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J. Moll. Stud. (2003) 69: 288-289

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## Growth and reproduction in Hawaiian succineid land snails

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The native land snail fauna of the Hawaiian Islands is one of the most threatened snail faunas in the world;<sup>1</sup> a large proportion of the species, perhaps as many as 90%, may now be extinct.<sup>2,3</sup> The impacts of introduced predators [e.g. rats and the predatory snail *Euglandina rosea* (Férussac)] and other human-related impacts (e.g. habitat destruction, collecting by shell collectors), super-imposed upon long pre-reproductive life and low fecundity (as in achatinelline tree snails),<sup>4-7</sup> have been implicated in the demise of many of the species. Certain native snails, however, have remained relatively abundant. Among these are some of the rainforest succineids.

Aside from the Achatinellinae,<sup>4–7</sup> little is known of the life histories of most Hawaiian land snails. However, just as knowledge of life-history characteristics has been important in understanding the high extinction rate of the achatinelline tree snails, such information may also be key to understanding why some succineid species remain abundant in the face of similar pressures.

In this study, the oviparous rainforest succineids *Succinea thaanumi*Ancey and *Catinella rotundata* (Gould), which lay gelatinous, translucent egg masses, usually on aboveground vegetation, were raised in captivity to investigate a range of life-history characteristics.

Three recently hatched juvenile *Succinea thaanumi* and one egg mass from Olaa, Island of Hawaii, were brought into a captiverearing facility on 3 November 1999. The juveniles were assumed to have hatched very recently because their bodies appeared white through the transparent shells and their digestive glands were not dark, indicating that they probably had not yet fed. Fifteen *Catinella rotundata* from Makaleha, Waianae Mountains, Island of Oahu, were brought into the facility on 30 March 2000.

Snails and egg masses were maintained as colonies in plastic containers (10 cm wide, 10 cm deep, 16 cm tall, with mesh tops; one for each species) subject to night (12 h) and day (12 h) light cycles, and intermittent spraying with water to simulate rain (3 min, every 8 h) in an environmental chamber (16°C at night, 20°C during the daytime), as used for achatinelline tree snail breeding.<sup>8</sup> The natural diet of these succineids is poorly known, but probably includes fungal material obtained from leaf surfaces.<sup>9</sup> Each container was provisioned with fresh leaves and branches of the native Hawaiian tree *Metrosideros polymorpha* (Myrtaceae), partly covered with fungus, plus supplemental cul-

tured fungus fortified with a trace of calcium carbonate.<sup>8</sup> The *M. polymorpha* and fungus were replaced approximately every 14 days when the containers were cleaned. At that time, maximum shell dimension (length) of adults and offspring, number of births and deaths, and number of eggs laid were recorded.

Reproductive characteristics of *Succinea thaanumi* are summarized in Table 1. Average shell length of the three juveniles (termed Cohort A) on 10 November 1999 (7 days after they were collected) was 1.8 mm. The mean maximum length attained by these three individuals was 9.3 mm, on 15 March 2000, after a period of 134 days in captivity. The first egg mass laid by them was found on 1 March 2000, when their average length was 8.8 mm, about 4 months after they had been brought into captivity (as juveniles). Additionally, two of them were observed mating (by 'shell-mounting'<sup>10</sup>) on 15 March 2000 (shell lengths 9.8 and 10.1 mm). One was found dead on 30 March 2000, the other two on 28 April 2000, giving a life span of at least 178 days for these latter two snails.

The first *S. thaanumi* hatched from the wild-collected egg mass (Cohort B) was observed on 22 December 1999. Because the previous observation date was 8 December 1999, the snail could have hatched any time during this period and the time to hatching was, therefore, at least 36–50 days.

The average shell length of juveniles that were first seen on 28 April 2000 was 0.85 mm (n = 15) and for those first seen on 9 May 2000 was 0.90 mm (n = 26). Data from the two hatchings were combined after 9 May 2000 as Cohort C. They reached a mean maximum length of 7.8 mm on 13 October 2000, approximately 5 months from birth.

The first reproductive event witnessed for Cohort C snails was a mating on 4 August 2000. Shell lengths of these snails were 7.0 and 7.7 mm, when the average length of Cohort C snails was  $6.0 \pm 1.1$  mm (mean and SD; n = 11). Time to reproductive maturity is therefore approx. 3 months. The first egg mass laid by Cohort C snails was found on 1 September 2000, when the snails were about four months old.

