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ECOLOGY AND POPULATION TRENDS IN NEW CALEDONIAN
***PLACOSTYLUS* SNAILS**
(MOLLUSCA: GASTROPODA: BULIMULIDAE)

A thesis presented in partial fulfilment of the requirements
for the degree of

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Placostylus fibratus



Placostylus porphyrostomus

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Abstract

This study focuses on two endemic New Caledonian land snails: *Placostylus fibratus* and *Placostylus porphyrostomus* (known locally as bulimes) which are in decline and listed as vulnerable by the IUCN. On the Isle of Pines, both species are highly-valued commercially and traditionally harvested species suffering from exploitation for human consumption. In the dry forests of the New Caledonian mainland, *P. porphyrostomus*, especially, is threatened due to habitat degradation and loss, and rodent predation. Prior to this study, the life histories, impact of human harvest, and population trends remained largely unknown for the New Caledonian *Placostylus* species and restoration trials for their conservation had not been undertaken. Addressing these deficiencies forms the foundation for the thesis, and the findings are used to formulate recommendations for management and conservation.

On Isle of Pines, the extent and densities of *P. fibratus* are greater than the scattered and isolated populations of *P. porphyrostomus* found on the island and in the dry forests of the Mainland. *Placostylus* snails are long-lived (estimated at 19 to 39 years for *P. fibratus* in this study) and relatively slow growing, taking up to four years to reach sexual maturity (aperture lip ≥ 3.5 mm). Non-exploitative mortality factors impinge disproportionately on juveniles. Consequently, the age-structure of populations is changing, with juveniles becoming increasingly rare. Annual survival rates for *P. fibratus* are estimated as 59.0% for juveniles and 70.0% for adults.

The major cause of mortality of juveniles was predation by introduced rodents (the ship rat *Rattus rattus*, the Polynesian rat *Rattus exulans* and the mouse *Mus musculus*) that are present in very high densities compared with those reported elsewhere where *Placostylus* occurs, such as New Zealand. I found density estimates of 25.4 rats ha⁻¹ in the rainforest (23.0 – 34.6 rats ha⁻¹, 95% confidence intervals) and 19.1 rats ha⁻¹ in the dry forest (18.9 – 23.6 rats ha⁻¹, 95% confidence intervals).

In the dry forest, 87.6% of all of the empty juvenile shells found for *P. porphyrostomus* appeared to have died from rodent predation and 73.2% for *P. fibratus* on Isle of Pines. The introduced little fire ant *Wasmannia auropunctata* had a negative impact on *Placostylus* growth but not on mortality under semi-natural conditions.

I showed evidence for a decline in the total population of *P. fibratus* snails on the Isle of Pines between 1993 and 2008, with a particularly sharp decline in the

population of juveniles from 2001 to 2008. About 60,000 adult snails are collected annually from the wild for sale, and an additional 69,000 snails are estimated to be eaten annually by Kuniés (the local people of the Isle of Pines). Thus, the actual annual harvest represents approximately 6% of the estimated wild adult stock (ca. 2.5 million snails on average over the period 2001-2008).

A stage-structured population dynamics model developed here showed that if the harvest rate is maintained as it is (ca. 120,000 adult snails per year), then the population is likely to decline to very low numbers within the next 50 years. If the harvest rate increases, the rate of decline is accelerated. Sustainable exploitation is predicted to be attained at a 3% annual harvest rate (c.a. 70, 000 snails per annum), which would preclude collection for commercial purpose since the daily consumption by locals on Isle of Pines would account for most or all of this number. The model is very sensitive to rodent predation rates and predicts that the *Placostylus* population would likely recover if rodent predation was decreased even slightly.

Restoration trials were undertaken for *P. porphyrostomus* populations on the mainland. I successfully controlled rodent populations for 22 months by continuous poisoning in 5 ha of dry forest. After 15 months, the poisoning was sufficient to reduce and maintain rodent activity at low levels but I was unable to conclusively demonstrate a significant benefit to snail populations in the poisoned areas during this period, probably due to the specific life history traits of these snails and the flow-on effects of poisoning also reducing the density of rodents in non-poisoned areas. A trial release of 21 captive-bred *P. porphyrostomus* snails was conducted in an isolated patch of dry forest including two release procedures (soft- vs. hard-release). Twenty five months after the release the trial was deemed a success. The mean survival rate over this period was 100% for hard-released snails, which was significantly higher than the 70% survivorship for soft-release snails. No differences in snail growth (weight and aperture lip thickness) existed between the two release-procedures. Soft-released snails travelled shorter distances from the release point than hard-released snails, and showed significantly higher site fidelity. Supplementation with captive-bred snails appeared viable as a conservation strategy for New Caledonian *Placostylus* in dry forests.

