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Systematic Review of Sexual Dimorphism in the Genus *Draco* (Lacertilia: Agamidae)

Faiq Khoerul Umam
Study Program of Biology Faculty of Military Mathematics and Natural Sciences
The Republic of Indonesia Defense University
Correspondence: khoerulfu@gmail.com

ABSTRACT
This systematic literature review synthesizes morphological, ecological, and evolutionary information to understand variation in sexual dimorphism in Draco. The literature indicates that males generally possess conspicuous marking structures such as brightly colored neck skin folds and more differentiated patagia that function in territorial defense and mate attraction. In contrast, females often exhibit proportionally larger body size and patagia area, reflecting natural selection pressures related to reproductive costs and the need to maintain gliding performance while carrying eggs. Patterns of sexual dimorphism in Draco vary widely across species and regions, influenced by local environmental conditions, habitat noise levels, and interspecific competition.

Keywords: Dewlap, Draco, Patagium, Reptile, Sexual Dimorphism.

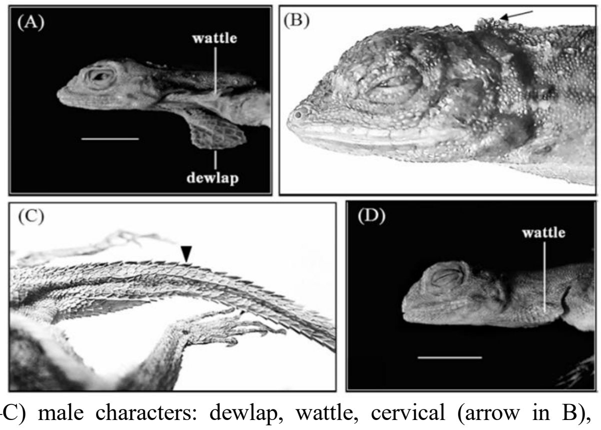
ABSTRAK
Tinjauan literatur sistematis ini mensintesis informasi morfologis, ekologis, dan evolusioner untuk memahami variasi dimorfisme seksual pada Draco. Literatur menunjukkan bahwa jantan umumnya memiliki struktur penanda yang mencolok seperti lipatan kulit leher berwarna cerah dan patagia yang lebih terdiferensiasi yang berfungsi dalam pertahanan teritorial dan daya tarik pasangan. Sebaliknya, betina seringkali menunjukkan ukuran tubuh dan luas patagia yang proporsional lebih besar, mencerminkan tekanan seleksi alam yang terkait dengan biaya reproduksi dan kebutuhan untuk mempertahankan kinerja meluncur saat membawa telur. Pola dimorfisme seksual pada Draco sangat bervariasi di berbagai spesies dan wilayah, dipengaruhi oleh kondisi lingkungan lokal, tingkat kebisingan habitat, dan persaingan antarspesifik.

Kata kunci: Gelambir, Draco, Patagium, Reptil, Dimorfisme Seksual.

INTRODUCTION

Sexual dimorphism is the systematic difference between male and female individuals of the same species. In reptiles, sexual dimorphism is generally influenced by sexual selection, often resulting in larger males, particularly in territorial lizards such as Agamidae (Carothers, 1984). The genus *Draco*, which consists of approximately 42 species of arboreal lizards unique for their gliding ability, exhibits distinctive and complex patterns of sexual dimorphism (Uetz, 2021). *Draco* inhabits the forests of Southeast Asia and uses gliding membranes (patagia) supported by elongated ribs to move from tree to tree. In addition to the patagium, male *Draco* possess a large, brightly pigmented, and sexually dimorphic dewlap, which functions as a visual signal for social communication, territorial defense, and mate attraction (Mori & Hikida, 1994; Srichairat et al., 2017; Sharma et al., 2025).

Draco exhibits Reversed Sexual Size Dimorphism (SSD-R), in which females have larger body size (SVL) (Mori & Hikida, 1992; Shine et al., 1998). This SSD-R is associated with natural selection arising from gliding performance, as females have relatively larger patagia to compensate for the burden of carrying eggs (Russell & Dijkstra, 2001; Shine et al., 1998). In addition to the patagium, differences are also observed in head morphometrics (Sexual Head Dimorphism) (Srichairat et al., 2016).



