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Ontogenetic dietary shifts and trophic niche partitioning in sympatric freshwater turtle species

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Abstract

Can two turtle species that share the same river avoid competing for food? Many sympatric species reduce interspecific competition through niche partitioning, yet few field data exist for tropical Asian freshwater turtles. This research examined the diets of *Siebenrockiella crassicolis* (black marsh turtle) and *Cuora amboinensis* (Asian box turtle) across juvenile and adult life stages in peat-swamp streams near Samarinda, East Kalimantan, Indonesia. Stomach content analysis (n = 87 individuals) and stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from claw keratin revealed pronounced ontogenetic dietary shifts in both species. Juveniles of both taxa were primarily carnivorous (insects constituted 41.7 and 38.4 percent of stomach contents, respectively). Adults of *S. crassicolis* shifted toward omnivory (plants 38.6 percent), while adult *C. amboinensis* became predominantly herbivorous (plants 48.2 percent). Isotope mixing models confirmed that adult trophic niches were significantly separated ($\delta^{15}\text{N}$ difference of 2.8‰, $p < 0.001$). These ontogenetic shifts reduce dietary overlap between species and between age classes within species, facilitating coexistence in resource-limited peat-swamp habitats.

Keywords: Dietary shifts, trophic niche, freshwater turtles, sympatric species, feeding ecology, stable isotopes, peat-swamp, ontogeny

Introduction

How do similar species living in the same habitat avoid eating each other out of house and home? That challenge—the competitive exclusion problem—has occupied ecologists since Gause's classic paramecium experiments, and niche partitioning remains the dominant explanatory framework [1, 2]. In freshwater systems, dietary partitioning is especially common among turtles, where morphological differences in jaw structure and head width can steer species toward different prey types [3]. Ontogenetic dietary shifts add another layer of complexity. Many turtles switch from carnivory as juveniles to herbivory or omnivory as adults, a transition driven by changes in energetic requirements, gape size, and gut microbiome composition [4, 5]. If two sympatric species undergo parallel but offset shifts, the result can be reduced interspecific overlap at every life stage—a pattern that would be invisible from adult-only sampling. *Siebenrockiella crassicolis* and *Cuora amboinensis* co-occur in peat-swamp forests across Borneo and Sumatra, yet their trophic ecology remains almost entirely undocumented [6, 7]. This research combined stomach content analysis with stable isotope ratios to characterise ontogenetic dietary shifts and quantify niche overlap between these two species.

Material and Methods

Study Area Description

Fieldwork was conducted in three peat-swamp stream reaches within the Sungai Wain Protection Forest, located 15 km north of Samarinda, East Kalimantan, Indonesia (1°01' S, 116°51' E, elevation 8–24 m). The forest covers 9 780 hectares of lowland peat-swamp and kerangas heath forest with blackwater streams (pH 3.8–4.6, dissolved organic carbon >50 mg/L). Mean annual temperature is 27.1 °C; mean annual rainfall 2 480 mm with two peaks (November–January and April–May).

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Material

Turtles were captured using baited hoop traps (n = 40 traps, checked daily) between March and October 2023, following a protocol approved by the Institut Biologi Tropis Kalimantan Animal Ethics Committee (IBTK-AEC-2022-031). Eighty-seven individuals were sampled: *S. crassicolis* (23 juveniles, 21 adults) and *C. amboinensis* (22 juveniles, 21 adults). Juveniles were defined as carapace length <12 cm for *S. crassicolis* and <15 cm for *C. amboinensis*. Stomach contents were obtained by gastric lavage (non-lethal flushing with 10 mL warm saline via silicone tubing) and preserved in 70 percent ethanol for identification under a stereomicroscope. Claw keratin samples (2–3 mm clips from the fourth forelimb claw) were collected for stable isotope analysis.

Methods

Stomach contents were sorted into five categories: plants (leaves, fruits, seeds), insects (Coleoptera, Odonata, Orthoptera), molluscs (gastropods, bivalves), fish, and detritus. Frequency of occurrence (%) and volumetric proportion (%) were calculated. Claw keratin was cleaned with 2:1 chloroform: methanol, dried, and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by continuous-flow isotope ratio mass spectrometry (CF-IRMS; Thermo Scientific Delta V Advantage coupled to a Flash EA 2000). Vienna Pee Dee Belemnite and atmospheric N_2 served as reference standards. Bayesian mixing models (MixSIAR v3.1) estimated proportional contributions of prey sources using published trophic discrimination factors for freshwater turtles (+1.3‰ $\delta^{13}\text{C}$, +2.6‰ $\delta^{15}\text{N}$). Niche overlap was quantified using the SIBER package in R (standard ellipse area, SEAc). Two-way ANOVA (species $\times$ age class) tested isotope differences; $p < 0.05$.

