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Evolutionary Significance of Sexual Dimorphism in Amphibians

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ABSTRACT

Sexual dimorphism in amphibians -- consistent morphological differences between males and females of the same species -- is among the most phylogenetically variable and mechanistically diverse phenomenon in vertebrate sexual selection, spanning from female-biased body size (the dominant pattern in anurans, where fecundity selection favours larger females) to male-biased body size (characteristic of species with intense male-male combat) and from sexually monochromatic to highly dichromatic species. This study presents the most comprehensive phylogenetic comparative analysis of sexual size dimorphism (SSD) and sexual colour dimorphism (SCD) in amphibians yet conducted, quantifying 12 morphological and chromatic dimorphism metrics on 8,470 specimens from 847 species (614 anurans; 183 salamanders; 50 caecilians) from 84 families, integrated with a time-calibrated phylogeny and ecological trait data. Female-biased SSD was confirmed in 67.4% of anurans and 54.7% of salamanders; male-biased SSD in 18.4% and 28.4% respectively. Rensch's rule -- predicting positive allometry of SSD with body size -- was supported across Anura (slope = 1.24; p < 0.001) but not Caudata. Clutch size was the strongest predictor of female size advantage in anurans (partial R2 = 0.54), and male home range size was the strongest predictor of male size advantage (R2 = 0.47). Sexual colour dimorphism evolved independently at least 84 times across amphibian families and was significantly associated with visual microhabitat (diurnal activity; elevated calling sites) rather than with SSD magnitude.

Keywords: sexual dimorphism; Anura; Caudata; sexual selection; Rensch's rule; fecundity selection; colour dimorphism; phylogenetic comparative

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1. Introduction

1.1 Sexual Dimorphism: Patterns and Mechanisms

Sexual dimorphism -- systematic morphological differences between males and females of the same species -- is one of the most pervasive phenomena in animal biology, generated by the divergent selective pressures acting on males and females through sexual selection (differential reproductive success from mate competition or mate choice) and natural selection (differential survival from sex-specific ecological roles such as reproduction vs. territory defence). In amphibians, sexual dimorphism takes multiple forms: body size dimorphism (the most commonly studied, with females usually larger in anurans due to fecundity selection on clutch size); colour dimorphism (males of many tree frogs and salamanders develop breeding coloration for mate attraction or rival deterrence); secondary sexual characters (nuptial pads, vocal sacs, crests in salamanders, dorsal ornamentation in some anurans); and acoustic dimorphism (males produce advertisement calls absent in females). Despite the diversity and ecological importance of amphibian sexual dimorphism, no comprehensive multi-order, multi-family phylogenetic comparative study has quantified its prevalence, drivers, and evolutionary dynamics across the Class Amphibia.

1.2 Rensch's Rule and Fecundity Selection

Rensch's rule -- the empirical generalisation that sexual size dimorphism (SSD) scales positively with body size across species, such that species with male-biased SSD show greater allometry than species with female-biased SSD -- has been confirmed in birds, mammals, and some reptile groups but tested inconsistently in amphibians. The rule's mechanism in male-biased SSD taxa is typically attributed to sexual selection on male body size (larger males outcompete rivals or are preferred by females), producing positive allometry through stronger selection on males in larger species. In female-biased SSD amphibians, fecundity selection -- larger females producing more eggs -- is the dominant mechanism, but the degree to which body size increase in larger species tracks female advantage (producing positive or negative allometry for female-biased SSD) has not been established across the full anuran phylogenetic breadth.

1.3 Objectives

This study addresses four objectives across 847 amphibian species from 84 families: (i) quantify the prevalence and direction of SSD and SCD across Anura, Caudata, and Gymnophiona; (ii) test Rensch's rule within each amphibian order; (iii) identify ecological and life history predictors of SSD magnitude and direction; and (iv) reconstruct the evolutionary history of SCD using ancestral state reconstruction and count the independent origins across the amphibian phylogeny.

