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Distinct sexual dimorphism in a vulnerable lizard, *Physignathus cocincinus*, in Vietnam: an indirect cause for male-biased exploitation?

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Abstract. Besides habitat destruction, unsustainable exploitation of wildlife can be a key threat to endangered reptiles. The Asian Water Dragon (*Physignathus cocincinus*), which is found in Vietnam and other Southeast-Asian countries, has been recently assessed as "Vulnerable" in the IUCN Red List due to severe human impacts. In particular, the species has been overexploited in Vietnam for local consumption and the international pet trade. We herein analyzed sexual dimorphism of *P. cocincinus* relating to alterations of sexual structure in exploited populations. A total of 90 adult Asian Water Dragons, including 50 females and 40 males, were examined with 15 morphometric and other external characters (e.g. coloration, crest size, tubercle form). There were significant inter-sexual differences in the dewlap with eye-catching colors, and development of nuchals, dorsal crest and tubercles on the neck and chin shields in males. Rensch's rule favoring the male-biased pattern in some morphometrics of *P. cocincinus* (e.g. body length, head traits and weight) was also confirmed. Based on interviews and observations at restaurants, larger and heavier males were intensively harvested by hunters because of their higher suitability for food consumption and higher profits. We hypothesized that this apparent sexual dimorphism of *P. cocincinus* might indirectly cause a decrease in the number of male adults and impacting the demographic structure in disturbed populations due to selective exploitation. Thus, it needs to be further assessed to what extent wild populations can sustain male-biased harvest. In terms of conservation actions, we propose enhanced patrols to better protect and captive-breeding programs to re-stabilize wild populations of *P. cocincinus*.

Key words. Squamata, Agamidae, Asian Water Dragon, conservation, intentional exploitation, male-biased dimorphism, morphology, population.

Introduction

During the ongoing sixth global mass extinction of wildlife, the human impacts of over-exploitation, habitat degradation, environmental pollution and climate change pose significant threats to reptiles (Böhm et al. 2013, Auliya et al. 2016, Cox et al. 2022). The over-exploitation of wildlife indeed leads to a substantial decline in populations and even to extirpation of threatened reptiles (Böhm et al. 2013). However, concrete conservation measures are often missing due to a lack of science-based understanding of the population demography (Böhm et al. 2013). Comprehensive data on the population abundance, structure and growth – vital rates are essential to assess the level of endangerment and species' ability to withstand certain levels of exploitation (Beissinger & Westphal 1998, Coulson et al. 2001, Jones et al. 2017, Iucn 2023).

High profits from the pet trade and food consumption are the main causes of poaching wildlife. Their intra-specific demand may be unbalanced in exploited species. Accordingly, intra-specific phenotypic distinctions could be a paramount cause of the non-randomness of human harvest, in which a group of individuals characterizing a certain size, an attractive coloration or a unique behavior is more likely at risk of exploitation than others from the breeding pool (Kingsolver 2007). Such "unnatural" selective removal may alter the long-term stability of the population structure (Mills 2007, Allendorf et al. 2008. Coltman 2008, Allendorf & Hard 2009, van Schingen et al. 2016). In terms of age structure, larger and heavier adult individuals may face intensified harvesting for food consumption, consequently reducing the effective population density. In *Shinisaurus crocodilurus*, it was documented that the number of adult animals in populations were significantly decreased within a short period of time, by poaching (van Schingen et al. 2016). The sexual dimorphism (SD), such as various colorations or phenotypic differences between males and females (Cooper & Vitt 1993, Andrews & Stamps 1994, Olsson et al. 2002), which may drive the intentional collections, may thereby change the sex ratio in populations. Impacts of selective exploitations have already been documented in some mammal and bird species (Harris et al. 2002, Jones et al. 2017).

The Asian Water Dragon, *Physignathus cocincinus* Cuvier, 1829 is widely distributed in Southeast Asia (e.g. Cambodia, southern China, Laos, Thailand and Vietnam), and its introductions are noted in Hong Kong, Malaysia, Taiwan and Florida, USA (Nguyen et al. 2009, Nguyen et al. 2018a, Lee et al. 2019, Chan et al. 2020, Gewiss et al. 2020). Evergreen lowland rainforests comprising rocky streams represent the typical habitat of *P. cocincinus* (Nguyen et al. 2009, Chan et al. 2020, Gewiss et al. 2020). Recently, the species has been classified as "Vulnerable" in the International Union for Conservation of Nature (IUCN) Red List, the Red Data Book of Vietnam (Tran et al. 2007, Stuart et al. 2019), and was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) at CoP19, as unregulated trade in the species was considered one of its key threats. Since its CITES listing, the species is also nationally protected in Vietnam and harvest of the species is illegal. Habitat degradation and fragmentation by infrastructure development, deforestation, tourism activities and water pollution are further threats to *P. cocincinus* (Nguyen et al. 2018a, Gewiss et al. 2020). Over-exploitation was considered to have critical impacts on wild populations of this species in central and northern Vietnam, where populations were occurring in low densities (Nguyen et al. 2018a, Gewiss et al. 2020). According to the CITES trade and the LEMIS databases, over one million live individuals of *P. cocincinus* were imported into the European Union (EU) and the United States (US) for the pet trade during the last two decades, whereof Vietnam was the major source (Gewiss et al. 2020). The majority of these specimens were most likely of wild origin, as large scale captive-breeding facilities are lacking in Vietnam and are not considered profitable due to rather low prices on the international market.