The minimum maximal lifespan for *Succinea thaanumi*, calculated for Cohort C from the earliest possible birth date (13 April 2000) and the date of death of the last Cohort C snails (22 December 2000), was 253 days.

Reproductive characteristics of *Catinella rotundata* are also summarized in Table 1. All wild collected individuals except the largest died soon after coming into captivity, most before reach-

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Characteristic	S. thaanumi	Cohort	C. rotundata	Cohort
Mean shell length at hatching	$0.9 \pm 0.2 \mathrm{mm} (n = 41)$	С	$1.6 \pm 0.5 \mathrm{mm} (n = 20)$	D
Maximum shell length	$9.3 \pm 1.1 \text{ mm} (n = 3)$	А	12.0 mm ( <i>n</i> = 1)	[1 adult]
	$7.8 \pm 1.4 \text{ mm} (n = 36)$	С		
Time to reach maximum shell length	126 days	А	-	-
	140–155 days	С		
Mean shell length at reproductive maturity	$8.8 \pm 1.3 \mathrm{mm} (n = 3)$	А	-	-
	$7.4 \pm 0.5 \text{ mm} (n = 2)$	С		
Time to reproductive maturity	<4 months	А	-	-
	~3 months	С		
Mean number of eggs per egg mass	9 (range 1–16, <i>n</i> = 21)	_	12 (range 3–19; <i>n</i> = 4)	-
Egg mass time to hatching	At least 36–50 days	В	43–70 days	D
Minimum maximal life-span	253 days	С	267 days	[1 adult]
	at least 178 days	А		

**Table 1.** Life-history characteristics (mean ± SD, if appropriate) of *Succinea thaanumi* and *Catinella rotundata*, and the cohorts from which the data were derived.

ing the presumed adult size. The sole survivor reached a length of 12.0 mm. An egg mass was found on 9 May 2000, but subsequently decomposed. Two egg masses were then found on 19 August 2000 (could have been laid as early as 5 August) and a third on 1 September 2000 (combined as Cohort D). The first hatchlings were observed on 13 October 2000, giving a hatching period of 43–70 days. Average length of a random sample of newborn snails was 1.55 mm. Overall hatching success rate was 80% (40 snails from 50 eggs). The average number of eggs per egg mass was 12. The single surviving adult snail, which was a subadult when collected, lived for 267 days in captivity. All the hatchlings died before reaching adulthood so it was not possible to infer lifespan from them and their growth was not measured.

Age at reproductive maturity in *Succinea thaanumi*, approximately 3 months, contrasts with that of the endangered achatinelline tree snails: 3–5 years in *Achatinella mustelina* Mighels<sup>6</sup> and 5–7 years in *Partulina proxima* (Pease).<sup>5</sup> Both *S. thaanumi* and *C. rotundata* also lay a relatively large number of eggs in each egg mass and lay them frequently. For instance, the single *C. rotundata* laid 50 eggs, of which 40 hatched, in 267 days. This contrasts with the slow reproductive rate of achatinelline species, which are ovoviviparous, averaging six or seven offspring per year.<sup>5,6</sup>

The life spans of these two succineid species are much shorter than those of many achatinelline tree snail species, which may live up to at least 19 years.<sup>5</sup> Even if the lifespan values reported here (7–8 months) are under-estimates, based upon the rapid time to maximum length (126 days for *S. thaanumi*) and comparison with other land snails,<sup>11,12</sup> it is unlikely that these species live much longer than 1 or 2 years in the wild.

Rapid maturation, high fecundity and year-round breeding may be critical life history traits that have allowed some rainforest succineid species to maintain relatively high population levels despite alien predation pressures. There are 42 endemic Hawaiian succineid species occupying many different habitats.<sup>1</sup> While some remain relatively abundant, others are extremely rare or perhaps extinct. Differences in life history may partly explain these disparities. For instance, dry land species, about which little is known, may have rather different life history characteristics, perhaps breeding only infrequently when conditions are appropriate, like the North American xerophilous succineid *Succinea vaginacontorta* Lea,<sup>13</sup> and perhaps thereby increasing their susceptibility to sustained predation episodes.

This study was based on a small number of laboratory-raised snails. Nevertheless, the results are an important addition to the scant recorded natural history of Hawaiian succineids. Although these succineids do not appear as threatened as the better-known Achatinellinae, all native Hawaiian snails are arguably threatened to some degree. The more that is known about them, the better chance they have of being conserved.

We thank Mike Hadfield for the opportunity to undertake this study in his captive rearing facility, Kevin Olival for assistance with collecting and maintaining the snails, and Dan Gruner for assistance with collecting.

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