

Differential survival among Tahitian tree snails during a mass extinction event: persistence of the rare and fecund

C.S. BICK, DIARMAID Ó FOIGHIL and TREVOR COOTE

Abstract The deliberate introduction of the rosy wolf snail *Euglandina rosea* to the Society Islands in the 1970s led to the mass extirpation of its rich Partulidae (Pilsbry, 1900) fauna, comprising approximately half of all species in this Pacific island tree snail family. On Tahiti ongoing field surveys have documented the survival of two of seven endemic species of *Partula* (*P. hyalina* and/or *P. clara*) in 38 valleys. *E. rosea* is now a potent extinction agent across Oceania and determining the factors enabling these two taxa to endure may have wide conservation import. We hypothesized that *P. hyalina* and *P. clara* have survived because they were the most abundant and/or widespread species and that they will eventually become extinct. We lack demographic data contemporaneous with predator introduction, but an early 20th century study by H.E. Crampton provides historical demographic data for intact Tahitian partulid populations. Crampton found that *P. clara* and *P. hyalina*, although widespread, were consistently rarer than their now-extirpated congeners, including in the 23 valleys he surveyed that retain surviving populations. Given this result, and the recent finding that *P. clara* and *P. hyalina* comprise a discrete founding lineage in Tahiti, it is plausible that some shared biological attribute(s) may have contributed to their survival. Crampton recorded the clutch sizes of thousands of gravid Tahitian partulids and found that these two taxa had higher instantaneous mean clutch sizes than did co-occurring congeners. Higher fecundities may have contributed to the survival of *P. hyalina* and *P. clara* in the valleys of Tahiti.

Keywords Differential survival, mass extinction, oceanic islands, Partulidae, Tahiti, tree snail

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Introduction

Oceanic islands represent some of the most isolated habitats on earth and their endemic biotas are characterized by small ranges and the absence of highly co-evolved defensive capabilities, such as anti-predator behaviours and morphologies (Paulay, 1994; Vermeij, 1999; Roff & Roff, 2003; Fullard et al., 2007). Consequently, island biotas are exceptionally vulnerable to introduced continental predators (Paulay, 1994; D'Antonio & Dudley, 1998). This is perhaps best exemplified by Guam's 'empty forest' (Redford, 1992) phenomenon, where a single introduced predator, the brown tree snake *Boiga irregularis*, has severely affected the endemic forest fauna (Savidge, 1987; Wiles et al., 2003; Mortensen et al., 2008), prompting extraordinary conservation interventions (Clark & Savarie, 2012).

Another alien predator, the carnivorous rosy wolf snail *Euglandina rosea*, has also had an outsized impact on oceanic island endemic faunas, being implicated in the extinction of at least 134 terrestrial snail species (Régner et al., 2009). A North American native, *E. rosea* stalks its gastropod prey by following their mucous trails, consuming small prey whole and larger individuals piecemeal (Gerlach, 2001; Shaheen et al., 2005; Davis-Berg, 2012). It is highly mobile and can climb trees, a detrimental characteristic for many arboreal Pacific island terrestrial snails (Kinzie, 1992; Meyer & Cowie, 2011). *Euglandina rosea* was introduced to multiple Pacific island archipelagos in a misguided strategy to control outbreaks of the introduced giant African snail *Lissachatina fulica*, most notably to the Hawaiian Islands in 1955 (Cowie, 1998) and to the Society Islands in 1974 (Coote, 2007). It rapidly extirpated large numbers of endemic land snail species on both archipelagos, including members of the Achatinellidae in Hawaii (Hadfield et al., 1993) and Partulidae in the Society Islands (Clarke et al., 1984).

The loss of the Partulidae of the Society Islands has been of particular concern because this archipelago is home to c. 50% of partulid species diversity (Cowie, 1992). It has also been the main setting for 20th century partulid studies, starting with the classic work of H.E. Crampton (1916, 1932) and continuing with decades of research by B. Clarke, J. Murray, M. Johnson and associates (Clarke & Murray, 1969; Murray & Clarke, 1980; Johnson et al., 1993). The collapse of Society Islands partulid populations following the introduction of *E. rosea* prompted the emergency establishment of off-archipelago captive populations for 15