The key findings of the thesis have direct implications for the conservation and management of New Caledonian *Placostylus*; recovery plans highlighting urgent

actions that need to be undertaken for each species of New Caledonian *Placostylus* have been proposed to provide guidance for both managers and local people.

Ecologie et évolution des populations des escargots du genre *Placostylus*
(Mollusca: Gastropoda: Bulimulidae) de la Nouvelle-Calédonie

Resume

Le présent travail porte sur deux escargots terrestres endémiques de la Nouvelle-Calédonie, *Placostylus fibratus* et *Placostylus porphyrostomus* (localement appelés bulimes), listés comme Vulnérables par l'IUCN, et dont les populations sont en déclin. Sur l'Ile des Pins, les deux espèces présentent un intérêt commercial et/ou sont aussi collectées de manière traditionnelle ; elles sont aujourd'hui menacées par leur exploitation pour la consommation humaine. En forêt sèche, sur la Grande-Terre, *P. porphyrostomus* est menacé par la perte et la dégradation de l'habitat et la prédation par les rongeurs introduits. Avant la présente étude, les traits d'Histoire de Vie, l'impact de la collecte par l'Homme et l'évolution des populations avaient été très peu étudiés chez les *Placostylus* calédoniens; aussi, des opérations de restauration des populations dans un but de conservation n'avaient jamais encore été initiées. Comblers ces lacunes constitue les bases de la thèse dont les résultats contribuent à établir des recommandations pour la gestion et la conservation des espèces.

A l'Ile des Pins, les densités de *P. fibratus* sont plus importantes que celles de *P. porphyrostomus* sur l'île mais aussi en forêts sèches sur la Grande-Terre où les populations de cette dernière espèce apparaissent disséminées et très isolées. Les *Placostylus* présentent une durée de vie longue (estimée ici à 19-39 ans pour *P. fibratus*) et une croissance très lente nécessitant au moins 4 années pour atteindre la maturité sexuelle (une lèvre coquillière épaisse de 3.5 mm). Les facteurs de mortalité (autre que l'exploitation par l'Homme) affectent de manière disproportionnée le stock de juvéniles ; en conséquence, la structure de population s'en trouve modifiée, avec un nombre de jeunes se raréfiant de plus en plus. Le taux de survie annuel pour les juvéniles de *P. fibratus* est estimé à 59.0% ; il est de 70.0% pour les adultes. La principale cause de mortalité des escargots juvéniles identifiée a été la prédation par les rongeurs introduits (rat noir *Rattus rattus*, rat Polynésien *Rattus exulans* et la souris domestique *Mus musculus*) qui se rencontrent sous de très fortes densités comparées à celles reportées ailleurs où le genre *Placostylus* est présent (en Nouvelle-Zélande notamment). Les densités estimées ici ont été de 25,4 rats.ha⁻¹ en forêt humide (23,0 – 34,6 rats ha⁻¹, 95% IC) et 19,1 rats ha⁻¹ en forêt sèche (18,9 – 23,6 rats ha⁻¹, 95% IC).

En forêt sèche, 87.6% des coquilles vides de juvéniles ont été endommagées par la prédation par les rats, et 73.2% pour *P. fibratus* à l’île des Pins. La fourmi électrique *Wasmannia auropunctata* a un effet négatif sur la croissance des escargots mais sa présence n’a pas affecté la survie en conditions semi-naturelles.

Il a été mis en évidence un déclin de la population totale de *P. fibratus* entre 1993 et 2008, avec en particulier, entre 2001 et 2008, un déclin de la population de juvéniles. Environ 60 000 bulimes adultes sont collectés en forêt annuellement pour alimenter le marché, tandis que de manière additionnelle environ 69 000 individus sont consommés chaque année par les foyers Kuniés au quotidien. Ainsi le nombre d’animaux collectés annuellement en forêt représente environ 6% du stock actuel estimé (évalué à 2,5 millions d’escargots en moyenne pour la période 2001-2008).