(A–C) male characters: dewlap, wattle, cervical (arrow in B), and caudal crests (arrow in C); (D) female characters (bar scale = 1 cm).
Source: Srichairat et al. (2017)

Figure 1
Sexual Dimorphism Genus *Draco*

This literature review aims to synthesize key findings on sexual dimorphism in the genus *Draco* from various scientific sources. Specifically, this review categorizes and analyzes the morphological patterns of dimorphism in *Draco*, particularly in key organs such as the body, dewlap, and patagium, as well as the selective mechanisms both sexual and natural that drive the evolution of these patterns of sexual dimorphism.

METHOD

The research method used is a Systematic Narrative Review, which aims to synthesize key findings on sexual dimorphism in the genus *Draco* from various primary scientific literature. This method emphasizes critical analysis and thematic synthesis of qualitative and quantitative data from the included studies.The data for this review are derived from a collection of scientific articles focusing on the genus *Draco*. This collection includes studies in the fields of morphometrics, functional ecology, taxonomy, and evolution of major *Draco* species in Southeast Asia.

The analyzed articles were selected based on the following inclusion criteria: (1) type of Publication: The published articles must be original empirical studies (original research) or taxonomic/systematic monographs. Other literature reviews are excluded as primary data sources but may be used as supporting references; (2) topical Focus: The article must explicitly present comparative data and analyses between males and females regarding sexually dimorphic characters, including at least one morphological trait (e.g., Snout-Vent Length (SVL), head size, dewlap, or patagium); and (3) taxa: The article must focus on the genus *Draco* L. (Agamidae, Lacertilia, Reptilia).

After identifying the relevant articles, the analysis process was carried out through the following stages: (a) extraction of key data: Specific data extracted from each study included the species examined, the SSD patterns identified, quantitative findings regarding dimorphic organs (dewlap and patagium), and the hypothesized selective mechanisms (Sexual Selection or Natural Selection); (b) thematic categorization: The extracted data were grouped into two main analytical themes to form the structure of the journal's discussion, namely morphological patterns of sexual dimorphism and the evolutionary driving factors; and (c) narrative synthesis: The grouped findings were then critically analyzed and synthesized to construct a cohesive narrative. The main focus of the synthesis was to identify evolutionary trade-offs that explain variation in SD patterns among species (*D. maculatus* vs. *D. spilopterus*) and to draw general implications from the fragmented findings across the genus.

RESULT

Morphometric Patterns of Sexual Dimorphism and SSD Variation

Sexual dimorphism in the genus *Draco* is consistently recorded in three primary morphological dimensions, namely body size, signaling organs, and the gliding membrane.

Body Size Dimorphism (Sexual Size Dimorphism)

SSD in *Draco* exhibits significant interspecific variability, reflecting differences in the dominant selective pressures. General literature (Mori & Hikida, 1992) often reports a trend of Reversed SSD (SSD-R), in which females have a greater Snout–Vent Length than adult males. This pattern is consistent with the findings of Tabug et al. (2023) on *Draco spilopterus*, where females show larger SVL. This SSD-R is associated with the need for females to accommodate substantial reproductive burden (eggs) and maintain locomotor performance during gravidity (Shine et al., 1998). Srichairat et al. (2016) explicitly identified a male-biased SSD pattern in *Draco maculatus*, in which males possess significantly larger SVL than females. This pattern is also supported by the study of Srichairat et al. (2014) on *D. blanfordii*. These interspecific differences in SSD patterns (SSD-R in *D. spilopterus* and *D. melanopogon* vs. male-biased SSD in *D. maculatus*) indicate that:

1. In species with male-biased SSD, sexual selection associated with male–male competition or dominance signaling becomes the stronger evolutionary force, favoring larger male body size.
2. In species with SSD-R, natural selection related to reproductive constraints becomes the principal mechanism shaping the evolution of larger female body size.

Table 1
Morphometric variation (mm) in the mean and standard deviation of SVL and head dimensions of *Draco* at each location