Society Island species (Murray et al., 1988; Tonge & Bloxam, 1991; Pearce-Kelly et al., 1997). Until recently, only 5 of 61 endemic Society Islands partulid species were thought to persist in the wild (Coote & Loève, 2003) but subsequent field surveys have found scattered extant populations on Raiatea, Moorea and Tahiti representing four additional species (Lee et al., 2008, 2009). Seven of these surviving taxa (*Partula otaheitana*, *Partula hyalina*, *Partula clara*, *Partula affinis*, *Samoana attenuata*, *Samoana burchi*, *Samoana diaphana*) occur on Tahiti, the largest and highest island in the archipelago (Coote, 2007; Lee et al., 2007a, 2009). The predominant Tahitian pattern is one of low elevation extirpation and montane persistence: partulid survivors are most common in cloud forest refuges of >1,000 m altitude (Coote, 2007; Lee et al., 2007a, 2009), where predator activity is probably impaired by cooler temperatures (Gerlach, 1994, 2001). However, extensive field surveys beginning in 2004 have located small clusters of low elevation survivors in a number of Tahitian valleys (Coote, 2007), currently totalling 38 (Fig. 1; Table 1). Of Tahiti's eight species of *Partula*, two now dominate low elevation extant populations; i.e. 37 of the 38 valleys with known survivors were exclusively populated by *P. clara* and/or *P. hyalina* (Fig. 1; Table 1).

Partula hyalina and *P. clara* are closely-related species, distinguished by shell coloration, which together represent a discrete Tahitian founder lineage of Moorean origin (Lee et al., 2009). Their ability to endure almost 40 years of predation by *E. rosea* in the valleys of Tahiti is surprising because predation models predict partulid extirpation within 3 years of initial predator contact (Gerlach, 2001). We are interested in understanding what aspect(s) of their biology underlies this survival, not only for their individual conservation but because of the possible implications for the survival of the many endemic land snails across Oceania now threatened by *E. rosea* (Régnier et al., 2009).

The inverse relationships of population size (Pimm et al., 1988; Schoener & Spiller, 1992) and geographical range (Payne & Finnegan, 2007; Cardillo et al., 2008) to extinction risk have been well documented. Our initial hypothesis is therefore that *P. hyalina* and *P. clara* have survived because they were the most abundant and/or widespread species in Tahitian valleys and that they will eventually be driven to extinction by the predator. To test this, ideally we need a detailed census of Tahitian partulid populations contemporaneous with the 1974 introduction of *E. rosea*. Such a resource is not available but we do have access to a century-old dataset of Tahiti's intact partulid populations. During 1906–1909 Crampton (1916) surveyed and collected Tahitian valley tree snail populations, publishing a detailed account that has been lauded as 'among the finest work ever done on the evolution of land snails' (Gould, 1994). We therefore have an extensive demographic profile of intact Tahitian partulid populations with individual valley-level resolution. This allows us to calibrate present-day extant

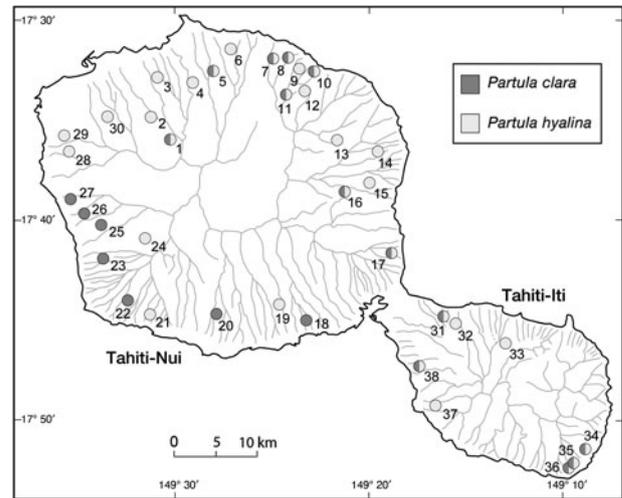


FIG. 1 Tahiti, showing the distribution of surviving low elevation partulid populations detected by Coote (2007; unpubl. data) in surveys during 2004–2010. The survivors in 37 of 38 valleys exclusively comprised *Partula clara* and/or *Partula hyalina*. A third species, *Partula affinis*, was found in one valley (36, Faaroa), together with *P. clara* and *P. hyalina*. See Table 1 for the names of the numbered valleys and the number of survivors.

populations with their pre *E. Rosea* introduction equivalents across the island as a whole, as well as for the 23 valleys Crampton surveyed that retain surviving populations (Table 1).