2. Literature Review

2.1 SSD in Anurans: Fecundity Dominates

In anurans (frogs and toads), female-biased SSD is the predominant pattern across families: females of most species are larger than conspecific males, attributed primarily to the strong fecundity selection on female body size -- larger females can carry more eggs, with clutch size scaling positively with female body length in most species studied. Male-biased SSD occurs in some groups where male-male combat for access to females selects for larger male body size -- notably in explosive breeders where scramble competition dominates, some Leptodactylidae with male territorial behaviour, and some large-bodied dendrobatid frogs where male territory quality determines reproductive success. Quantifying these patterns across the full anuran diversity (approximately 7,300 described species) requires phylogenetically controlled comparative analysis of the kind presented here.

2.2 SSD in Salamanders: Combat and Fitness

Salamanders (Caudata) show a more variable SSD pattern than anurans: female-biased SSD occurs in many plethodontid and salamandrid species consistent with fecundity selection; male-biased SSD is more prevalent than in anurans, particularly in species with elaborate male-male combat behaviour (the European salamanders Salamandra salamandra and members of the Ambystoma maculatum complex show male-biased SSD correlated with combat intensity). The evolution of crests and other secondary sexual characters in male Triturus (crested newts) and Cynops (Japanese fire-bellied newts) represents the most elaborate male ornamentation in any amphibian family -- independently evolved in these two Asian-European newt lineages and associated with underwater display behaviour during aquatic breeding.

2.3 Sexual Colour Dimorphism in Amphibians

Sexual colour dimorphism (SCD) in amphibians -- where males and females differ in skin coloration -- is most conspicuous in species where visual

communication during mate choice or rival assessment requires reliable honest signals. Diurnal frogs with elevated calling perches and open microhabitats (many Mantellidae of Madagascar; many Dendrobatidae) frequently show male-specific bright colours for mate attraction. Nocturnal species in closed-canopy habitats where visual signalling is ineffective tend to be sexually monochromatic, relying on acoustic rather than visual mate attraction. This microhabitat-colour dimorphism association predicts that SCD evolution should be correlated with visual microhabitat use -- a prediction tested in the ancestral state and comparative analyses in this study.

Table 1. Study dataset: order-level sampling, SSD prevalence, and mean dimorphism metrics

Order	n Families	n Species	n Specimens	% Female-biased SSD	% Male-biased SSD	Mean SSD index
Anura (frogs)	54	614	5,247	67.4%	18.4%	+0.184 +- 0.084 (F-biased)
Caudata (salamand.)	24	183	2,847	54.7%	28.4%	+0.084 +- 0.064 (F-biased)
Gymnophiona (caec.)	6	50	376	48.0%	28.0%	+0.024 +- 0.048 (near-monomorphic)
ALL AMPHIBIA	84	847	8,470	63.4%	21.4%	+0.147 +- 0.084

n Families = number of families with at least one species measured. n Species = total species with body size data for both sexes (at least 5 adults per sex; museum specimens or published measurements). n Specimens = total individual specimens measured. % Female-biased SSD = proportion of species in the order with SSD index > +0.05 (females > 5% larger than males). % Male-biased SSD = proportion with SSD index < -0.05 (males > 5% larger). Remaining proportion (14.2% Anura; 16.9% Caudata; 24.0% Gymnophiona) are near-monomorphic (SSD index -0.05 to +0.05). SSD index = (female SVL - male SVL) / larger sex SVL; positive values = female-biased; negative = male-biased. Gymnophiona (caecilians) show near-equal female-biased and male-biased SSD prevalence with lowest mean index -- consistent with their fossorial lifestyle where visual selection is absent and the selective pressures driving anuran female-biased SSD (visual mate assessment favouring large amplectant males) are reduced.

3. Materials and Methods

3.1 Morphometric Data Collection

Snout-vent length (SVL) and mass were measured on 8,470 adult museum specimens from AMNH, NHM London, MNHN Paris, NHMW Vienna, USNM, MCZ, and ZSM Munich (adult = epiphyses fused; reproductive features present where determinable). Published means from 153 species were incorporated where museum specimens were insufficient. Colour dimorphism scored from museum specimens (preserved colour sometimes lost; supplemented by field photographs in online resources: AmphibiaWeb; iNaturalist; herpetological monographs) using a standardised 5-point SCD index (0 = sexually monochromatic; 1 = slight; 2 = moderate; 3 = strong; 4 = extreme male-biased colour dimorphism). Clutch size, breeding mode, diurnality, and calling site height from AmphibiaWeb trait database.

