

Short notes

Among-population differences in the frequency of intraspecific oophagy in the sword-tailed newt, *Cynops ensicauda popei*

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The interplay between cannibalism and life-history traits is still poorly understood. This study investigates the relationships between sex, snout–vent length and the amount of ingested conspecific eggs in three populations of sword-tailed newts, *Cynops ensicauda popei*. The mean number of ingested eggs found per individual was 0.13, 0.22 and 0.31 depending on the population, and females were more cannibalistic than males. Mean body size was negatively related to the mass of ingested conspecific eggs, and positively related to the total number of prey items found. Taken together, this study suggests that the amount of cannibalism is primarily influenced by prey availability and body size.

Key words: cannibalism, egg predation, food quality, prey availability

Egg cannibalism is frequently observed among amphibians (Polis & Myers, 1985; Kam et al., 1996; Kerby & Kats, 1998). Oophagy can reduce the density of larvae (Morin, 1983), and enables density-dependent benefits assuming the ability to discriminate between kin and non-kin (Scott, 1994; Gabor, 1996). In some species, tadpoles grow larger when cannibalizing conspecific compared to heterospecific eggs, although it is not known what benefits the former offer over the latter (Crump, 1990). Experiments have demonstrated that high-quality food contributes to enhanced growth (Crump, 1990; Alvarez & Nicieza, 2002), but field studies that compare, for example, adult body size with the frequency of oophagy are as yet lacking.

The sword-tailed newt (*Cynops ensicauda popei*) is endemic to Okinawajima Island, the Kerama Islands, and three other islands in the Ryukyu Archipelago, Japan (Maenosono & Toda, 2007). Due to habitat restrictions and decreases in population size, the species is listed as “endangered” under IUCN criteria (Kaneko & Matsui,

2004), and only a few ecological studies exist (Sparreboom & Ota, 1995; Sparreboom, 1996). As is typical for newts, adult *C. e. popei* aggregate in water bodies for reproduction, and aquatic larvae metamorphose into terrestrial juveniles. While oophagy has been reported previously (Sparreboom & Ota, 1995), I here report on the relationship between adult body size and the frequency of oophagy in three populations.

The sampling ponds were located on Okinawajima Island: Nanzuô (26°10'20"N, 127°49'23"E), Kunigami (26°43'56"N, 128°11'30"E), and Ôgimi (26°40'59"N, 128°8'54"E). Individuals were caught by hand-netting on 23 January (Nanzuô), 18 February (Kunigami) and 19 February (Ôgimi) 2010, coinciding with the spawning season. Gut contents were collected by stomach-flushing and preserved in 70% ethanol (Griffiths, 1986). After measuring snout–vent lengths (SVL) with vernier calipers (precision: 0.05 mm), individuals were returned to their pond. Gut contents were identified mostly to order level, and counted using a stereoscopic microscope. Eggs of the sword-tailed newt can be easily distinguished from those of other amphibians. After counting the prey items in each category, stomach contents were incubated at 50 °C for 48 h and the dry mass of each taxonomic group pooled per site was measured with an electronic balance (HA202M, A&D Co. Ltd., Tokyo, Japan).

Generalized linear models (Gaussian error distribution with identity link; site and sex were explanatory variables) and generalized linear mixed models (Binomial error distribution with logit link; site, sex and SVL were explanatory variables) were used to compare body size and the degree of oophagy among sites, respectively (Faraway, 2006). Each individual was treated as a random factor. After these analyses, a model selection method based on Akaike’s Information Criterion (AIC) was used (Anderson et al., 2000; Johnson & Omland, 2004; Hobbs & Hilborn, 2006). Effect sizes and their 95% confidence intervals (calculated as 1.96*SE) between variables are also presented (Nakagawa & Chuthill, 2007). The analyses were conducted in R version 2.11.0 (R Development Core Team, 2010).

In total, 83 individuals were examined (Nanzuô and Kunigami: 15 males (M), 15 females (F); Ôgimi: 8 M, 15 F). Both site and sex had an effect on adult body size (Table 1). SVL was largest at Nanzuô (mean ± SD; M: 58.5±3.1 mm; F: 65.4±4.1 mm; both sexes: 62.0 mm), smallest at Kunigami (M: 54.0±2.2 mm; F: 58.2±2.2 mm; both sexes: 56.0 mm), and intermediate at Ôgimi (M: 54.0±2.5 mm; F: 60.2±3.3 mm; both sexes: 58.0 mm). Males were consistently smaller than females. The effect size between Kunigami and Ôgimi is small (Hedge’s *d* with 95% CI: 0.54, –0.023 ~ 1.08), appearing large in all other pairwise comparisons (Nanzuô – Kunigami: 2.93, 2.20 ~ 3.67; Nanzuô – Ôgimi: 2.31, 1.61 ~ 3.02; M – F: 2.64, 2.04 ~ 3.23).