Methods

Crampton (1916) systematically surveyed the partulid populations of Tahiti. He divided the island of Tahiti into five subunits: Tahiti-Nui, comprising four quadrants (north, south, east and west) and the peninsula Tahiti-Iti (Taiarapu). Over four annual surveys during 1906–1909 he surveyed a large fraction of the coastal valleys present in each geographical subunit: 10 western, 20 southern, 10 northern, 10 eastern and 12 in Tahiti-Iti. Crampton (1916) did not detail his sampling methodology except to state that he walked into each valley along the primary trails during daylight hours, collecting snails from the adjacent trees and vegetation. He was particularly interested in population-level variation and typically obtained large sample sizes (hundreds) from each valley.

Modern-day surveys of Tahitian valleys for surviving partulids largely follow Crampton's (1916) methodology, except that the snails are much rarer and that more valleys have been surveyed (Coote, 2007). Each survey of a valley is restricted to a single day and involves walking along existing forest trails as deep as possible into the valley, stopping at regular intervals for intense searches of adjacent 5-m² patches of habitat. Where snails are encountered, all individuals within the immediate patch are enumerated within a 20-minute search period (Coote, 2007).

TABLE 1 The 38 Tahitian valleys with surviving low elevation populations of *Partula clara*, *Partula hyalina* and *Partula affinis* detected by T. Coote (2007, unpubl. data) during 2004–2010 (given as number of snail populations and/or number of snails located per 20-minute search), and the species and number of snails in 23 of these 38 valleys where Crampton (1916) collected partulids during 1906–1909. The valley names used by Crampton (1916) are indicated in parentheses if they differ from the current names. See Fig. 1 for numbered locations of the valleys.

Valley	Coote		Crampton's counts of adult snails per valley ²
	No. of snail populations ^{1,2}	Snails per 20-minute search ²	
Tahiti-Nui			
1, Fautaua	Several (<i>hy</i> , <i>cl</i>)		129 (<i>hy</i>), 955 (<i>otah</i>)
2, Fautaua-Faaiti	1	10 (<i>hy</i>)	
3, Nahoata (Pirai)	Several (<i>hy</i>)		55 (<i>hy</i>), 211 (<i>filo</i>), 988 (<i>otah</i>)
4, Tuauru	1 (<i>hy</i>)		14 (<i>hy</i>), 374 (<i>aff</i>)
5, Ahonu	2 (<i>hy</i> , <i>cl</i>)	5 (<i>hy</i>)	5 (<i>hy</i>), 295 (<i>otah</i>)
6, Orofara	1 (<i>hy</i>)		
7, Puhi	2 (<i>hy</i> , <i>cl</i>)	2 (<i>cl</i>)	
8, Faarapa (Farapa)	Several	8 (<i>hy</i>), 4 (<i>cl</i>)	9 (<i>hy</i>), 591 (<i>otah</i>)
9, Farromai (Faarumai)	1	2 (<i>hy</i>)	12 (<i>hy</i>), 1 (<i>cl</i>), 353 (<i>otah</i>)
10, Haapoponi	Several	27 (<i>hy</i>), 7(<i>cl</i>)	
11, Onohea-Faaiti	2	12 (<i>hy</i>), 17 (<i>cl</i>)	
12, Onohea-Faarahi (Tiarei)	1	3 (<i>hy</i>)	1(<i>hy</i>), 166 (<i>otah</i>)
13, Tahaute (Mahaena)	1	2 (<i>hy</i>)	2 (<i>hy</i>), 3 (<i>cl</i>), 147 (<i>otah</i>)
14, Faaiti	1	2 (<i>hy</i>)	
15, Faatautia	1	2 (<i>hy</i>)	12 (<i>aff</i>)
16, Vaiiha (Papeiha)	2	11 (<i>hy</i>), 2 (<i>cl</i>)	6 (<i>hy</i>), 3 (<i>cl</i>), 273 (<i>otah</i>)
17, Vaitoare	Several	24 (<i>hy</i>), 3(<i>cl</i>)	
18, Vaioo	2	8 (<i>cl</i>)	
19, Faurahi (Faarahi)	1 (<i>hy</i>)		2 (<i>hy</i>), 10 (<i>cl</i>), 467 (<i>otah</i>), 29 (<i>prod</i>)
20, Taapua (Taharua)	1	1 (<i>cl</i>)	2 (<i>hy</i>), 2 (<i>cl</i>), 325 (<i>otah</i>)
21, Afererii	1	1 (<i>hy</i>)	
22, Tereia (Tereehia)	2	4 (<i>cl</i>)	33 (<i>cl</i>), 130 (<i>otah</i>)
23, Vaipoe (Atitara)	2	10 (<i>cl</i>)	36 (<i>cl</i>), 154 (<i>otah</i>)
24, Orofero (Orofere)	Several (<i>hy</i>)		2 (<i>hy</i>), 49 (<i>cl</i>), 18 (<i>nod</i>), 197 (<i>otah</i>)
25, Tiapa (Aoua)	2	14 (<i>hy</i>)	19 (<i>hy</i>), 67 (<i>cl</i>), 396 (<i>nod</i>), 650 (<i>otah</i>)
26, Papehue	1	1 (<i>cl</i>)	4 (<i>hy</i>), 35 (<i>cl</i>), 210 (<i>nod</i>), 143 (<i>otah</i>)
27, Maruapo (Maruapoo)	1	4 (<i>cl</i>)	11 (<i>hy</i>), 4 (<i>cl</i>), 795 (<i>nod</i>), 135 (<i>otah</i>)
28, Matatia (Taapuna)	Several	3 (<i>hy</i>)	13 (<i>hy</i>), 313 (<i>nod</i>), 225 (<i>otah</i>)
29, Tihite	1 (<i>hy</i>)		
30, Tipaerui-Faaiti	1 (<i>hy</i>)		22 (<i>hy</i>), 937 (<i>otah</i>)
Tahiti-Iti (Tairapu)			
31, Rarouri	Several (<i>hy</i> , <i>cl</i>)		
32, Tehoro	Several (<i>hy</i>)	1	11 (<i>hy</i>), 1 (<i>cl</i>), 306 (<i>aff</i>)
33, Ahaavini (Haavini)	1	1 (<i>hy</i>)	20 (<i>hy</i>), 40 (<i>cl</i>), 273 (<i>otah</i>)
34, Vaita	Several (<i>hy</i> , <i>cl</i>)		
35, Taapeha	Several (<i>hy</i> , <i>cl</i>)		
36, Faaroa	Several (<i>hy</i> , <i>cl</i> , <i>aff</i>)		
37, Vavi (Vavii)	1 (<i>hy</i>)		26 (<i>hy</i>), 22 (<i>cl</i>), 225 (<i>otah</i>)
38, Faaana	1 (<i>hy</i> , <i>cl</i>)		