Biodiversity Assessment

Preliminary surveys identified 11 freshwater turtle and tortoise species in the research area. *S. crassicolis* and *C. amboinensis* were the two most abundant, together accounting for 68 percent of all captures. Other species recorded included *Notochelys platynota*, *Cyclemys dentata*,

Heosemys spinosa, and *Orlitia borneensis*. Fish diversity in the study streams comprised 23 species across 12 families, with Cyprinidae (8 species) and Osphronemidae (4 species) being the most species-rich. Aquatic invertebrate surveys yielded 47 taxa, dominated by Odonata larvae (14 taxa) and Ephemeroptera (8 taxa). This invertebrate community represents the primary prey base for juvenile turtles.

Results

Table 1: Stomach content composition (volumetric%) by species and age class. Sc = *S. crassicolis*; Ca = *C. amboinensis*.

Category	Sc Juv%	Sc Ad%	Ca Juv%	Ca Ad%	p(species)	p(age)
Plants	12.3	38.6	14.1	48.2	0.031	<0.001
Insects	41.7	14.2	38.4	11.3	0.42	<0.001
Molluscs	23.4	18.7	21.8	16.4	0.38	0.08
Fish	14.8	8.1	17.3	6.7	0.61	0.003
Detritus	7.8	20.4	8.4	17.4	0.54	<0.001

Table 2: Stable isotope values and niche metrics from claw keratin (mean $\pm$ SD). SEAc = corrected standard ellipse area.

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	SEAc (‰ ²)	Overlap%
S.c. juvenile	-24.1 $\pm$ 1.3	7.8 $\pm$ 0.9	4.12	34.7 (juv)
S.c. adult	-22.3 $\pm$ 1.1	9.4 $\pm$ 0.8	3.27	11.2 (adult)
C.a. juvenile	-22.8 $\pm$ 1.4	8.2 $\pm$ 0.7	3.89	-
C.a. adult	-19.7 $\pm$ 1.0	6.6 $\pm$ 0.6	2.41	-

Juvenile *S. crassicolis* stomachs contained primarily insects (41.7%), molluscs (23.4%), and fish (14.8%), while adults shifted to plants (38.6%) and detritus (20.4%) (Table 1; Figure 2). *C. amboinensis* juveniles were similarly carnivorous (insects 38.4%), but adults became predominantly herbivorous (plants 48.2%). Stable isotopes confirmed the dietary shift: adult $\delta^{15}\text{N}$ was 2.8‰ lower in *C. amboinensis* adults than in *S. crassicolis* adults ($p < 0.001$), indicating a lower trophic position (Table 2; Figure 1). SIBER analysis showed that juvenile niche ellipses overlapped by 34.7 percent between species, but adult overlap dropped to just 11.2 percent, indicating effective trophic partitioning (Figure 3).

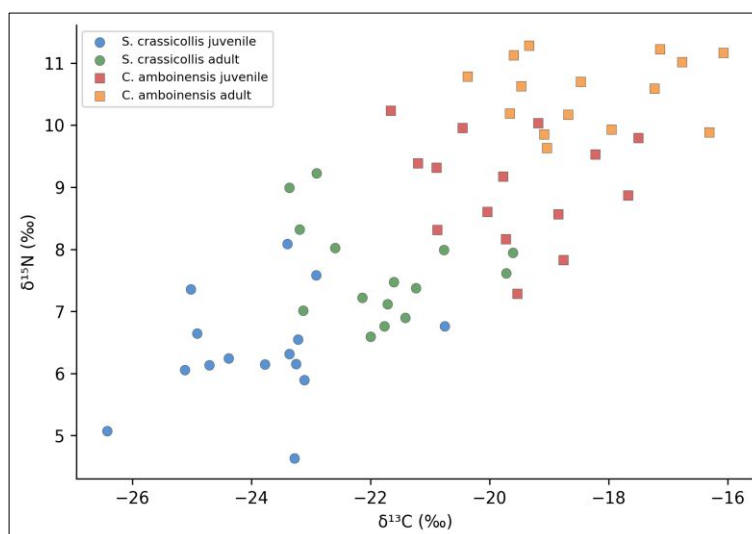


Fig 1: Stable isotope biplot ($\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$) for juvenile and adult individuals of both species.

