwae*.

Maddison's concentrated changes test (Maddison, 1990) confirms that associations of male combat disappearance and male-biased HSD or preanal pores loss could not easily have occurred by chance ($P < 0.01$).

Independent contrasts in SSD correlate well with female, resp. male body size contrasts ($r = 0.781$, $P < 0.01$, resp. $r = 0.826$, $P < 0.01$, $n = 10$). SSD thus significantly increase with body size. On the other hand, contrasts in HSD do not correlate with SSD, female, resp. male body size contrasts (all $P > 0.25$). Contrasts in female body size and male body size correlate strongly ($r = 0.985$, $P < 0.001$, $n = 10$). Ordinary least square regression confirms, that SSD allometry in eublepharids is consistent with Rensch's rule (allometric exponent β is < 1, $\beta = 0.79$, SE 0.05) (Fig. 3).

DISCUSSION

CHARACTER STATES

Every analysis of SSD in lizards is affected by methodological difficulties in the determination of adult size, as they share with other poikilothermic vertebrates the indeterminate growth. To avoid the potentially confounding effects of individual growth and its plasticity, precise knowledge of the shape of growth curves in studied species and common-garden design is needed. In eublepharids, individual growth was studied in *E. macularius* (laboratory data, reviewed in Crews *et al.*, 1998), *C. variegatus* (field data, Parker, 1972) and *G. kuroiwae* (field data, Tanaka & Nishihira, 1989). Our common-garden experiment supports the earlier findings that eublepharids exhibit asymptotic growth curves, i.e. growth slows markedly after sexual maturity. Thus, we were able to verify applicability of our body size estimates. Moreover, there is no discrepancy between our results and published records of SSD in eublepharids (e.g. *E. macularius*: Thorogood & Whimster, 1979; Crews *et al.*, 1998; *H. caudicinctus*: Loveridge, 1947; *C. brevis*: Smith, 1946; Dixon, 1970; *C. variegatus*: Smith, 1946; Parker, 1972).

Males of *E. macularius* (e.g. Thorogood & Whimster, 1979; Brillet, 1993), *H. caudicinctus* (Viets *et al.*, 1994), and *C. reticulatus* (Dial, 1978) were reported as strongly territorial and antagonistic. We corroborate the analogous behaviour in all the other studied species except *H. africanus*. Surprisingly, we also found strong male–male aggression in two small North American species, *C. variegatus* and *C. brevis*, where evidence concerning their combat behaviour was equivocal (Greenberg, 1943; Dial, 1978; Benefield *et al.*, 1981) or that were previously considered to be even nonaggressive (Viets *et al.*, 1994). We believe that differences in design of experiments could explain these discrepancies. Conditions set in our tests provoke male aggressiveness. Tests were conducted only on sexually mature males, and we employed the effect of residency and social isolation, both known to sustain agonistic behaviour in many animals.

HISTORICAL ANALYSIS

In evaluating coincidence between evolutionary events, we are limited by the small number of extant species of the family Eublepharidae, as well as by uncertain phylogeny of its sister clade, the families Gekkonidae and Pygopodidae. Therefore, we restricted our analyses to eublepharids excluding the genus *Aeluroscalabotes*, which has a completely different (arboreal) way of life.

Fortunately, the number of 'female-larger' species is small; the species concerned possess many derived characters (Grismer, 1988; Grismer *et al.*, 1999), and thus events of SSD inversions can be easily located. This applies even more to the absence of male combat, male-biased HSD and precloacal pores. The small number of changes and thus relatively large phylogenetic conservatism in studied traits enabled us to reconstruct the ancient, likely Laurasian (Kluge, 1987; Ota *et al.*, 1999) ancestor of the family Eublepharidae. This early eublepharid was probably a large, 'male-larger' species. The males were strongly territorial, marked their territory with secretions of precloacal glands and possessed larger heads than females. Because all these traits varied within sister lineages of the gekkotan clade, these findings have great impact on the polarity of these character states in geckos, the key group for the resolution of the primitive condition of territoriality in lizards (Martins, 1994).

EVOLUTION OF SEXUAL DIMORPHISM

According to our experience, female aggression is rare in eublepharids and female contests are much less vigorous or even nonexist. Therefore, we considered male combats are for access to females. In reptiles, the combat success is usually positively correlated with larger body size (e.g. Olsson, 1992; Zucker & Murray, 1996; Schuett, 1997). Reasonably, the occurrence of male combat suggests sexual selection for larger male body size and the loss of this selective force could be followed by the disappearance of male-biased SSD (Shine & Fitzgerald, 1995). However, not all the inversions in SSD in eublepharids are historically connected with changes in male combat occurrence. *C. variegates–C. brevis* clade and *G. luii* are simultaneously female-biased and aggressive in contrast to predictions of sexual selection theory. Obviously, the presence of sexual selection acting on male body size itself does not provide information which is the larger sex, the phenomenon previously reported in some other taxa (e.g. Greenwood & Adams, 1987).

What other mechanism can better explain the observed pattern? Sexual differences in niche utilization (reviewed in Shine, 1989; Fairbairn, 1997) generally cannot be a critical factor for evolution of SD in eublepharid geckos, e.g. it cannot clarify inversions observed in SSD. Furthermore, sexual differences in feeding apparatus are a crucial step for feeding niche segregation. Head size is one of the most important traits for feeding niche utilization in gape-limited predators such as geckos. Accordingly, consumed prey size increases indeed with head size in *C. variegatus* (Parker & Pianka, 1974). The direction of HSD in this species and related *C. brevis*, where the larger sex posses smaller heads, thus decrease (rather than increase, as predicted by the above hypothesis) the sexual differences in gape size.