¹Several, ≥ 2 remnant populations

²*hy*, *P. hyalina*; *otah*, *P. otaheitana*; *filo*, *P. filosa*; *aff*, *P. affinis*; *cl*, *P. clara*; *prod*, *P. producta*; *nod*, *P. nodosa*

At the end of each day's sampling Crampton (1916) preserved the snails for later analyses (identification, measurement, dissection) in his Columbia University laboratory. In total, Crampton (1916) collected 24,085 individuals of seven Tahitian species: *P. affinis* [as *P. otaheitana affinis*; reclassified by Kondo (1980)], *P. clara*, *Partula filosa*, *P. hyalina*, *Partula nodosa*, *P. otaheitana* and *Partula producta*. We extracted his frequency data for each valley surveyed,

combining data for subspecies categories into totals for each species. Although the scale of Crampton's (1916) collecting was extraordinary by today's standards, it is unlikely to have been the main driver in their subsequent extirpation. His sampling was restricted to snails adjacent to the main valley paths and, as late as 1970, the valleys of Tahiti continued to support significant populations of partulids (John B. Burch, pers. comm.).

Partulids are ovoviviparous hermaphrodites and adults typically contain a small number of progeny at different stages of development, giving birth to single young at multi-week intervals (Murray & Clarke, 1966). Crampton (1916) dissected the adults he collected, recording the number of eggs, embryos and shelled young present in the reproductive tracts of individual gravid females when collected (i.e. instantaneous clutch size). He presented these data as means per valley population for five species: *P. affinis*, *P. filosa*, *P. nodosa*, *P. otaheitana* and *P. producta*. As a result of the relatively low abundance of *P. clara* and *P. hyalina*, he calculated their mean instantaneous clutch sizes over multiple valleys, grouped into his five geographical subunits.

We compiled Crampton's (1916) mean instantaneous clutch size data, combining his subspecies data into single species values for each valley/quadrant. We then calculated estimates of mean clutch sizes across the entire island for each species.