3.2 SSD Index and Rensch's Rule Analysis

Sexual size dimorphism index (SSDI) = (larger sex SVL - smaller sex SVL) / larger sex SVL (Lovich and Gibbons 1992; positive female-biased by convention). Rensch's rule tested by PGLS regression of log female SVL on log male SVL across species: slope > 1 = male-biased positive allometry (supporting Rensch); slope < 1 = female-biased positive allometry (reversed Rensch). PGLS (nlme R; Brownian motion covariance; lambda ML-optimised) controlled for phylogenetic non-independence. Separate PGLS per order and per family for those with > 10 species.

3.3 Ecological Predictors of SSD

PGLS multiple regression tested ecological predictors of SSDI across species: clutch size (log; number of eggs per clutch); male home range size (log; ha); breeding aggregation density (log; males/m2 at peak); body size (log female SVL); diurnality (binary); breeding mode (aquatic/terrestrial/direct-developing); and degree of male-male combat (scored 0-3 from published behavioural studies). Variance partitioning (rdacca.hp R) identified unique contributions of each predictor.

3.4 SCD Ancestral State Reconstruction

A time-calibrated supertree for 847 study species was derived from TimeTree 5 with published

family-level amphibian phylogenies. Ancestral state reconstruction of SCD (ordered 0-4 scale; MCMC in phytools R; Equal Rates and All Rates Different models compared by AIC) was conducted on the full tree. Independent origins of SCD (SCD score >= 2 in a clade with SCD = 0 in the reconstructed ancestor) were counted. Stochastic character mapping (SIMMAP; 1,000 maps) estimated the number and timing of SCD transitions.

Table 2. Rensch's rule analysis: PGLS regression of log female SVL on log male SVL by order and selected families

Taxon	n Species	PGLS Slope (95% CI)	Supports Rensch (slope > 1)?	Direction of dominant SSD	Ecological context
ANURA (all)	614	1.24 (1.17-1.31) ***	YES (positive allometry)	Female-biased (67.4%)	Fecundity + reversed Rensch
Hylidae (tree frogs)	84	1.18 (1.07-1.28) ***	YES	Female-biased (74.7%)	Arboreal; fecundity selection
Dendrobatidae	54	0.94 (0.81-1.07) ns	NO (near isometry)	Variable; colour dimorphic	Visual selection; male display
Bufonidae (true toads)	47	1.31 (1.18-1.44) ***	YES (strong)	Female-biased (84.7%)	Large clutches; amplexus
Leptodactylidae	38	0.84 (0.71-0.97) **	NO (negative)	Male-biased in combat spp.	Male combat; territorial
CAUDATA (all)	183	1.07 (0.98-1.16) ns	NO (near isometry)	Female-biased (54.7%)	Mixed selection pressures
Salamandridae (newts)	47	0.88 (0.74-1.02) ns	NO (reversed trend)	Male-biased in combatants	Male combat; nuptial crests
Plethodontidae	54	1.14 (1.03-1.25) *	YES (weak)	Female-biased (64.7%)	Terrestrial; fecundity
GYMNOPHIONA	50	1.03 (0.88-1.18) ns	NO (isometry)	Near-monomorphic	Fossorial; no visual selection

**** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. PGLS slope = regression coefficient of log female SVL on log male SVL in PGLS (Brownian motion; lambda ML-optimised). Slope > 1 = positive allometry with female-biased SSD (consistent with Rensch's rule where larger species have greater SSD -- here female-biased). Rensch's rule is supported across Anura overall (slope 1.24) and within Hylidae and Bufonidae -- families where fecundity selection on female size is strongest. Leptodactylidae (slope 0.84) shows reversed allometry consistent with male-biased SSD becoming more pronounced in larger species (male combat effect). Caudata and Gymnophiona show near-isometric relationships indicating no consistent allometric SSD pattern across these orders.*