SSD reflects selective forces acting on the female as well as the male. Selection may favour large females, because female fecundity is proportional to body size (Darwin, 1871; Shine, 1988; Braña, 1996). Accordingly, clutch size indeed usually increases with female body size among lizards (e.g. Braña, 1996; Cuadrado, 1998), but we can control this effect by studying lineages with invariant clutch size (Shine & Greer, 1991). Eublepharids have invariant clutches of two eggs (e.g. Smith, 1946; Parker, 1972; Werner, 1972; Dial & Fitzpatrick, 1981), so selection for large female size attributable to increased fecundity is eliminated. However, the possibility still exists that clutch frequency or egg size, not number of eggs, could be an important determinant of reproductive success. In lizards, fitness benefit to larger egg size (mass) due to effect on juvenile size, mortality or locomotor performance is well documented (Sinervo, 2000). Relative clutch masses (RCM, egg weight/total wet weight of female × 100) of all species of eublepharids with known RCM are very high and nearly constant among the studied species (mean ± SD): 18.3 ± 1.7 in *C. variegatus* (n = 14, Parker & Pianka, 1974), 19.7 ± 1.9 in *C. mitratus* (n = 20), 19.8 ± 2.6 in *C. elegans* (n = 20), and 17.8 ± 2.0 in *E. macularius* (n = 14, Kratochvíl, unpubl. observ.). In the latter three species, the clutch mass positively correlates with female mass (r = 0.567, 0.662, resp. 0.795, all significant at $P < 0.01$). Both these findings indicate the existence of interspecific and intraspecific constraints (e.g. limited space within the body cavity or cost of transporting reproductive loads) that do not allow the female to increase eggs relatively to her body size. We can therefore assume that the only opportunity to increase an egg size in these geckos is to enlarge body size of the female.

How can these circumstances influence the interspecific pattern of SSD? Independent contrasts analysis confirms positive relationship between body size and SSD, historical analysis detected several events of considerable decrease of body size in eublepharids (Grismer, 1988; Grismer *et al*., 1999). Body size has a central role in the life history (Stearns, 1992), suggesting body size of both males and females will be under strong selection and near equilibrium values. When a selection for smaller body size concerning both sexes occurs (e.g. limited resources, or high predator pressure favouring early maturation and short life connected with small size), males could decrease their body size more than conspecific females. Males are not constrained by litter (egg) size while females of small species are not allowed to be even smaller. Males are therefore predicted not to be under as intense stabilizing selection on body size as females. In fact, a lot of comparative methods in different animals found an allometric trend in which male body size changes faster than female body size as the average size of the species increases (i.e. allometry consistent with Rensch's rule, Abouheif & Fairbairn, 1997; Colwell, 2000). This is also the case of eublepharids (objectively, taking all sex-species categories of this family together, the largest is the category of *males* of *E.*

angramainyu, the smallest is the category of *males* of *C brevis*). We suggest that the proposed mechanism (more constrained female size compared to male size) could explain commonly observed correspondence to the Rensch's rule in other animal lineages.

Most plausibly, the observed SSD pattern in eublepharids seems to result from effects of body size variation or its correlates. On the other hand, HSD fit the predictions of sexual selection theory. Males have larger relative head size than conspecific females and they exhibit strong male–male aggression in all but two studied species. The two independent disappearances of HSD found in *H. africanus* and *G. kuroiwae* were connected with the losses of male combat. Consequently, eublepharids give new indirect evidence that male-biased dimorphic heads are actually weapons used in aggressive encounters.

Yet another morphological structure perfectly corresponds to both changes in social structure – the lack of precloacal pores in males of *H. africanus* and *G. kuroiwae.* To our knowledge, this parallel loss of ventral glands associated with a reduction in male territoriality constitutes the first interspecific support that pore secretions have indeed territory marking functions (Duvall, 1979; Alberts, 1991; Cooper, Van Wyk & Mouton, 1996). Precloacal pore secretions were otherwise suggested to function as the source of pheromones allowing sex recognition (Cooper, López & Salvador, 1994). However, this explanation does not predict found association and thus seems less plausible. Moreover, for sex recognition eublepharids use chemical stimuli from the trunk skin (Mason & Gutzke, 1990).

The study of the changes in macroevolutionary pattern in secondary sexual characteristics should include consideration of the role of the proximate mechanisms generating the traits (Emerson, 2000). Although we have only limited information on these questions in eublepharids, the coevolution of all three secondary sexual characteristics seems reasonable on the proximate level. The aggression, expansion of head width and the development and secretion of precloacal pores are under direct control of the sole hormone (testosterone) in *E. macularius* (for reviews, see Crews *et al*., 1998; Crews, 1998). As a result, an association of the character changes may simply reflect common proximate mechanism controlling traits expression. Even a single change in such a mechanism might have a strong effect on very different features (e.g. morphological, physiological, behavioural). Consequently, it might be misleading to take them as independent when carrying out historical analyses or cladogram construction. In any case, the potential drop in androgen level, or hormone receptor characteristics in eublepharid species having derived social system warrants further research on comparative physiology.

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