Regarding poaching for local consumption, adults of *P. cocincinus*, especially males, were the preferred target by local hunters due to their larger size making them more suitable and valuable for food consumption (Nguyen et al. 2018a, Gewiss et al. 2020). Our previous surveys in the disturbed populations in Thua Thien Hue Province, central Vietnam documented a significant change in sexual structure by a decrease in the number of adult males during the hunting season (Nguyen et al. 2018a).

In this study, we investigated the difference between males and females in phenotypic characters, such as coloration, crests, tubercles and morphometrics. There may be an inter-sexual variation in coloration and the male-biased sexual dimorphism in surveyed populations of *P. cocincinus*. Based on population data provided by Nguyen et al. (2018a) and evidence from interviews with local hunters, we further assessed whether the sexual dimorphism in *P. cocincinus* may indirectly contribute to the selective harvest, and likely drives its natural population structure towards less adult males.

Materials and methods

Field surveys

Field surveys were conducted in Vietnam from 2014 to 2023. In particular, adult individuals of *P. cocincinus* were found in Ha Giang Province (2 individuals), Quang Ninh Province (3 individuals) and Vinh Phuc Province, northern Vietnam (9 individuals), in Thua Thien Hue Province, central Vietnam (60 individuals), and Binh Phuoc, Kien Giang, Phu Yen provinces, southern Vietnam (16 individuals) (Fig. 1C). All adults were captured by hand and subsequently released after taking measurements and photos in their natural habitats.

Interviews

We conducted interviews with six local hunters (3 from Phu Yen, 1 from Binh Phuoc and 1 from Kien Giang provinces in May 2023, and 1 from Thua Thien Hue Province in January 2024) and one local dealer from Phu Yen Province, to obtain information on preferences for hunting and selling between males and females of *P. cocincinus*. Furthermore, we visited two local restaurants selling food containing *P. cocincinus.*

Morphological characters

A total of 90 adult individuals (50 females and 40 males) of *P. cocincinus* were examined for their morphological characteristics. According to Nguyen et al. (2018b), mature individuals of *P. cocincinus* were categorized based on the snout–vent length (SVL ≥ 130 mm). The dimorphism in coloration was assessed by taking photos from four directions (e.g. lateral, ventral and both dorsal sides). The weight of each individual was also measured.

Further measurements were taken with dial calipers to the nearest 0.1 mm from the right side of each individual. Abbreviations: AD = diameter of auditory meatus; AG = axilla to groin length, from posterior edge of forelimb insertion to anterior edge of hindlimb insertion; ED = diameter of eye, greatest diameter of orbit; EE = eye to ear distance, from posterior margin of eye to anterior margin of ear; FLL = forelimb length, from axilla to the tip of the fourth finger; HH = maximum head height; HL = head