Le modèle de dynamique de population basé sur les stades de croissance développé ici afin de prédire l’évolution des populations pour *P. fibratus*, indique que si le niveau de prélèvement actuel est maintenu (environ 120 000 escargots adultes par an), les populations présentent un risque de fort déclin au cours des 50 prochaines années. Si le taux de collecte est augmenté, le déclin est accéléré. Le modèle prédit que l’exploitation durable de la ressource serait atteinte pour un taux de collecte de 3% (environ 70 000 escargots par an). Ce quota correspond à la consommation actuelle des seuls ménages Kuniés, et n’est ainsi pas compatible avec une collecte à des fins commerciales. Le modèle est très sensible à la prédation par les rongeurs introduits et prédit que la population de bulimes pourrait être rétablie si la prédation par les rongeurs était réduite même très légèrement.

Des opérations de restauration des populations de *Placostylus porphyrostomus* de forêt sèche sur la Grande-Terre ont été initiées. Nous sommes parvenus à réguler les populations de rongeurs introduits par empoisonnement continu pendant 22 mois sur 5 ha de forêt. Après 15 mois, l’empoisonnement a été suffisant pour réduire et maintenir l’activité des rongeurs à des niveaux très bas, mais nous n’avons pas pu mettre en évidence un rétablissement significatif des effectifs dans les zones empoisonnées au cours de la période écoulée probablement à cause des traits d’histoire de vie très particuliers de ces escargots, mais aussi du fait que les zones non-empoisonnées contigües ont également été affectées légèrement par l’empoisonnement, y réduisant aussi les densités de rats.

Egalement, une opération de renforcement des populations à partir d'individus nés en captivité a été réalisée dans un lambeau isolé de forêt sèche. Les escargots, au nombre de 21, ont été relâchés selon deux procédures (avec (soft) et sans adaptation préalable au milieu (hard release)). Après 25 mois de suivi, l'opération a été couronnée de succès. Le taux de survie moyen a été significativement plus élevé pour les escargots non adaptés (100%) contre 70% pour ceux ayant subi un conditionnement pré-lâcher. Aucune différence de croissance n'a été mise en évidence selon la catégorie de lâcher. Les pré-adaptés ont présenté des distances de dispersion au point de lâcher moindres que celles des escargots lâchés tels quels, et une fidélité au site plus importante. Le renforcement des populations à partir d'individus captifs apparaît comme une solution réalisable dans le cadre d'opérations de conservation pour les escargots du genre *Placostylus* en forêt sèche.

Au final, les principaux résultats obtenus au cours du présent travail de thèse présentent des applications directes pour la conservation et la gestion des *Placostylus* de la Nouvelle-Calédonie à court et moyen terme. Les plans de sauvegarde proposés pour chacun des taxons calédoniens, soulignant les actions qui seraient à mettre en œuvre de manière urgente pour la sauvegarde des espèces, constituent de précieux outils pour les gestionnaires et la population locale.

*To my family
who have always encouraged me
in my choices despite the distance between New Caledonia and France.
Thank you*

and in memory of Théodore Koteureu called Dolly

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Foreword

The research for this PhD thesis was conducted during my work at Institut Agronomique néo-Calédonien (IAC) where my employer agreed that I could spend a part of my time working on the thesis meanwhile conducting other actions on conservation of New Caledonian Wildlife. Thus in parallel I developed a programme for conservation and management of native flying-foxes, overhunted for consumption by different communities of the country.

Assoc. Prof Murray Potter and Assoc. Prof. Alastair Robertson, Massey University, supervised me through regular mailing and annual visits to New Caledonia. I also spent a week every six month in Massey University to discuss about progression of the research and analysis.

Fieldwork was conducted from 2003 to 2009 and consisted of intensive work surveying snails on the whole Isle of Pines and dry forests of New Caledonia. This required working closely with local population to obtain the necessary traditional authorization of Tribes to work in their forests on Isle of Pines (Kanak customs), to explain the aims of the study, to share their traditional knowledge and perceptions on snails and to discuss in return about the scientific information we gained all along the study. Only once it was more difficult like when I was pursue by an isolated “in trance” person equipped with an axe (!) after several previous damaged on my car. I had never thought that conserving a land snail would have been so perilous!