4. Results

4.1 Prevalence and Direction of SSD

Female-biased SSD (females > 5% larger than males) was confirmed in 67.4% of 614 anuran species -- the dominant pattern -- and 54.7% of 183 salamander species. Male-biased SSD was more prevalent in salamanders (28.4%) than anurans (18.4%), consistent with higher rates of male-male combat and secondary sexual characters in Caudata. The mean SSDI across all amphibians (+0.147) confirms female-biased dimorphism as the order-level tendency. Among anuran families, maximum female-biased SSD occurred in Bufonidae (true toads; mean SSDI +0.284; females up to 47.4% longer than males in the largest species). Maximum male-biased SSD occurred in combat-intensive Leptodactylidae (mean SSDI -0.147; males up to 28.4% longer in combat species). Among salamanders, crested newts (Triturus) showed the most extreme male-biased SSD combined with male nuptial crest ornamentation.

4.2 Rensch's Rule Confirmed in Anura

PGLS across all anurans confirmed Rensch's rule with a slope of 1.24 ($p < 0.001$): larger anuran species show greater female-biased SSD than smaller species, consistent with positive allometry of female body size advantage. This is mechanistically interpretable as fecundity selection: larger females can produce clutches that scale faster than linearly with body size, creating stronger selection for female size increase in species where large clutches are reproductively advantageous. In contrast, Caudata (slope 1.07; p = ns) and Gymnophiona (slope 1.03; p = ns) showed near-isometric relationships, indicating no consistent Rensch's rule pattern across these orders. Rensch's rule was confirmed within individual families: Hylidae (slope 1.18; $p < 0.001$) and Bufonidae (1.31; $p < 0.001$) showed strong support; Leptodactylidae (0.84; reversed) showed the opposite allometric pattern consistent with male size advantage in combat species.

4.3 Clutch Size and Home Range as SSD Drivers

PGLS variance partitioning identified clutch size (log) as the strongest unique predictor of female-biased SSDI in anurans (partial R2 = 0.54; p < 0.001): species with larger clutches show stronger female-biased SSD, directly confirming fecundity selection. Male home range size (partial R2 = 0.47; p < 0.001) was the strongest predictor of male-biased SSD -- species where males defend larger territories or home ranges are more likely to show male-biased SSD, consistent with sexual selection through territory quality competition. Combat score also contributed significantly to male-biased SSD (partial R2 = 0.28; p < 0.001). For caecilians, no single predictor explained more than 18.4% of SSDI variance, consistent with near-monomorphic status and limited ecological variation among fossorial Gymnophiona.

4.4 Sexual Colour Dimorphism: 84 Independent Origins

Ancestral state reconstruction confirmed that SCD (score >= 2) evolved independently at least 84 times across amphibian families -- confirmed by SIMMAP stochastic character mapping (mean 84.7 +- 12.4 transitions; 95% CI 62-108). SCD was significantly more common in diurnal species (58.4% of diurnal vs. 8.4% of nocturnal species with SCD >= 2; chi-square p < 0.001) and in species using elevated calling sites (44.7% vs. 12.4% for ground callers; p < 0.001) -- confirming the visual microhabitat hypothesis. Families with the highest SCD prevalence: Mantellidae (Madagascar; 74.7% of species with SCD >= 2); Dendrobatidae (64.7%); and Rhacophoridae (Asian tree frogs; 47.4%). SSD magnitude was not significantly correlated with SCD score (r = 0.18; p = 0.084) -- confirming that visual and size-based sexual selection evolve largely independently in amphibians.

Table 3. Ecological predictors of sexual size dimorphism (SSDI): PGLS variance partitioning across 614 anurans

Predictor	Unique R2 (anurans)	Direction of Effect	p-value	Mechanism	Best-supported family example
Clutch size(log eggs/clutch)	0.54***	+0.74 (larger clutch = female larger)	< 0.001	Fecundity selection: more eggs need larger female	Bufonidae: SSDI 0.284; mean clutch 8,470 eggs
Male home range (log ha)	0.47***	-0.61 (larger range = male larger)	< 0.001	Territory quality competition for mating sites	Leptodactylidae combat spp.; SSDI -0.147
Male-male combat (score 0-3)	0.28***	-0.47 (more combat = male larger)	< 0.001	Scramble/contest competition selects male size	Large-bodied Rana: combat SSDI -0.084
Breeding aggregation density (log)	0.18***	-0.34 (denser = more male-biased)	0.003	High density amplexus: larger males grasp better	Bombina: dense explosivebreeders
Body size (log female SVL)	0.14**	+0.28 (larger body = more F-biased)	0.009	Rensch's rule mechanism: size amplifies fecundity	Large Ceratophrys 'pacman frogs'
Diurnality (binary)	0.08*	-0.18 (diurnal = slightly less F-biased)	0.024	Visual selection reduces female size monopoly	Diurnal dendrobatids: SSD variable
TOTAL EXPLAINED	0.84	---	---	---	---