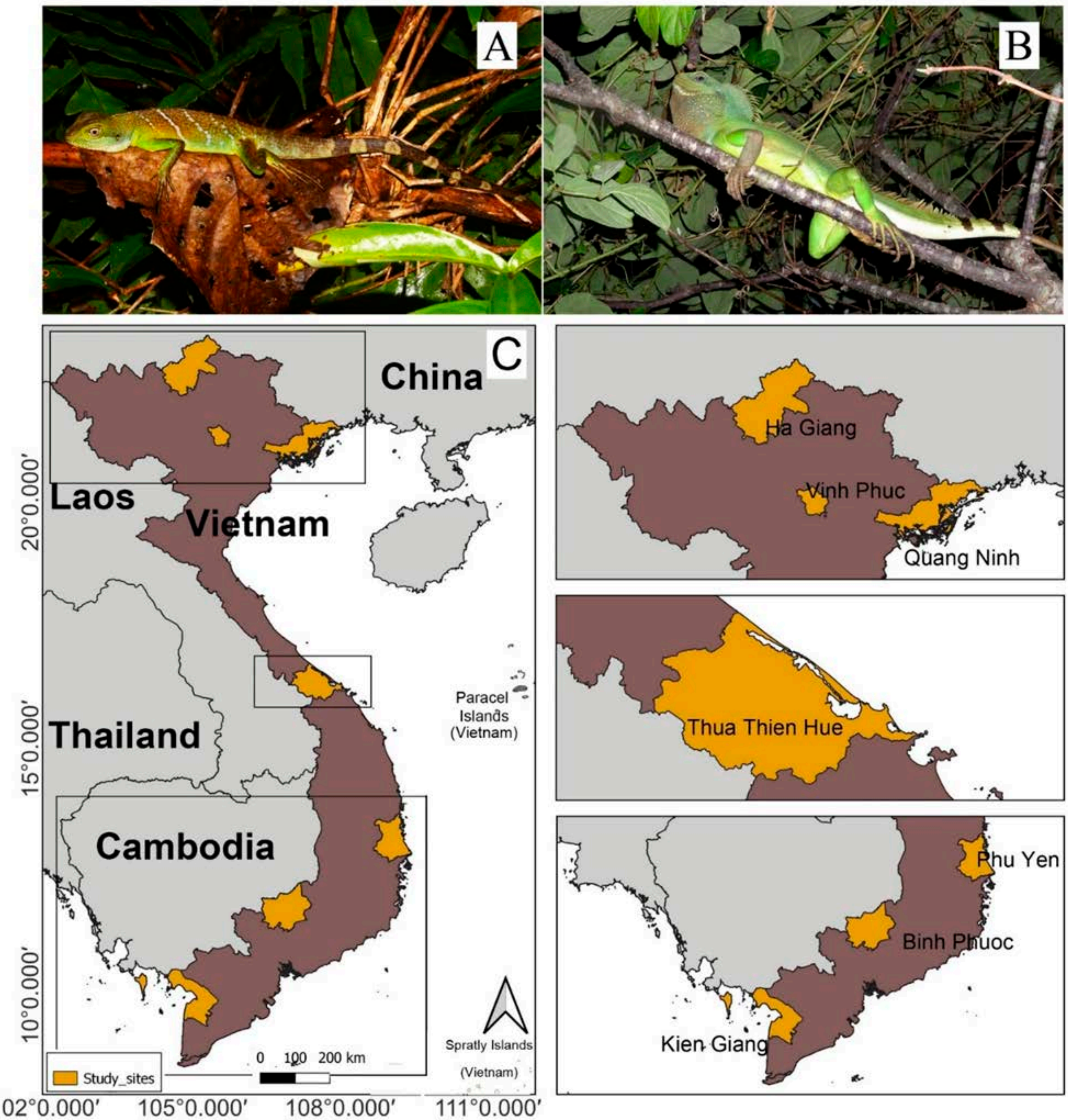

Figure 1. (A) Female; (B) male of *Physignathus cocincinus* resting on a tree branch; (C) study sites in northern Vietnam (Ha Giang, Quang Ninh, Vinh Phuc provinces), central Vietnam (Thua Thien Hue Province) and southern Vietnam (Binh Phuoc, Kien Giang, Phu Yen provinces).

length, from the tip of snout to posterior edge of occiput; HLL = hindlimb length, from groin to the tip of the fourth toe; HW = maximum head width; ML = mouth length, from tip of snout to last posterior labial edge; MW = mouth width, distance between last posterior labial edges on each side; SE = snout to eye distance, from tip of snout to anteriormost point of eye; SVL = snout–vent length, from tip of snout to vent; TaL = tail length, from vent to tip of tail.

Statistical comparisons

The sexual dimorphism index (SDI) was calculated to identify the pattern of sexual size dimorphism (SSD) using the formula suggested by Lovich & Gibbons (1992), in which

SDI = (mean size of males / mean size of females) – 1.

Accordingly, SDI is a positive value when males are the larger sex (SDI > 0) as a male-biased pattern, a negative value when females are the larger sex (SDI < 0) as a female-biased pattern and zero when the sexes are equal in size (SDI=0) as unbiased pattern). Shapiro-Wilk's test was used to test the assumption of normality. A Wilcoxon test was performed to determine the difference in the SVL between males and females. All statistical analyses were performed by using the software environment R.3.1.2 (RStudio Team 2018).

Due to high collinearity, the raw differences in other morphological characteristics of *P. cocincinus* may be intrinsically affected by the differences in overall body size. To independently assess the differences and limit the correlative effects, a normalization equation following an allometric growth model first suggested by Thorpe (1975) was applied to adjust raw data of morphology through the allom() function in R package GroupStruct (Chan & Grismer 2021). Accordingly, the allometric formula calculates the value:

$X_{adj} = \log_{10}(X) - b[\log_{10}(SVL) - \log_{10}(SVL_{mean})]$,

where X_{adj} = size corrected variable; X = unadjusted dependent variable; b = regression coefficient or slope of the relationship between $\log_{10}(X)$ and $\log_{10}(SVL)$. Subsequently, we used the t-test approach to examine the inter-sexual differences in these adjusted variables. For all of these tests, we applied a significance level of P = 0.05.

We further used a Principal Component Analysis (PCA) of seven adjusted variables (namely AG, HL, HW, HH, TaL, FLL and HLL) to assess overall inter-sexual morphological variation. Morphological spaces between sexes were visually illustrated by clustering all individual points of similar coded colors in a spatial coordinate of the PC1 and PC2 axes in the PCA analysis to evaluate the possibility of overlap. The values of the PCs were individually extracted to examine the inter-sexual difference by using the t-test. This PCA test was performed using the packages "factoextra" (Kassambara & Mundt 2020) and "FactoMinerR" (Le et al. 2008).