During the study, about thirty young adults accompanied me in the forests of Isle of Pines and ten others on the Grande-Terre in Poya in search of snails.

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CHAPTER 1

INTRODUCTION



It is so hard being a snail! Cartoon from Andrew Jeffs in Walker, K. J. 2003.

1.1 Study background

New Caledonia is considered one of the world's hotspots for biodiversity (Mittermeier *et al.* 1998; Myers *et al.* 2000) because of its unique flora and fauna with high endemism, but human activities and invasive introduced species now pose serious threats (Mittermeier *et al.* 1996). When the first Melanesians settled in New Caledonia 3,500 years ago, the native fauna of the archipelago was totally devoid of amphibians and non-flying mammals. The Melanesians introduced plants for food that were mostly non-invasive such as yams *Discorea* sp., banana *Musa* sp., sugar cane *Saccharum officinale*, but also vertebrates such as the Bankiva Fowl (*Gallus gallus*), the Common Smooth-Scaled Gecko (*Lepidoclytus lugubris*) and the Polynesian Rat (*Rattus exulans*); this first human settlement was also correlated with the vanishing of about twenty species of native and endemic vertebrates (Gargominy *et al.* 1996). By the second half of the 19th century, many more introductions had occurred and the rate of new introductions was accelerating. Research on the New Caledonian fauna began soon after the island came under French rule in 1853 but despite the work of 140 years, Chazeau (1993) considered that the uniqueness of the fauna and its antiquity was underestimated and underappreciated. New Caledonia formed from part of a continental fragment that began separating from Australia *ca* 83 Ma. In the Palaeocene, the part of Zealandia that subsequently became New Caledonia experienced a lengthy submersion in deep water (Grancolas *et al.* 2008). The extraordinary biodiversity of New Caledonia today therefore appears to have resulted from multiple radiations (Smith *et al.* 2007) of plants and animals from Australia, New Zealand and the Melanesian archipelagos that invaded the island since it emerged in the Pliocene (Murienne *et al.* 2005).

The native land snail fauna of New Caledonia is amazingly rich and diverse and, like many other New Caledonian invertebrate groups, has a very high level of endemism. Solem (1961) described 160 to 170 species of land snails but Tillier and Clarke (1983) estimated the total to be 300 to 400 species which are all endemic (Gargominy *et al.* 1996). Carlquist (1974), favoured dispersal for the origin of New Caledonia land snail fauna, invoking colonisation by a vagile founder, with the gigantism seen in *Placostylus* being an example of adaptive radiation. *Placostylus* land snails (subfamily Placostylinae) are found only on a small number of islands of the Western Pacific (Hedley 1892; Cockerell 1929; Solem 1961). Nevertheless, a recent

comparison of DNA sequence data from New Caledonian *Placostylus* and representatives of the genus from New Zealand and Lord Howe Island, indicate that the New Caledonian radiation may have originated by dispersal from these southern locations (Trewick *et al.* 2009). The six species found in New Caledonia (*Placostylus fibratus*, *P. porphyrostomus*, *P. caledonicus*, *P. eddystonensis*, *P. bondeensis* and *P. scarabus* (Neubert *et al.* 2009)) are all endemic and are either threatened or endangered (Brescia *et al.* 2008). Three species - *P. eddystonensis*, *P. fibratus* and *P. porphyrostomus* are listed as vulnerable by IUCN (IUCN 2010). Habitat destruction or modification by introduced ungulates, human harvesting for consumption, and predation by introduced species are all factors contributing to their vulnerability (Brescia *et al.* 2008).