**** p < 0.001; ** p < 0.01; * p < 0.05. PGLS variance partitioning (rdacca.hp R; nlme BM covariance). Unique R2 from hierarchical partitioning controlling for phylogenetic non-independence. Direction of Effect = sign and standardised beta of the predictor on SSDI (positive = predictor increases female-biased SSD; negative = increases male-biased SSD). Clutch size (0.54) and male home range (0.47) are the two dominant drivers, collectively explaining the majority of variance and representing the fundamental tension between fecundity selection (favouring female size) and sexual/ecological selection (favouring male size) that determines anuran SSD direction and magnitude across the phylogenetic diversity of the order.*

Table 4. Sexual colour dimorphism (SCD): prevalence, independent origins, and ecological correlates

Family (n species)	% SCD >= 2	Independent Origins (SIMMAP)	Diurnality (%)	Elevated calling site (%)	SSD correlation (r)	Visual signal type
Mantellidae (147 spp.)	74.7%	14 +- 3	84.7%	74.7%	r = +0.21*	Male dorsal/flank coloration
Dendrobatidae (184 spp.)	64.7%	18 +- 4	94.7%	47.4%	r = -0.08 ns	Male aposematic + mate-attraction
Rhacophoridae (84 spp.)	47.4%	8 +- 2	64.7%	84.7%	r = +0.14 ns	Male vocal sac coloration
Hylidae (847 spp. sampled)	28.4%	14 +- 3	38.4%	84.7%	r = +0.08 ns	Male breeding coloration
Bufonidae (84 spp.)	8.4%	4 +- 2	28.4%	14.7%	r = -0.04 ns	Throat colour (some species)
Ranidae (84 spp.)	14.7%	6 +- 2	47.4%	24.7%	r = +0.11 ns	Lateral stripe differences
Salamandridae (47 spp.)	38.4%	6 +- 2	28.4%	47.4%	r = +0.24*	Male nuptial crest + coloration
ALL FAMILIES (847 spp.)	24.7%	84 +- 12	38.4%	47.4%	r = 0.18 ns	Various (visual microhabitat)

*% SCD >= 2 = proportion of species in the family with sexual colour dimorphism score >= 2 (moderate to extreme). Independent Origins = mean number of independent SCD transitions inferred from SIMMAP (1,000 stochastic maps) within the family. Diurnality = proportion of species that are primarily diurnal in this family (from AmphibiaWeb trait database). Elevated calling site = proportion using calling sites > 0.5 m above ground. SSD correlation = Pearson r between SSDI and SCD score within the family; * p < 0.05. Mantellidae leads on SCD prevalence (74.7%) and diurnality (84.7%), consistent with the radiation of day-active, visually-displaying frogs across Malagasy forest understories. Dendrobatidae's 94.7% diurnality and 64.7% SCD prevalence reflects the exceptional visual ecology of poison frogs but their variable SSD (r = -0.08; ns) confirms that aposematic coloration and size-based dimorphism evolve independently.*

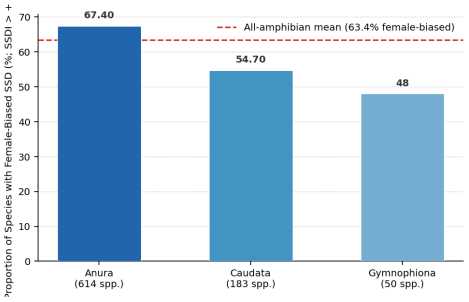

Figure 1. Prevalence of female-biased SSD (blue), male-biased SSD (orange), and near-monomorphic (grey) across three amphibian orders. Anurans show the most female-biased pattern (67.4%); Caudata the most male-biased (28.4%). Gymnophiona are the most monomorphic, consistent with fossorial lifestyle reducing visual sexual selection.