Results

Sexual dimorphism

Phenotypic characters are distinctive between males and females, once individuals of *P. cocincinus* reach maturity. In particular, well-developed nuchal and dorsal crests are present in adult males (Figs 1B, 2B1; Nguyen et al. 2018a, Gewiss et al. 2020), while these characters are slightly raised in females (Figs 1A, 2A1). We further recorded larger sharp tubercles on the neck sides and their presence on chin shields in adult males only (Fig. 2B). The dewlap is not well-developed in males, but an inter-sexual color variation is observed. In particular, males show a relatively bright violet color (Fig. 2B2), while females are characterized by red and pear colors (Fig. 2A2).

The mean values and ranges (minimum – maximum) of 15 raw morphometrics of *P. cocincinus* males and females are presented in Table 1. The mean SVL of males (187.3 ± 6.35 mm) is significantly longer than that of females (152.7 ± 2.5 mm) (Wilcox-test, W = 416; P < 0.001; Fig. 3, Table 1). Furthermore, the value of SDI = 0.23 (> 0) confirms that SSD of *P. cocincinus* follows the male-biased pattern. Our results also indicate that males are considerably heavier than females on average (Wilcox-test, W = 161; P < 0.001), with a maximum weight of 600 g, while females only reach a maximum of 300 g (Table 1).

Using adjusted data of remaining morphometrics, our inter-sexual comparisons in *P. cocincinus* reveal that males have significantly longer, wider and higher head dimensions (HL, HW and HH, respectively), and other head characters (SE, EE and ML), and longer forelimbs (FLL), indicating the male-biased pattern (Fig. 3, Table 1).

The PCA using seven adjusted morphometrics estimated the first two principal components to explain 61.5% (whereof PC1: 37.5% and PC2: 24.0%) of the overall variance between males and females of *P. cocincinus*. We found that forelimbs (FLL) and head dimensions (HL, HW and HH) are the most important variables accounting for PC1 and PC2, respectively (Fig. 4). The ordination test shows that the morphological space of females relatively overlays that of males (Fig. 4). However, our statistic tests document that the averages of PC1 (t = -3.6; df = 59; P < 0.001) and PC2 (t = -3.6; df = 49; P < 0.001) between males and females are both significantly different.

Interviews on selective harvest

We interviewed local hunters and noted that large adults are the preferred target for collection over juveniles, among which adult males are the most favored. Local dealers collected juveniles only for the pet trade and their price was recorded to be very low with 10,000–20,000 Vnd/ind (~ 0.4–0.8 USD). In comparison, prices to buy two or three adult males of *P. cocincinus* (~ 1 kg) ranged from 300,000–450,000 Vnd (~ 12–20 USD) which were twice as expensive as prices for adult females. Two hunters from

Table 1. Descriptive statistics of morphometrics in males and females of *Physignathus cocincinus* and Wilcoxon-test analyses (* indicating the significant difference).

Characters	Males Min–Max (Mean ± SD)	Females Min–Max (Mean ± SD)	P-values
Body characters			
SVL*	131.2–280 (189.0 ± 34.9, n=40)	130.0–219.0 (155.7 ± 18.9, n=50)	W=416; P < 0.001
TaL	320.0–675.0 (461.9 ± 84.7, n=40)	314.0–527.0 (392.6 ± 49.0, n=50)	t=-0.4; df=69.5; P > 0.05
AG	53.0–125.0 (85.0 ± 22.1, n=39)	48.1–104.0 (70.4 ± 11.6, n=50)	t=1.0; df=73.3; P > 0.05
FLL*	71.0–115.4 (91.7 ± 14.5, n=29)	53.8–94.0 (73.5 ± 8.3, n=44)	t=-2.6; df=58.9; P < 0.05
HLL	119.0–194.7 (156.7 ± 24.1, n=29)	100.3–162.0 (131.4 ± 14.2, n=44)	t=-1.4; df=63.5; P > 0.05
Weight*	86.0–600.0 (268.3 ± 22.8, n=29)	64.0–300.0 (140.9 ± 8.9, n=41)	W=161; P < 0.001
Head characters			
HL*	45.0–78.9 (59.6 ± 10.0, n=29)	34.3–59.0 (42.3 ± 5.1, n=44)	t=-6.4; df=47.1; P < 0.001
HW*	24.5–40.0 (30.0 ± 4.4, n=29)	19.7–32.0 (24.6 ± 2.7, n=44)	t=-2.6; df=47.9; P < 0.05
HH*	20.0–38.5 (30.2 ± 5.6, n=29)	17.0–29.4 (22.6 ± 2.8, n=44)	t=-3.6; df=52.4; P < 0.001
SE*	17.5–26.9 (22.1 ± 2.8, n=25)	14.1–21.7 (17.3 ± 1.9, n=35)	t=-3.2; df=56.0; P < 0.05
ED	11.3–17.7 (14.3 ± 1.7, n=25)	9.1–15.9 (12.0 ± 1.7, n=35)	t=-1.8; df=56.9; P > 0.05
EE*	11.2–20.7 (14.9 ± 3.1, n=25)	8.1–16.4 (10.7 ± 2.0, n=35)	t=-2.1; df=57.9; P < 0.05
AD	4.2–9.6 (6.4 ± 1.6, n=25)	3.9–5.7 (4.7 ± 0.4, n=35)	t=-1.5; df=52.6; P > 0.05
MW	21.8–40.2 (32.2 ± 6.0, n=25)	20.1–31.9 (25.9 ± 2.7, n=35)	t=-0.6; df=35.6; P > 0.05
ML*	32.4–44.8 (39.0 ± 4.1, n=25)	24.6–37.2 (29.8 ± 3.0, n=35)	t=-4.6; df=44.6; P < 0.001