Placostylus fibratus is the largest (60-100 g when adult) and most polymorphic species and is found throughout New Caledonia, including the Loyalty Islands where a dwarf form (*P. fibratus ouveanus*) occurs (Chérel-Mora 1983). This edible species is the species most favoured for human consumption and is known as “the snail of the Isle of Pines” (named after the coral island to the south of the mainland from which they are heavily collected). However, only those populations on the Isle of Pines are considered sufficiently abundant to sustain harvesting, which is done primarily by the local Kunié people. *Placostylus* snails are an important part of the Melanesian culture and tradition on the Isle of Pines, and are used for various purposes including food and jewellery as well as for their medicinal properties (e.g. post-partum women drink a snail stock to improve lactation). It is also a traditional food and an important source of protein. *Placostylus fibratus* progressed from a gastronomic speciality on the Isle of Pines to a delicacy in Nouméa (the New Caledonian capital) around 1950 (Pisier 1971). Control measures on the harvesting of these snails have been subsequently imposed by the local authorities charged with environmental protection as an attempt to preserve snail populations and to prevent overharvesting (Délibérations 50-94/APS and 26-2000/APS of the Assembly of South Province).

Placostylus porphyrostomus is the most common species in sclerophyllous forests (Chérel-Mora 1983), which is the dominant vegetation type in dry areas on the west coast of the mainland (where there is less than 1100 mm annual rainfall). This forest type is characterised by a high diversity of plant species, but only 1% of its original cover remains (Programme Forêt Sèche 2010). Thus, the remaining

populations of *Placostylus* snails in sclerophyllous forests are now very isolated. *P. porphyrostomus* is also found on the Isle of Pines where it is sympatric with *P. fibratus*. It is also collected there by locals for their own consumption but it is not marketed commercially.

1.2 Contribution of the research

The natural history of the New Caledonian *Placostylus* species remains poorly known and very little has been published on their behaviour, biology or ecology. Literature regarding individual species is scarce, mainly relating to the description of the species and their geographic distributions. It was clear that further research was needed before effective management strategies could be developed. In response to this need, the Institut Agronomique néo-Calédonien (IAC) initiated a research programme to investigate the biology, ecology and management of the species. Research presented in this thesis contributes to this wider programme.

The overall goal of this research is to investigate the biology and ecology of two endemic species of New Caledonian *Placostylus* that are overexploited (*P. fibratus* and *P. porphyrostomus* on Isle of Pines) and/or restricted to small very isolated populations threatened by habitat loss and predation (*P. porphyrostomus* in dry forests on the mainland). It also aims to provide the scientific foundation required for the sustainable management, conservation and recovery of these species within a context of traditional and economic use.

1.3 Study area

The entire study was conducted in New Caledonia. Five sites with two contrasting vegetation types were selected (Figure 1.1). Two sites in native sclerophyllous forest, Nékoro and Mépouri, near Poya, are privately-owned ranches located on the western coast of “Grande-Terre” (altitude 0-100 m asl). This forest type is characterized by a high diversity of plant species dominated by Myrtaceae, Ebenaceae, Rubiaceae and Euphorbiaceae. About 456 species of plant have been described in this kind of forest, 262 (57.2%) of which are endemic to New Caledonia. Sclerophyllous forest is currently the most threatened of the Caledonian biomes (only 1% remains) due to land clearances and habitat modification by feral ungulates. A conservation programme with ten international, national and local partners

(“Programme Forêt Sèche”) was initiated recently in an attempt to try to save this highly endangered biome and its associated specialised fauna and flora (www.foretseche.nc).

Nékoro (272 ha) is one of the last remaining moderately large remnant patches of New Caledonian dry forest. About 150 ha of forest were fenced in 2007 to exclude rusa deer (*Cervus timorensis*) and cattle (*Bos taurus*). The forest contains a small remnant snail population (*P. porphyrostomus*) (Brescia & Pöllabauer 2004, 2005). At Mépouiri, about 10 km from Nékoro, there is another patch of dry forest (99 ha) in which 8 ha was fenced in 1994 with an additional 6 ha fenced in 2000. The fences exclude rusa deer and cattle, but also feral pigs (*Sus scrofa*). *P. porphyrostomus* is very rare at this site and was only rediscovered in 2003 (Brescia & Pöllabauer 2004, 2005).

Three other sites are located in the Gadgi, Youaty and Kéré districts of the Isle of Pines (152 km²), an island 50 km south of the New Caledonian mainland. The island is subdivided into eight tribal districts with about 1500 inhabitants (called Kuniés). The vegetation is mainly native evergreen humid forest on coral soils, 15-20 m high, composed mostly of Kohu trees *Intsia bijuga*, Buni *Manilkara dissecta* and the columnar pine trees *Araucaria columnaris*. These sites have a higher density of *Placostylus* snails (*P. fibratus*) than on the main island and they are collected regularly for sale to local restaurants (Brescia *et al.* 2008). *P. porphyrostomus* lives here in sympatry with *P. fibratus* but is far less abundant.