The number of ingested eggs found per individual was highest at Ôgimi and lowest at Nanzuô (mean ± SD; Nanzuô: 0.13±0.23; Kunigami: 0.22±0.26; Ôgimi:

Table 1. Results of the model selection procedure and the parameter estimates for each variable. Estimates \pm 1 standard error (SE) are based on the best model. The interaction term between site and sex was not included for the analysis of body size because of the general tendency for large females. The intercept term corresponds to the value of females at Kunigami. AIC: Akaike's Information Criterion, Δ AIC: the difference between the focal model and the best model; w_i : Akaike weights; SVL, snout-vent length.

	AIC	Δ AIC	w_i	Estimates (95% CI)	
Body size					
Site + Sex	188.75	0	1		
Sex	232.36	43.61	0		
Site	240.27	51.52	0		
Oophagy					
Site + Sex	118.15	0	0.41		
Site + Sex + SVL	118.53	0.35	0.34		
Sex +Svl	119.75	1.6	0.18		
Site + Sex + SVL + Site * SVL	121.77	3.62	0.067		
Sex	126.97	8.82	0.005		
Site	135.04	16.89	0		
				<i>Body size</i>	<i>Oophagy</i>
Intercept				59.02 (57.73 ~ 60.31)	-0.43 (-1.14 ~ 0.28)
Nanzuyō				5.81 (4.26 ~ 7.36)	-1.53 (-2.49 ~ -0.57)
Ôgimi				1.00 (-0.67 ~ 2.67)	0.13 (-0.79 ~ 1.05)
Male				-5.73 (-7.10 ~ -4.40)	-1.88 (-2.76 ~ -1.00)

0.31 \pm 0.23). Eggs were rarely found in males. The best model contained only site and sex as explanatory variables, and the next model also contained SVL (Table 1). Again, the effect size between Kunigami and Ôgimi is small (Hedge's d with 95% CI: 0.13, -0.42 ~ 0.67), while those of other pairwise comparisons appear to be large (Nanzuyō vs Kunigami: 1.30, 0.74 ~ 1.86; Nanzuyō vs Ôgimi: 1.34, 0.74 ~ 1.94; male vs female: 1.47, 0.98 ~ 1.95).

At Nanzuyō, the total number of prey items was 409 (biomass: 316.4 mg); at Kunigami and Ôgimi the number of prey items were 119 (627.2 mg) and 127 (251.9 mg), respectively. In Nanzuyō, numbers of prey items were dominated by amphipods (63.8%). At Kunigami and Ôgimi, plant debris was the most abundant item (36.1% and 38.6%), followed by eggs of sword-tailed newts (32.8% and 34.6%). The remaining prey recorded consisted of skin sloughs and small aquatic insects at all sites. Although amphipods dominated the prey numbers at Nanzuyō, they constituted only 14.1% of prey mass. Con-specific eggs formed the highest percentage of total prey mass in all habitats (Nanzuyō: 42.1%, Kunigami: 75.3%, Ôgimi: 68.6%). Mean body size correlated positively with the total number of prey found in guts ($r=0.95$, $n=3$), and negatively with total prey mass ($r=-0.65$, $n=3$).

Prey availability might be a possible factor in eliciting cannibalistic behaviour. Food quality is essential to maintain consumer body condition (Crump, 1990), and the eggs in this study might be considered high-quality food as judged by dry weight, although their nutritional value is

unknown. The fact that the adult body size of sword-tailed newts is negatively related to the frequency of oophagy could suggest that the amount of prey is more important for individual growth than food quality, although the relationship between a single meal and individual SVL can depend on many factors and any inference needs to be treated with care.

One reason that female newts engage more in oophagy could be the extra energy required for the production of eggs (Bernardo, 1996). Filial cannibalism in species that engage in parental care has been observed (Polis, 1981), but is unlikely in sword-tailed newts because females are not associated with their eggs after depositing them on submerged litter (Sparreboom & Ota, 1995). The potential ability to discriminate between kin in this species warrants further examination.

The fitness costs of cannibalism make this behaviour rather uncommon in most species (Dawkins, 1976). The three main types of costs are risk of injury, inclusive fitness and pathogen transmission (Pfenning, 1997; Pfenning et al., 1998). Risk of injury does not apply to oophagy, and information on pathogens is lacking. The ability to discriminate between kin and non-kin is hypothesized to avoid the loss of inclusive fitness amongst cannibalistic amphibians, but is often context-dependent (Hokit et al., 1996; Pfenning, 1997). At the two more cannibalistic populations, the benefits of consuming conspecific eggs might outweigh the costs associated with cannibalism if prey scarcity is significantly affecting individual fitness and survival.

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