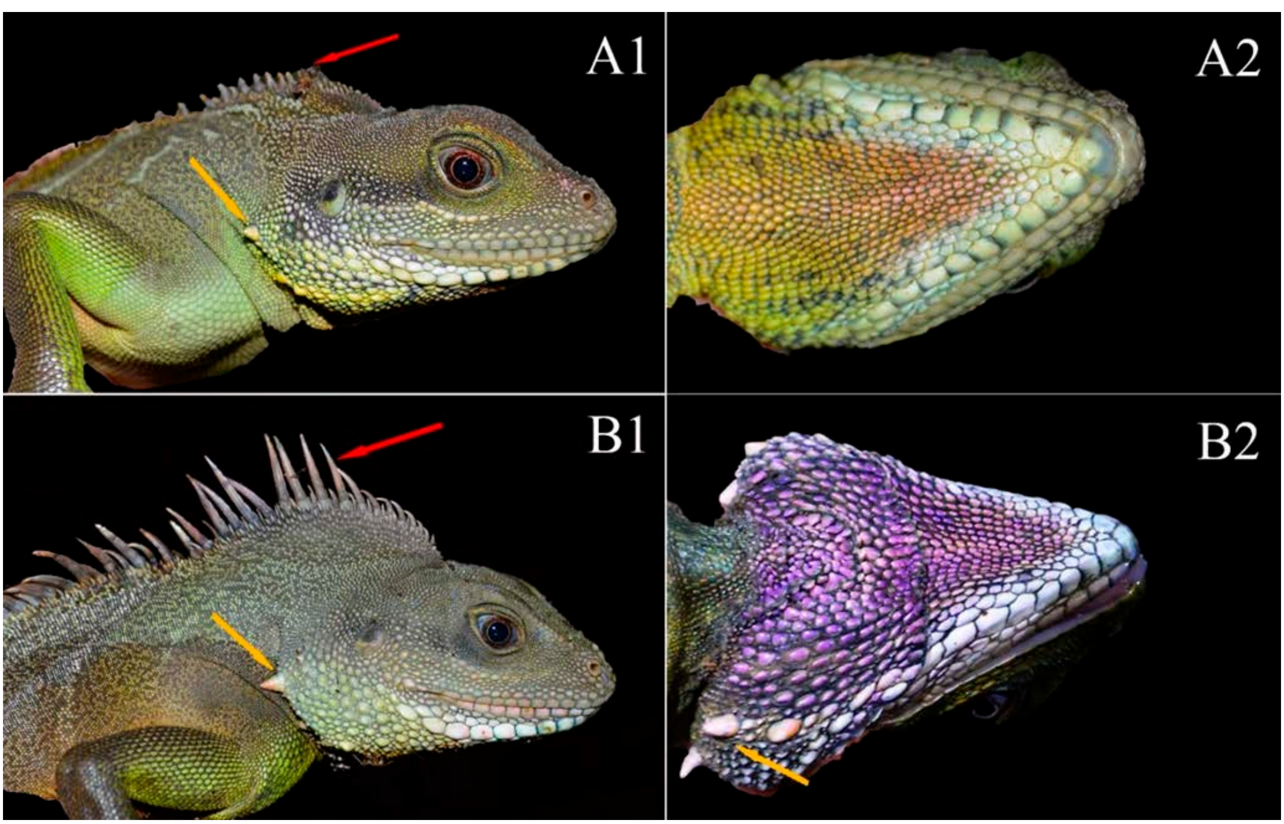

Figure 2. A few dimorphic characters for identification of females (A) and males (B) from the lateral side (1) and the ventral side (2) of *Physignathus cocincinus*, including nuchal and dorsal crests (red arrows), and tubercles (orange arrows).

Phu Yen Province shared information that they usually collected large adult males to sell them to dealers or restaurants, while they released encountered adult females, because they are necessary for reproduction. During visits at restaurants in Thua Thien Hue and Phu Yen provinces, we only found one adult female together with many large adult males (Figs 5A, B).