	Statistics	Ilocos	Laguna	Cavite	Bicol	t-test
		M (6) / F (3)	M (11) / F (4)	M (15) / F (3)	M (8) / F (4)	
SVL	Mean ± SD	75.9±10./ 80.89±5.37	81.85±8.86 / 83.86±15.74	71.32±5.03 / 66.78±2.84	71.89±4.01 / 75.62±10.44	0.148
	Min–Max	55.16–84.22 / 74.69–84.23	73.94–92.27 / 59.9–98.31	58.23–78.19 / 64.65–70.00	65.19–77.56 / 62.30–86.60	
JL	Mean ± SD	15.19±1.31 / 16.29±2.16	14.99±2.22 / 17.05±3.33	14.40±1.08 / 14.33±1.01	13.86±1.36 / 15.29±2.19	0.002*
	Min–Max	13.36–16.82 / 14.99–18.74	12.89–19.40 / 16.46–21.03	11.90–16.44 / 13.17–15.02	12.53–16.47 / 12.44–17.31	
JW	Mean ± SD	9.71±0.21 / 12.08±0.99	9.46±1.50 / 11.34±2.61	8.81±0.86 / 9.64±0.61	8.93±0.38 / 10.29±1.92	0.002*
	Min–Max	8.38–10.65 / 10.94–12.70	8.67–12.90 / 10.01–13.66	6.96–10.00 / 9.07–10.28	8.24–9.41 / 7.78–11.80	
HL	Mean ± SD	13.36±1.25 / 15.04±1.39	14.67±1.55 / 16.35±2.89	13.82±0.82 / 13.15±0.40	13.23±1.07 / 14.46±2.86	0.017*
	Min–Max	12.08–15.5 / 13.46–16.07	12.97–18.02 / 15.82–19.44	11.90–15.66 / 12.71–13.50	11.62–14.87 / 11.91–17.65	
HW	Mean ± SD	10.06±0.53 / 11.92±1.39	10.07±0.96 / 11.08±1.13	9.18±0.83 / 9.67±0.51	9.06±0.74 / 9.28±1.40	0.008*
	Min–Max	9.34–10.95 / 10.88–13.50	9.66–11.84 / 10.25–12.50	8.01–11.09 / 9.26–10.24	7.99–10.17 / 7.53–10.9	
HH	Mean ± SD	8.42±0.56 / 9.66±1.03	8.58±0.95 / 9.14±1.63	7.97±0.90 / 8.08±0.60	7.68±0.47 / 8.29±0.60	0.015*
	Min–Max	7.79–9.03 / 8.90–10.83	7.14–10.15 / 7.93–11.19	6.30–9.75 / 7.56–8.73	6.84–8.18 / 7.46–8.89	

Snout–Vent Length (SVL), Jaw Length (JL), Jaw Width (JW), Head Length (HL), Head Width (HW), Head Height (HH).
Source: Tabug et al. (2023)

Table 2
Descriptive analysis and t-test of morphometric characters of male and female *Draco maculatus* specimens from Thailand.