Results

Crampton (1916) calculated the relative frequency of each species he collected across Tahiti from 1906 to 1909 (Fig. 2a). Of the seven species of *Partula* he collected on Tahiti, *P. otaheitana* was the most abundant (a total of 18,955 individuals were collected) and the most widespread, being found in 51 of the 62 valleys surveyed. It was the most numerous partulid species in 48 of the 51 valleys in which it was recorded, usually comprising >90% of all individuals collected in each valley (Supplementary Fig. S1).

Partula nodosa was the second most abundant Tahitian partulid species collected by Crampton (1916). The 1,922 specimens he collected (Fig. 2a) had a regional distribution within the island, being restricted to seven western valleys and predominating in three of them (Supplementary Fig. S1). *Partula affinis* was almost as numerous: 1,560 individuals (Fig. 2a) were collected from 10 valleys distributed in the northern, eastern and southern quadrants, as well as on Tahiti-Iti (Crampton, 1916). In eight of these valleys *P. affinis* predominated, comprising >80% of all tree snails collected (Supplementary Fig. S1). The two rarest species collected, *P. filosa* and *P. producta* (Fig. 2a), were both single-valley endemics. They formed minor components of their respective valley partulid totals (*P. filosa* 17% and *P. producta* 6%; Supplementary Fig. S1) and both species are now extinct.

A century ago *P. clara* and *P. hyalina* were both widespread in Tahiti, recorded from 43 and 51 of the 62 valleys surveyed, respectively (Crampton, 1916). Although they approached *P. otaheitana*'s extensive range across the island of Tahiti, *P. clara* and *P. hyalina* were much rarer; the surveys yielded totals of 819 and 589 individuals, respectively (Fig. 2a). Each of these two species typically composed <5% of the tree snails collected in individual valleys, with their highest incidence being 28% for *P. clara* and 21% for *P. hyalina* (Supplementary Fig. S1).

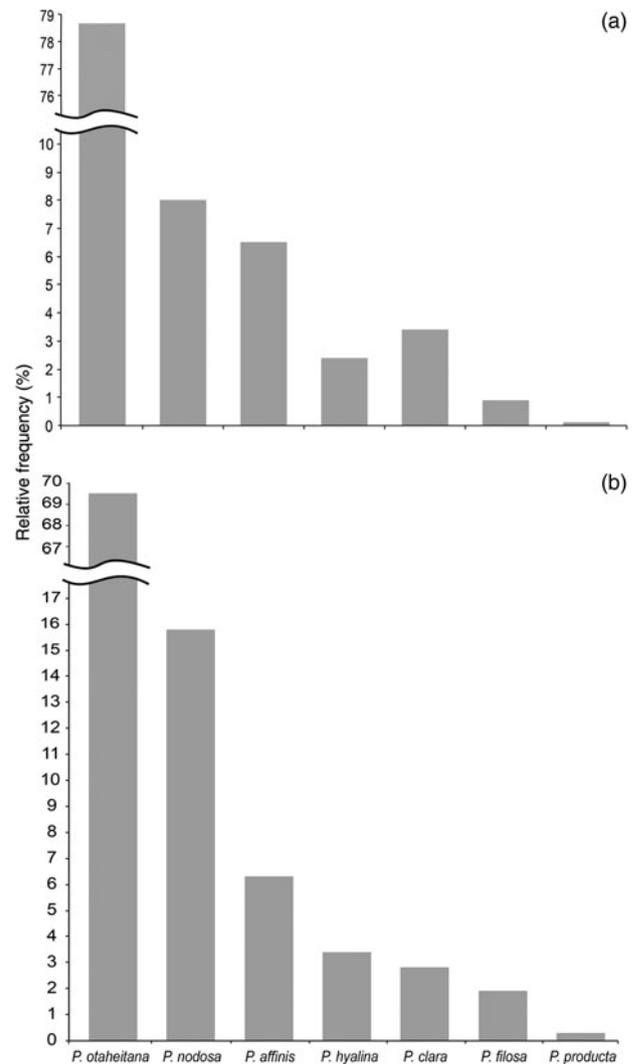


FIG. 2 The overall relative frequencies, on a logarithmic scale, of (a) seven endemic species of Tahitian *Partula* (*P. otaheitana*, $n = 18,955$; *P. nodosa*, $n = 1,922$; *P. affinis*, $n = 1,560$; *P. hyalina*, $n = 589$; *P. clara*, $n = 819$; *P. filosa*, $n = 211$; *P. producta*, $n = 29$) collected by Crampton (1916) in the 62 valleys he surveyed during 1906–1909, and (b) of these seven species (*P. otaheitana*, $n = 7,631$; *P. nodosa*, $n = 1,732$; *P. affinis*, $n = 692$; *P. hyalina*, $n = 369$; *P. clara*, $n = 306$; *P. filosa*, $n = 211$; *P. producta*, $n = 29$) in 23 Tahitian valleys that retain recent survivors (Table 1).