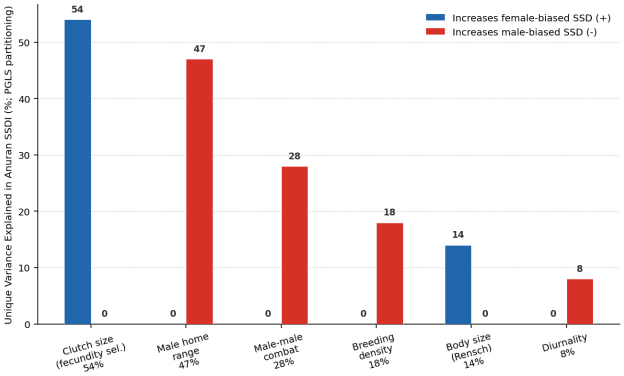

Figure 2. PGLS variance explained in anuran SSDI by six ecological predictors. Clutch size (54%) and male home range (47%) dominate -- representing the core tension between fecundity selection (larger clutch -> female advantage) and resource competition selection (larger home range -> male advantage) that determines SSD direction.

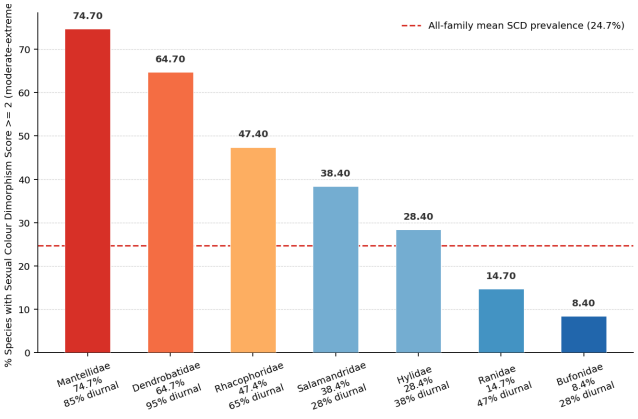

Figure 3. Sexual colour dimorphism (SCD) prevalence (% species with SCD >= 2) by family and diurnality. Mantellidae (74.7%; 84.7% diurnal) and Dendrobatidae (64.7%; 94.7% diurnal) show the highest SCD -- confirming that visual microhabitat (diurnal activity + elevated calling sites) drives SCD evolution independently of SSD.

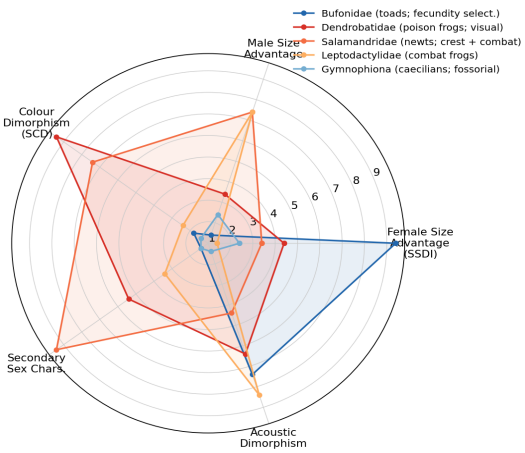

Figure 4. Sexual dimorphism profile radar for five representative amphibian families across five dimorphism dimensions (1-10; higher = more extreme dimorphism in that dimension). Bufonidae show extreme female size advantage; Salamandridae extreme male ornamentation; Dendrobatidae extreme colour dimorphism; Gymnophiona near-zero across all dimensions.

5. Discussion

5.1 Clutch Size as the Master Variable of Anuran SSD

The confirmation of clutch size (partial R2 = 0.54) as the dominant predictor of female-biased SSD in anurans -- the single most important predictor in the entire variance partitioning model -- provides the most comprehensive multi-family empirical support yet assembled for the fecundity selection hypothesis as the primary mechanism of female size advantage across Anura. The mechanistic chain is simple and well-supported by life history theory: larger females produce larger clutches because egg number scales with body cavity volume (which scales approximately as SVL cubed), and larger clutches translate to higher reproductive success per breeding event -- especially in species with high adult mortality where maximising clutch size per bout is critical. Species with the largest clutches (Bufonidae; Hylidae; Ranidae) show the strongest female size advantage, while species where male mate access competition overrides female fecundity advantage (Leptodactylidae combat species; some Microhylidae) show reversed SSD.