Morphometric Characters	Males (N=121)			Females (N=79)			p-Value
	Mean ± SD	Min	Max	Mean ± SD	Min	Max	
SVL	73.65 ± 9.61	38.70	90.70	69.43 ± 8.34	35.70	83.70	0.002*
SFL	24.23 ± 2.94	14.15	29.70	22.87 ± 2.73	13.10	26.85	0.001*
FL	31.04 ± 3.88	18.30	37.55	29.26 ± 3.41	16.00	35.35	0.001*
AGL	40.39 ± 5.51	21.20	49.20	39.17 ± 4.88	19.40	48.50	0.111
TaiL	112.21 ± 18.22	35.70	150.50	101.70 ± 13.76	53.90	126.35	0.000*
CL	5.02 ± 0.82	2.25	6.80	4.84 ± 0.95	2.05	6.95	0.149
HW	8.58 ± 1.03	4.85	10.55	8.62 ± 1.00	5.30	10.70	0.798
ID	2.70 ± 0.33	1.60	3.25	2.72 ± 0.36	1.70	3.65	0.662
HL	15.08 ± 1.60	8.70	17.55	14.60 ± 1.67	8.20	17.40	0.043*
HD	7.41 ± 0.80	4.15	8.90	7.11 ± 0.81	3.70	8.60	0.011*
ML	11.54 ± 1.28	6.60	14.05	11.15 ± 1.38	6.15	13.20	0.040*
DeL	26.73 ± 5.37	7.10	37.60	12.27 ± 2.34	5.20	18.15	0.000*
SN	1.74 ± 0.32	0.75	2.90	1.69 ± 0.32	0.60	2.90	0.257
DBNE	3.71 ± 0.50	1.85	4.65	3.57 ± 0.54	1.80	4.85	0.067
DBET	3.31 ± 0.44	1.70	4.10	3.17 ± 0.38	1.85	3.90	0.028*
EL	5.92 ± 0.51	4.25	7.20	5.81 ± 0.47	4.35	7.10	0.128
SL1	5.60 ± 0.74	2.70	6.90	5.41 ± 0.75	2.70	6.70	0.075
SL2	10.79 ± 1.16	6.25	13.20	10.46 ± 1.19	5.80	12.40	0.053
ST	12.97 ± 1.43	7.20	15.40	12.61 ± 1.47	6.65	14.65	0.089
TDV	1.87 ± 0.33	1.10	2.65	1.85 ± 0.33	1.00	2.45	0.649
TDH	1.55 ± 0.23	1.00	2.25	1.55 ± 0.24	0.85	2.00	0.923
SFL/SVL	0.33 ± 0.02	0.30	0.38	0.33 ± 0.02	0.29	0.38	0.631
FL/SVL	0.42 ± 0.03	0.35	0.52	0.42 ± 0.02	0.36	0.48	0.900
AGL/SVL	0.55 ± 0.02	0.49	0.60	0.56 ± 0.02	0.52	0.60	0.000*
TaiL/SVL	1.53 ± 0.17	0.53	1.78	1.47 ± 0.13	0.91	1.70	0.011*
CL/SVL	0.07 ± 0.01	0.05	0.09	0.07 ± 0.01	0.04	0.09	0.203
HW/SVL	0.12 ± 0.01	0.09	0.18	0.12 ± 0.01	0.11	0.16	0.000*
ID/SVL	0.04 ± 0.00	0.02	0.05	0.04 ± 0.00	0.03	0.05	0.000*
HL/SVL	0.21 ± 0.01	0.18	0.24	0.21 ± 0.01	0.18	0.23	0.000*
HD/SVL	0.10 ± 0.01	0.08	0.13	0.10 ± 0.01	0.08	0.12	0.081
ML/SVL	0.16 ± 0.01	0.14	0.18	0.16 ± 0.01	0.14	0.18	0.008*
DeL/SVL	0.36 ± 0.05	0.17	0.47	0.18 ± 0.02	0.13	0.24	0.000*
SN/SVL	0.02 ± 0.01	0.01	0.04	0.02 ± 0.01	0.02	0.04	0.529
DBNE/SVL	0.05 ± 0.00	0.04	0.06	0.05 ± 0.01	0.04	0.07	0.192
DBET/SVL	0.04 ± 0.01	0.03	0.05	0.05 ± 0.01	0.04	0.06	0.536
EL/SVL	0.08 ± 0.01	0.07	0.11	0.08 ± 0.01	0.07	0.12	0.018*
SL1/SVL	0.08 ± 0.01	0.06	0.09	0.08 ± 0.01	0.07	0.10	0.012*
SL2/SVL	0.15 ± 0.01	0.13	0.17	0.15 ± 0.01	0.14	0.18	0.001*
ST/SVL	0.18 ± 0.01	0.14	0.20	0.18 ± 0.01	0.17	0.21	0.002*
TDV/SVL	0.03 ± 0.01	0.01	0.04	0.03 ± 0.01	0.02	0.04	0.084
TDH/SVL	0.02 ± 0.00	0.01	0.03	0.02 ± 0.00	0.01	0.03	0.166
FL/AGL	0.77 ± 0.05	0.66	0.95	0.75 ± 0.05	0.64	0.87	0.004*
HW/HL	0.57 ± 0.04	0.47	0.80	0.59 ± 0.03	0.51	0.70	0.000*
HD/HW	0.87 ± 0.07	0.61	1.06	0.83 ± 0.06	0.65	0.95	0.000*
HD/HL	0.49 ± 0.03	0.42	0.56	0.49 ± 0.03	0.40	0.55	0.358
DeL/HL	1.75 ± 0.26	0.74	2.31	0.84 ± 0.11	0.57	1.11	0.000*

Source: Srichairat et al. (2016)

SVL = snout–vent length; SFL = snout–forelimb length; FL = forelimb length; AGL = axilla–groin length; TaiL = tail length; CL = cloacal length; HW = head width; ID = internarial distance; HL = head length; HD = head depth; ML = mouth length; DeL = dewlap length; SN = snout–nostril distance; DBNE = distance from nostril to anterior edge of eye; DBET = distance from posterior edge of eye to anterior edge of tympanum; EL = eye length; SL1 = snout to anterior edge of eye (snout length 1); SL2 = snout to posterior edge of eye (snout length 2); ST = snout to anterior edge of tympanum; TDV = tympanum diameter (vertical); TDH = tympanum diameter (horizontal).