Discussion

Male-biased sexual dimorphism

Sexual dimorphism has been widely recorded in many terrestrial organisms (Darwin 1871, Shine 1979, Anderson & Vitt 1990, Andersson 1994). This phenomenon refers to phenotypic differences between males and females within a species, in coloration, body size, skin texture, vocal sacs and many other morphological characteristics (Cooper & Vitt 1993, Andrews & Stamps 1994, Olsson et al. 2002). In this study, sexual dimorphism regarding well-developed crests and sharp tubercles, a longer snout–vent length (SVL) and other morphometrics (head dimensions and forelimbs) with larger values were documented in males of *P. cocincinus*, all of which highly favor the male-biased pattern and approve Rensch's rule (Rensch 1950). Accordingly, larger males have advantages in winning male–male contests for territory, food resources and mating opportunities (Anderson & Vitt 1990, Webster 1992, Fairbairn 1997, Kratochvíl & Frynta 2002, Olsson et al. 2002, Fairbairn 2005, Cox & Calsbeek 2010). In fact, male Water Dragons have been recorded as territorial and aggressive towards conspecifics with no overlapping home ranges (Werning 2010, Chan et al. 2020).

Another potential hypothesis of the diet niche partitioning may be considered relative to the SD in head dimensions. Accordingly, a feeding behavior with larger prey items consumed by males that likely increases the male-biased SD pattern in head characters of *P. cocincinus* (Vitt 2000, Chelsea 2013) avoids inter-sexual competition for food resources (Shine 1991, Cox et al. 2008).

Females tend to prefer males with optimal phenotypes for mating (Cooper & Vitt 1993, Cox & Calsbeek 2010, Chelsea 2013). Besides morphometrics, the dimorphic coloration of the dewlap and the presence of nuchal and dorsal crests in male Water Dragons are considered to be exceptional characteristics that attract females in the mating selection. Furthermore, the well-developed sharp tubercles on the chin shield may have advantages in the male–male contest and in holding the head of females during copulation.

We also documented the male-biased pattern in forelimbs of *P. cocincinus*. An increased limb length likely en-