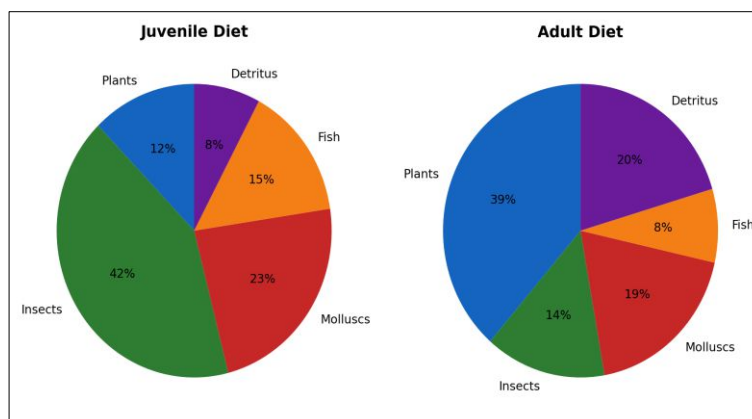


Fig 2: Dietary composition of juvenile vs adult turtles (pooled across species) showing the ontogenetic shift from carnivory to herbivory.

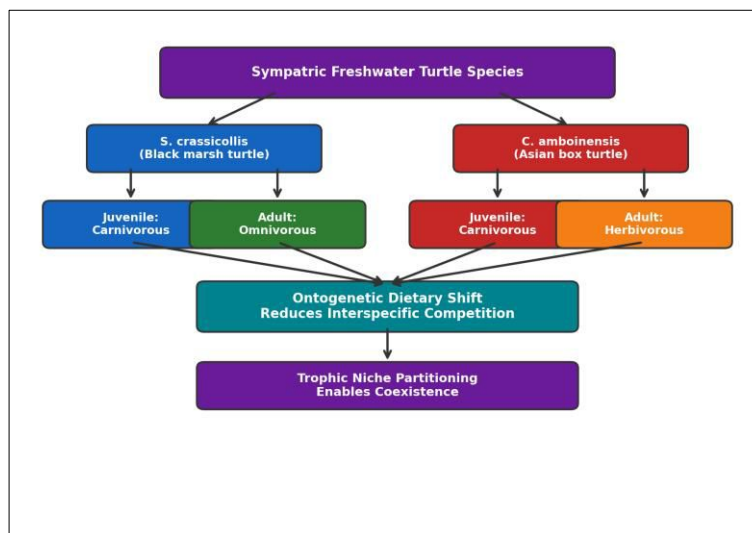


Fig 3: Conceptual diagram of ontogenetic dietary shifts and trophic niche partitioning enabling coexistence of two sympatric turtle species.

Discussion

The ontogenetic shift from carnivory to herbivory/omnivory mirrors patterns documented in North American emyids, where juveniles depend on protein-rich invertebrate prey for rapid growth before switching to more abundant but lower-quality plant resources as energetic demands shift from growth to reproduction [8, 9]. The 2.8‰ $\delta^{15}\text{N}$ separation between adult species is ecologically meaningful, roughly equivalent to one trophic level's worth of fractionation, confirming that *C. amboinensis* adults feed substantially lower on the food web than *S. crassicolis* adults [10]. The reduction in niche overlap from 34.7 percent (juveniles) to 11.2 percent (adults) suggests that ontogenetic shifts function as a coexistence mechanism. Both species start in similar dietary space as juveniles but diverge as they mature, reducing competition precisely when body size—and therefore total food demand—is greatest [11, 12]. This pattern is consistent with the size-structured competition hypothesis proposed by Werner and Gilliam [13]. Peat-swamp streams are nutrient-poor and highly acidic, limiting primary productivity and making interspecific competition more intense than in eutrophic lowland rivers. The strong niche separation we measured may therefore be an adaptive response to chronic resource limitation [14]. A limitation is that gastric lavage may underrepresent soft-bodied prey items that digest rapidly.

Conclusion: Both *S. crassicolis* and *C. amboinensis* undergo pronounced ontogenetic dietary shifts from juvenile

carnivory to adult omnivory or herbivory. These shifts reduce interspecific niche overlap from 34.7 percent in juveniles to 11.2 percent in adults. Stable isotope data confirmed species-level trophic separation among adults. The findings support the hypothesis that ontogenetic dietary shifts function as a mechanism for coexistence in sympatric freshwater turtles and have implications for conservation planning in peat-swamp forest habitats threatened by drainage and conversion.

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