Evolution of Dimorphic Structures Dewlap Dimorphism and Allometry

The dewlap in *Draco* is a primary dimorphic structure governed by sexual selection. Males possess a much larger dewlap with greater color variation, functioning as a long-distance visual signal for territorial communication and attracting mates (Sharma et al., 2025; Mori & Hikida, 1994). Allometric studies show that dewlap evolution is also influenced by natural selection through visual environmental noise. Summers & Ord (2022) found that dewlap allometry in *Draco* evolved to maximize signal detection, particularly in complex canopy environments. The development of this body structure reflects an evolutionary relationship between the need to attract mates (sexual selection) and the need to maintain signal visibility (natural selection/signal detection).

Patagium and Cost of Reproduction

The patagium (gliding membrane) exhibits sexual dimorphism that is predominantly female-biased. Shine et al. (1998) documented that the patagial area of females tends to be relatively larger in proportion to SVL compared to males, particularly in *D. melanopogon*. This difference is the direct result of adaptation to Natural Selection pressures. Egg production significantly increases the body mass of females, which aerodynamically elevates wing loading. A relatively broader patagium functions as a compensatory mechanism to mitigate the effects of increased wing loading, allowing gravid females to maintain sufficient gliding efficiency and performance for escaping predators and foraging. Russell & Dijkstra (2001) described interspecific variation in patagium morphology, emphasizing the close relationship between this locomotor structure and ecological demands.

Table 3
Sexual dimorphism of adult *Draco melanopogon* in Malaysia based on preserved museum specimens

Variables	Females	Males	Unpaired t- test		
	Mean±SD (range)	Mean±SD (range)	t	d.f.	P
SVL	77.9±4.1 (67-87)	75.7±3.4 (67-83)	4.17	212	<0.0001
Tail Length	145.1±7.1 (125-161)	136.8±7.7 (120-154)	6.91	155	<0.0001
Wing Span	78.4±5.0 (65-89)	73.6±5.0 (60-83)	6.05	212	<0.0001
Wing Attachment	45.6±3.1 (38-53)	43.6±3.0 (35-51)	4.60	212	<0.0001
Inter-limb length	43.8±2.7 (36-51)	42.2±2.5 (36-48)	4.22	212	<0.0001
Head length	14.5±0.7 (12.6-16.6)	13.6±0.8 (8.7-15.6)	8.60	212	<0.0001
Head Width	9.4±0.5 (8.1-10.3)	8.9±0.6 (7.7-12.3)	6.17	212	<0.0001
Axial Width	10.6±0.9 (8.9-13.2)	10.1±1.0 (7.7-12.7)	3.26	212	0.0013

Source: Shine et al. (1998)

Evolutionary Synthesis: A Trade-off Model of Sexual and Natural Selection

Overall, sexual dimorphism in the genus *Draco* is best explained through a dynamic, species-dependent trade-off model:

1. Male morphology is dominated by Sexual Selection (producing hyper-allometric dewlaps and, in some species, larger body size, such as in *D. maculatus*).
2. Female morphology is dominated by Natural Selection (driving relatively larger patagia and, in most species, larger body size/SSD-R) to compensate for reproductive costs and maintain locomotor performance essential for survival.

The interspecific variation in SSD observed (e.g., differences between *D. maculatus* and *D. spilopterus*) indicates that local environments and phylogenetic history determine which of the two selective pressures has the greatest impact on a given population.

Table 4
Summary of sexual dimorphism in *Draco*

Characteristics	Male	Female	Key Evolutionary Drivers
Body Size	Generally smaller	Generally bigger	Sexual Selection (male competition) vs. Natural Selection (costs of reproduction).
Dewlap	Bigger, longer, more colorful, and more frequently used in displays.	Smaller, less colorful, and less frequently used (generally nonexistent).	Sexual Selection (attracting mates, territoriality).
Patagium	The area is relatively smaller than the SVL. Often serves as a secondary ornament.	The area is relatively larger than the SVL.	Natural Selection (mitigation of wing loading during pregnancy).
Dominant Pattern	Communication and competition oriented adaptation.	Functional and survival oriented adaptation.	Sexual Selection

source: processed data

CONCLUSION

The diverse SSD patterns observed among species reveal that dimorphism in this genus is evolutionarily flexible and shaped by habitat-specific selective pressures. Sexual dimorphism in Draco arises from an evolutionary trade-off between intense sexual selection on males driving the development of conspicuous dewlaps and bright coloration and strong natural selection on females, which favors larger body size and proportionally broader patagia to maintain locomotor and gliding performance under reproductive constraints.

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