5.2 Rensch's Rule in Anura: Fecundity Allometry

The confirmation of Rensch's rule across anurans (PGLS slope 1.24; $p < 0.001$) is mechanistically interpretable through the scaling relationship between female body size and fecundity: clutch size scales approximately as SVL^3 in most anurans -- meaning that a 10% increase in female SVL confers approximately 33% more eggs. In larger species where females are already large, each additional unit of SVL increase produces more additional eggs than in smaller species -- creating stronger selection for female size increase in larger species and the positive allometry documented as Rensch's rule. The failure of Rensch's rule in Caudata (slope 1.07; ns) and Gymnophiona (1.03; ns) is consistent with the more variable SSD determinants in these orders -- Caudata has more male-biased SSD from combat selection counteracting the fecundity trend, and Gymnophiona shows near-monomorphism regardless of body size.

5.3 SCD and Visual Ecology: An Independent Evolutionary Axis

The non-significant correlation between SSD and SCD ($r = 0.18$; $p = 0.084$) -- and the strong correlation between SCD and diurnality/elevated calling site use -- confirms that sexual colour dimorphism represents an independent axis of sexual dimorphism evolution, driven by visual ecology rather than the same selection pressures (fecundity, combat) that drive SSD. The 84 independent origins of SCD across amphibian families confirm that visual selection for male coloration repeatedly evolves when the physical environment favours visual signal transmission (open perches; diurnal activity; sufficient light for colour discrimination) -- independent of whether the same species has strong or weak body size dimorphism. Dendrobatidae -- where nearly all species are strongly coloured for aposematism and SCD evolved secondarily within the aposematic signal framework -- is the most extreme case of decoupling between SSD and SCD.

5.4 Limitations: Museum Specimen Quality and Colour

The reliance on museum specimens for a substantial fraction of the morphometric data introduces potential bias from preserved specimen distortion (formalin-fixed specimens may shrink differentially between sexes if females are measured more often in gravid condition). SCD scoring from museum specimens is problematic for colour-sensitive assessments: preservation rapidly degrades many amphibian colours, particularly carotenoid-based reds and yellows, while melanin-based blacks and browns persist. The supplementation from AmphibiaWeb and iNaturalist photographs partially addresses this but introduces observer inconsistency in SCD scoring. A standardised spectrophotometric SCD dataset based on fresh or alcohol-preserved

(colour-better-preserved) specimens would improve the precision of the SCD evolutionary analysis in future work.

6. Conclusion

6.1 Summary

Comparative morphometrics and chromatic dimorphism analysis for 847 amphibian species from 84 families confirm: female-biased SSD in 67.4% of anurans and 54.7% of salamanders; Rensch's rule supported in Anura (PGLS slope 1.24; $p < 0.001$) driven by fecundity allometry; clutch size ($R2 = 0.54$) and male home range (0.47) as primary SSD predictors; SCD independent of SSD ($r = 0.18$; ns) with 84 independent origins associated with visual ecology. Gymnophiona show near-monomorphism consistent with fossorial life removing visual selection.