Ongoing field surveys of Tahitian valleys since 2004 have encountered remnant populations of *P. clara* and/or *P. hyalina* in 38 valleys (Coote, 2007; T. Coote, unpubl. data; Fig. 1; Table 1). We cross-referenced these with the 62 valleys that Crampton surveyed in 1906–1909 and identified 23 valleys containing present-day species that were also collected by Crampton (Table 1). Fig. 2b shows that, a century ago, the relative frequencies of *P. clara* and *P. hyalina* among the 23 Tahitian valleys where they survive today were not exceptional, but closely matched their relative frequencies across the island as a whole (Fig. 2a). *Partula otaheitana* was the most common species and *P. clara* and/or *P. hyalina* were minor constituents. This general pattern was

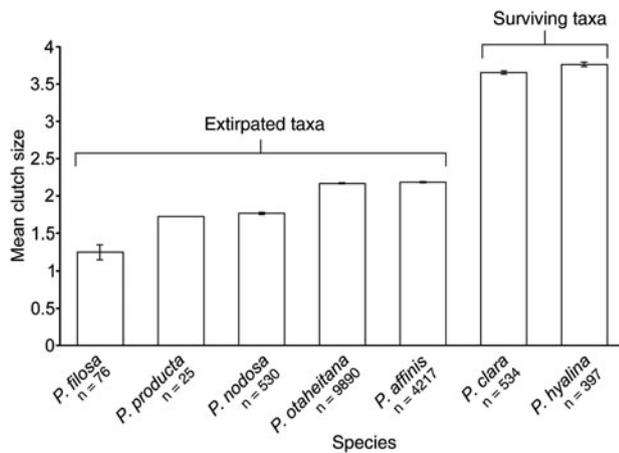


FIG. 3 Mean instantaneous clutch sizes for 15,669 gravid individuals of the seven endemic partulid species collected by Crampton (1916) across 62 Tahitian valleys during 1906–1909. Standard error bars are included for all taxa except *P. producta* (one sampling event). *Partula clara* and *P. hyalina* are labelled as surviving taxa because they dominate extant low elevation partulid populations on Tahiti (Fig. 1). The remaining five species, labelled as extirpated taxa, are absent from Tahitian valleys, with the exception of one valley population of *P. affinis* (Fig. 1).

maintained at the level of individual valleys, with the exception that *P. otaheitana* was replaced as the locally dominant species by either *P. affinis* or *P. nodosa* in a few valleys (Supplementary Fig. S1). *Partula clara* survives today in three valleys (Fautaua, Ahonu and Faarapa; Table 1) where it was sufficiently rare a century ago to go undetected by Crampton, despite his intensive collecting (e.g. his Fautaua Valley sample size was 1,084 snails). Given the very low migration rates of partulid tree snails (e.g. 1–10 m per year; Murray & Clarke, 1984), we consider it likely that these three valley populations of *P. clara* represent local survivors rather than de novo colonists from other valleys. The formerly locally dominant species in these three valleys, *P. otaheitana*, has been extirpated, despite having been at least 2–3 orders of magnitude more common than the surviving *P. clara*.

Fig. 3 is a summary of Crampton's (1916) mean instantaneous clutch sizes for Tahitian valley partulids. The surviving taxa, *P. clara* and *P. hyalina*, had markedly higher clutch sizes than their now-extirpated congeners.