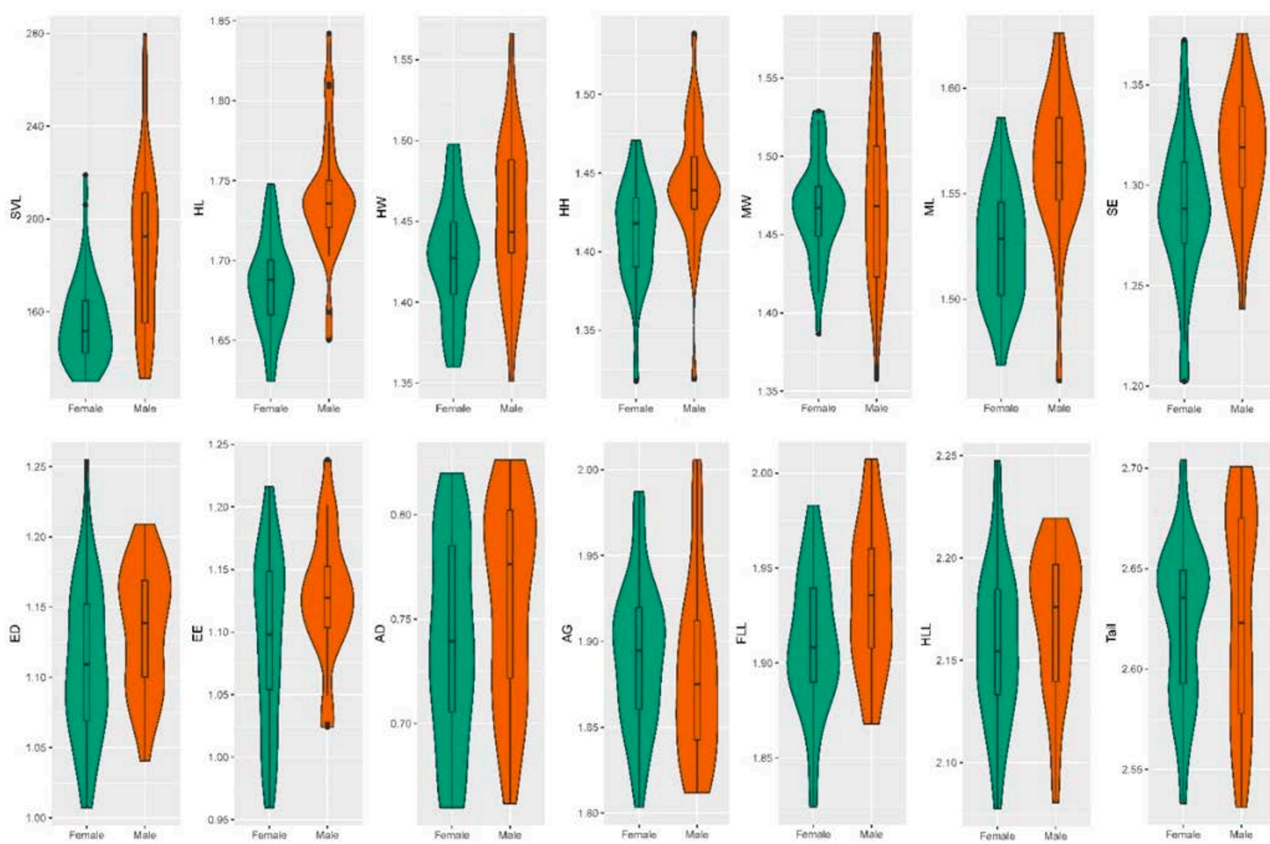

Figure 3. Violin plots overlayed with box plots show the range, frequency, mean, and 50% quartile (black rectangle) of snout–vent length (SVL) and remaining adjusted morphometrics of *Physignathus cocincinus*.

hances locomotor performance, such as more effective chasing of females to copulate and escape from predators (Butler & Losos 2002; Schwarzkopf 2005, Iraeta et al. 2010).

Implications for conservation

Over-exploitation for the pet trade and local food consumption have decisive impacts on wild *P. cocincinus* populations, such as decreasing population sizes and altered population structure (Nguyen et al. 2018a, Gewiss et al. 2020). While the approximate dimensions of the international pet trade are known based on recorded import numbers, the number of collected Water Dragons for the local consumptive trade in Vietnam has not been quantified but only reported on occasion (Nguyen et al. 2018a, Gewiss et al. 2020). Juveniles and young subadults are usually collected for the international pet trade. In contrast, based on interviews with hunters and observations at local restaurants, large adult males are favored by local dealers due to

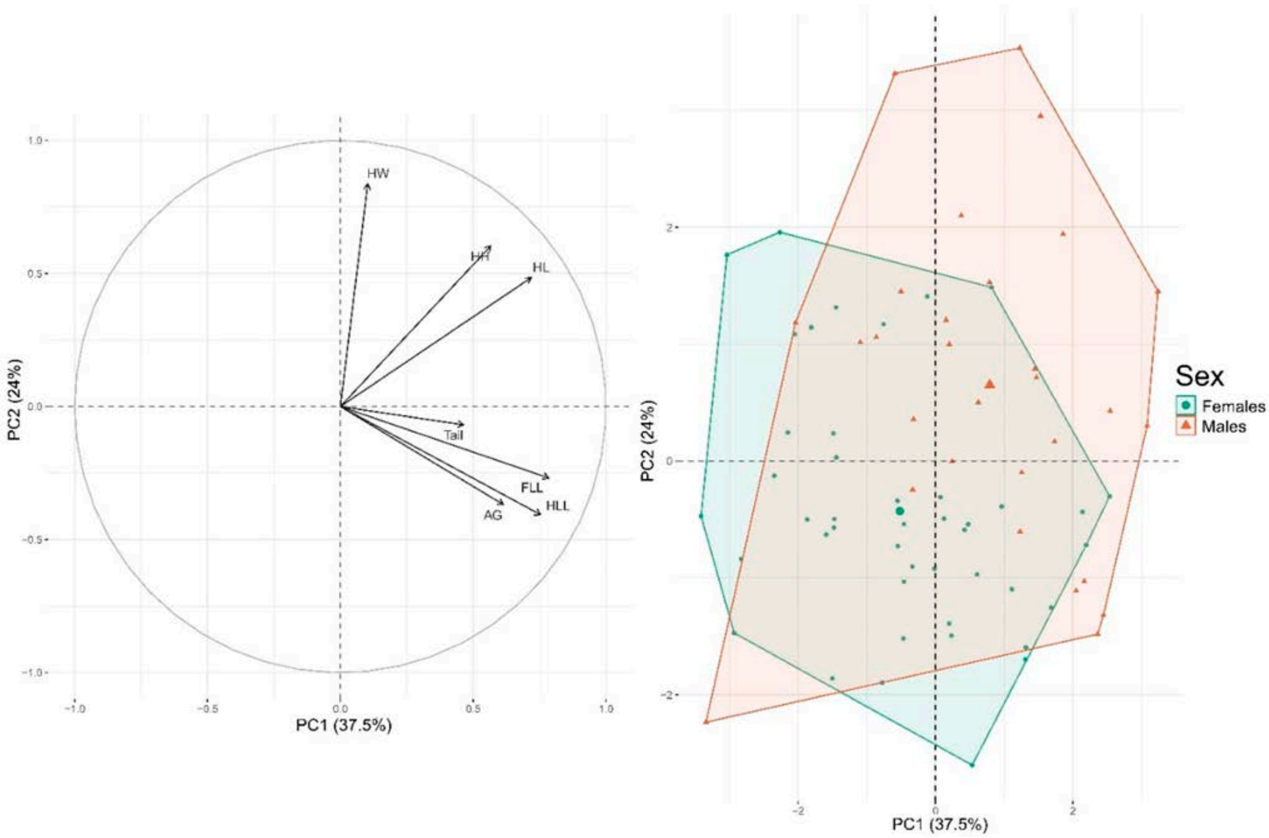

Figure 4. Principal Component Analysis of seven adjusted morphometrics from *Physignathus cocincinus* males and females.