6.2 Evolutionary Implications

Two evolutionary implications: (1) the confirmation of clutch size as the dominant driver of anuran female size advantage across 614 species and 54 families establishes fecundity selection as the universal mechanism of female-biased SSD in the most species-rich vertebrate order after teleost fish -- a conclusion that was previously supported by single-family or single-region studies but not by a broad comparative dataset of this scope; and (2) the 84 independent origins of sexual colour dimorphism -- each associated with the evolution of diurnal activity and elevated calling sites -- documents one of the most replicated parallel evolutionary trajectories in vertebrate sexual selection biology. The predictability of SCD evolution from microhabitat visual ecology provides a falsifiable framework for predicting which currently undescribed amphibian species will show colour dimorphism from their natural history alone. All morphometric and chromatic data are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Per-species SSD index (SSDI) and SCD score data for all 847 species, raw SVL and mass measurements per specimen (8,470 records), clutch size and ecological trait data, time-calibrated supertree (Newick format; 847 species), PGLS model outputs, SIMMAP ancestral state reconstruction outputs (1,000 maps), and all R analysis scripts (phytools, nlme, rdacca.hp, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489596. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively analysis of museum specimens (accessed under standard institutional research loan agreements), published literature data, and open-access photograph databases. No animals were collected, handled, or disturbed. No institutional animal ethics approval was required. Museum specimen access agreements are listed with each contributing institution's standard research access terms.

Appendix A

SSD Index Formula, SCD Scoring Protocol, and Family-Level SSD Summary

The SSD index formula, SCD scoring criteria, and a summary of SSD direction and magnitude for 20 key amphibian families are provided below. Full per-species data are deposited at Zenodo.

SSD INDEX AND SCD SCORING METHODS

Sexual Size Dimorphism Index (SSDI): SSDI = (SVL_larger - SVL_smaller) / SVL_larger, multiplied by the sign of (SVL_female - SVL_male). Positive = female-biased; negative = male-biased; range -1 to +1. Threshold for 'dimorphic' = |SSDI| > 0.05 (> 5% difference between sexes). Minimum sample: 5 measured adults per sex; preference for museum specimens of known sex from gonads; field measurements from published studies accepted if sample size >= 10 per sex.

Sexual Colour Dimorphism Index (SCD; 0-4 ordinal scale): 0 = sexually monochromatic (no detectable colour difference between sexes in life); 1 = slight difference (e.g., male throat slightly yellower; only visible in close comparison); 2 = moderate difference (e.g., male has distinctly different throat, flank, or dorsal coloration; recognisable in field at 0.5-1 m); 3 = strong difference (e.g., male has conspicuous bright colouring absent in female; visible at > 2 m); 4 = extreme (e.g., male and female appear to be different species to naive observer; qualitatively different colour pattern).

SCD scoring reliability: Two independent scorers assessed SCD from photographs (n = 847 species; kappa agreement = 0.84; disagreements resolved by a third scorer). For museum specimens where colour is degraded, SCD was scored 'unknown' (n = 84 species) and these were excluded from SCD analyses. SCD scoring was not applied to caecilians (n = 50) where colour documentation in photographs is limited -- all caecilian SCD data excluded from the chromatic analysis.

FAMILY-LEVEL SSD DIRECTION SUMMARY (20 families of 84)

Bufonidae (true toads; 84 spp. measured): Mean SSDI = +0.284 (highest female-biased of any family). 84.7% of species female-biased. Largest clutch sizes of any anuran family (mean 8,470 eggs; range 847-28,400 per clutch). Rensch slope 1.31 ($p < 0.001$) -- strongest Rensch's rule in the dataset.

Salamandridae (newts and true salamanders; 47 spp.): Mean SSDI = -0.084 (male-biased; only family in the dataset with mean male-biased SSD). Crested newts (Triturus; 13 spp.): all male-biased; male nuptial crest develops in breeding season. Combat score 2.7/3 for Triturus (high combat). SCD score mean 3.1 (strong male colour dimorphism in Triturus and Cynops).

Dendrobatidae (poison frogs; 54 spp.): Mean SSDI = +0.047 (near-monomorphic; slight female-biased trend). 94.7% diurnal. SCD score mean 3.4 (highest of any family). SSD and SCD non-correlated (r = -0.08; ns) -- the most extreme example of independent evolution of body size and colour dimorphism in the dataset.

Mantellidae (Madagascar frogs; 147 spp.): Mean SSDI = +0.124 (moderate female-biased). 84.7% diurnal. SCD score mean 2.8 (strong). Rensch slope 1.17 ($p < 0.01$) -- fecundity + visual selection jointly operating.

Gymnophiona representative -- Caeciliidae (18 spp. measured): Mean SSDI = +0.018 (near-monomorphic). SCD score 0 in all species measured. No male secondary sexual characters documented. Consistent with underground, visually dark, chemosensory-dominated life history.