Discussion

The introduction of *E. rosea* to Tahiti in 1974 exposed naïve endemic tree snails to an uncontrolled predator–prey experiment in which each valley population represented a discrete iteration. Outcomes in 37 of 38 valleys with known survivors have been strikingly uniform: persistence of two of seven endemic Tahitian species of *Partula*: *P. clara* and/or *P. hyalina* (Fig. 1; Table 1). Our initial hypothesis, that the surviving taxa endured because they were the most abundant and/or widespread species, is clearly refuted by Crampton's (1916) data. A

century ago these two species were relatively rare, typically representing <5% of the original species diversity in most valleys, including those valleys where they still persist (Fig. 2b; Table 1). Although *P. hyalina* and *P. clara* were widely distributed, this cannot explain their survival relative to the widespread, co-occurring and much more abundant *P. otaheitana*, now completely extirpated from the valleys of Tahiti (Coote, 2007; Fig. 1).

Molecular phylogenies have shown that *P. clara* and *P. hyalina* are two colour morphs of a founding lineage that is distinct from other Tahitian congeners (Lee et al., 2007b, 2009). It is therefore plausible that some shared phylogenetic trait has contributed to their differential survival. One such potential trait is evident in Crampton's (1916) dataset: *P. clara* and *P. hyalina* exhibited similar instantaneous clutch sizes that were markedly higher than those of their extinct congeners (Fig. 3). These data raise an obvious paradox regarding the population structure of tree snails in Tahitian valleys in 1906–1909. If mean clutch sizes in *P. clara* and *P. hyalina* were so much higher, why were they so rare relative to three of their congeners, especially *P. otaheitana*? This discrepancy implies that, a century ago, *P. clara* and *P. hyalina* were inferior competitors to their now-extirpated Tahitian valley congeners.

Species with a low intrinsic rate of increase, as a result of factors such as low fecundity, are at increased risk of extinction from stochastic events (Beissinger, 2000). Island endemics with greater reproductive effort are therefore predicted to have a higher likelihood of surviving the introduction of non-native predators. In the Guam avifauna, for example, species with larger clutch sizes have exhibited better survival (Wiles et al., 2003). Introduction of the alien predator *E. rosea* to the Society Islands affected the population dynamics of local partulids by increasing their mortality rates (Clarke et al., 1984). The significantly higher instantaneous clutch sizes of *P. clara* and *P. hyalina* relative to their extirpated congeners (Fig. 3) may be a major factor contributing to their continued survival in Tahitian valleys.

However, there are inherent shortcomings in Crampton's (1916) data that complicate the comparison of reproductive rate among Tahitian partulids. Instantaneous clutch size estimates were compiled from diverse valleys and individual valley-level clutch size estimates are not available for the two surviving taxa, making within-valley comparisons of survivors and non-survivors impossible. In addition, the exact gestation period is unknown for individual Tahitian species. We cannot at present rule out the possibility of longer gestation periods in *P. clara* and *P. hyalina* than in the extirpated species, a developmental pattern that could yield higher instantaneous clutch sizes (Fig. 3) but not necessarily higher birth rates.

The impact of introduced predators may vary across island microhabitats; e.g. in addition to larger clutch sizes, survival in the Guam avifauna is associated with the ability to nest in locations inaccessible to the brown tree snake

(Wiles et al., 2003). On Tahiti more low elevation sites with known survivors (Fig. 1; Table 1) contain *P. hyalina* (31 of 38) than *P. clara* (20 of 38) and this outcome may reflect microhabitat differences among the two taxa. Crampton (1916) noted a discrete distributional trait of *P. hyalina* that distinguished it from its Tahitian congeners. In addition to occurring in dense forest (the typical partulid habitat) he regularly observed *P. hyalina* at forest edges and in clearings where it was exposed to prolonged direct sunlight. *P. hyalina* has a distinctively white shell, and a correlation between light shell coloration and an enhanced ability to withstand exposure to direct sunlight is well known among land snail species (Jones, 1973, 1982; Hazel & Johnson, 1990; Ozgo, 2011). If *E. rosea* has a lower tolerance of direct sunlight, it is possible that this microhabitat distinction plays an additive role in the survival of *P. hyalina*.

The persistence of two of seven species of endemic Tahitian *Partula* under selection pressure from an introduced continental predator has some parallels with the fate of Guam's avifauna (Wiles et al., 2003). In both cases endemic species with larger clutch sizes exhibited better survival, being able to persist in the presence of the predator for multiple decades (40 years on Tahiti, 60–70 years on Guam). We suspect that this general pattern may also apply to diverse clades of endemic taxa across Oceania. If so, this could guide the prioritization of limited conservation resources for the preservation of Pacific island species that are threatened with extinction. For example, when a novel introduced predator appears on an island, it may be appropriate to give the highest conservation priority to endemic prey species that have lower reproductive potential.

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