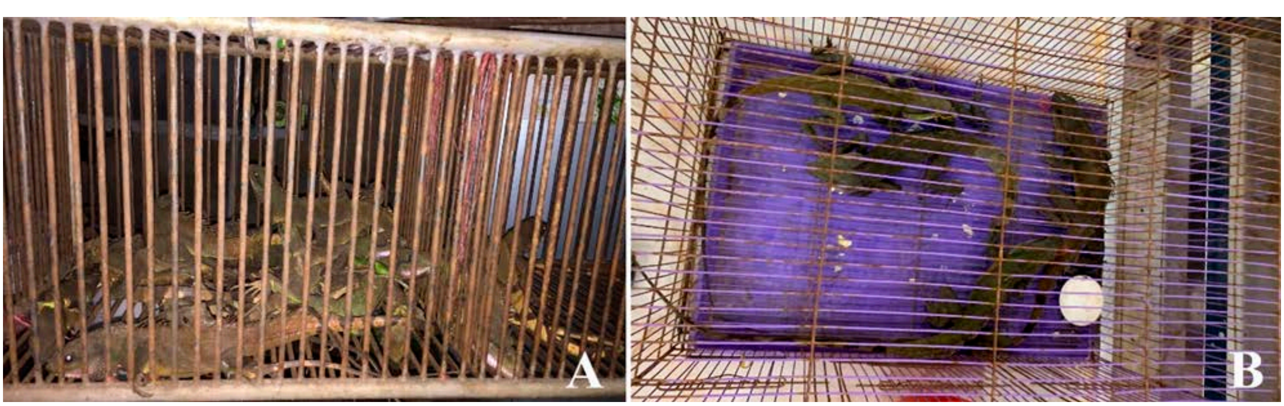

Figure 5. Adults of *Physignathus cocincinus* were caught in cages for food consumption in restaurants in (A) Thua Thien Hue and (B) Phu Yen provinces.

higher prices for sale in restaurants and the domestic pet trade (Nguyen et al. 2018a; Gewiss et al. 2020; this study). Male Water Dragons are characterized by their distinct phenotypes of larger sizes and heavier weight, attractive coloration and well-developed nuchal and dorsal crests. Among these, size and weight are considered important factors in terms of food consumption. Based on this information, we consider that the male-biased dimorphism in *P. cocincinus* might be an indirect factor influencing the abundance of males in nature. Nguyen et al. (2018a) documented a change in the demographic structure of the *P. cocincinus* population in Thua Thien Hue Province during the hunting season from April to June in two surveyed years. Accordingly, the proportion of adult males considerably decreased during the hunting season in comparison to adult females. The targeted harvest in males might shape a female-biased ratio in the adult population structure of *P. cocincinus* in exploited wild populations. Although this unbalanced ratio can occur in other undisturbed populations of *P. cocincinus* since it is a polygamous agamid species and males are reported to be very territorial and have no overlapping home ranges (Werning 2010, Chan et al. 2020), this ongoing selective over-harvest certainly changes of the natural ratio towards the significant reduction of adult males. Therefore, it needs to be further evaluated in the future as to which wild populations can withstand illegal exploitation and reduction in adult males.

The alteration in the population structure of *P. cocincinus* with such a significant decrease of adult males during the hunting season is considered one of many negative consequences of human activities. The exploitation of wildlife causes decreasing population size and genetic diversity, and may even lead to wild extirpation. In fact, the exploitation was completely unregulated until *P. cocincinus* was recently included in CITES Appendix II to prevent over-harvesting of wild animals for international trade. Consequently, the international legislation came into force in November 2022. Since then, no exports of wild specimens have been recorded so far. However, considering the additional pressure on wild populations by the harvest for local food consumption, despite being illegal further conservation actions on the domestic level are necessary that may include an adaptive management of wild populations. As *P. cocincinus* has a fast life history that can reach maturity within 12 months and may lay multiple clutches of up to 16 eggs per year (Werning 2010), we assume that the species can generally sustain a certain offtake, if carried out in a controlled manner taking into account the status of the targeted local populations. We further propose to increase patrol activities, improve capacity-building measures for local rangers and develop community education programs to enhance awareness about the biodiversity value. Captive-breeding programs may establish reserve populations that could be used to restock depleted wild populations. Furthermore, it can be assessed whether regulated captive-breeding in the species for commercial purposes is suitable to meet persisting demand for consumption and thereby decrease the pressure on wild populations.

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