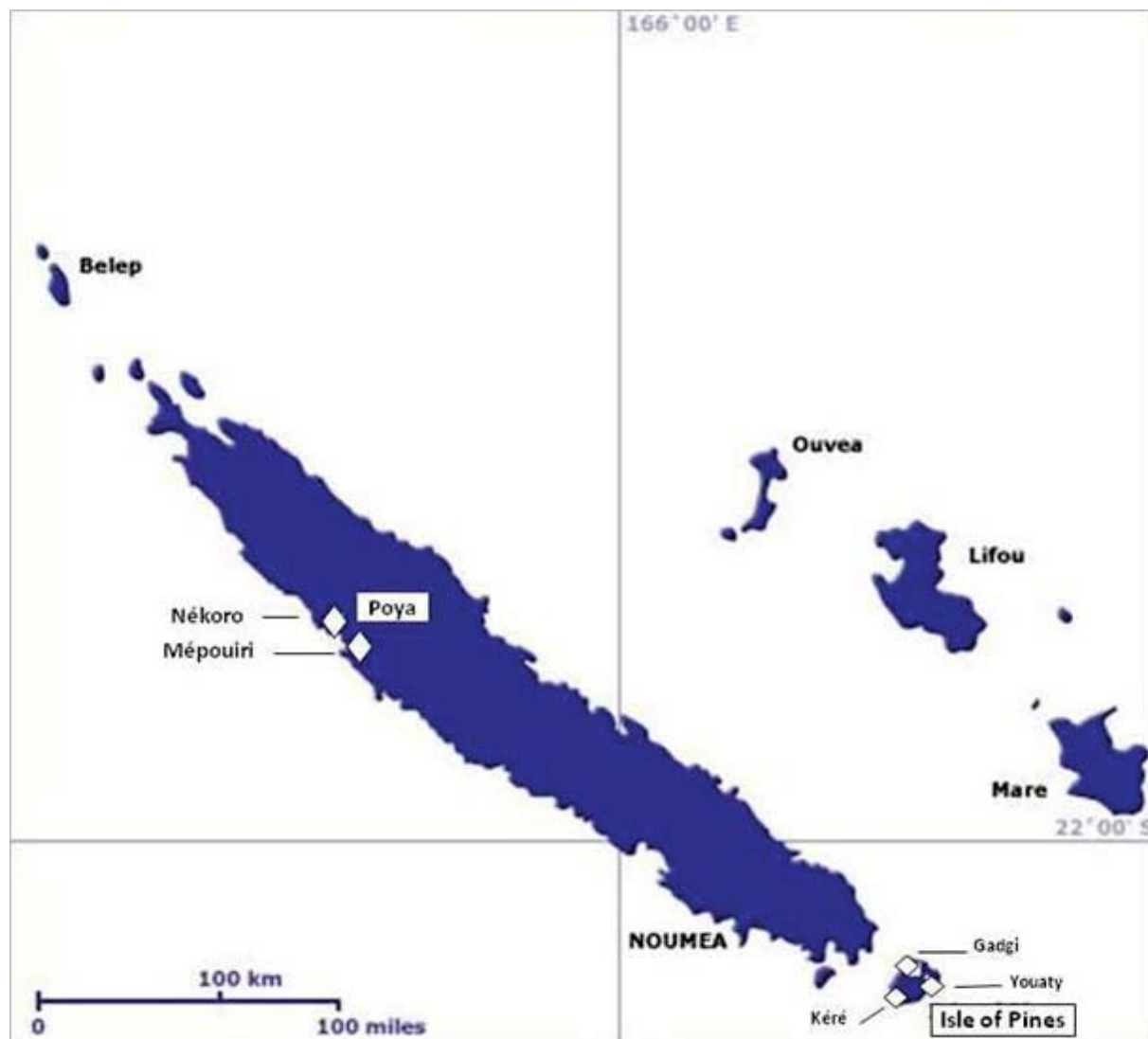


Figure 1.1: the study area with the three sites on Isle of Pines (Gadgi, Youaty and Kéré) and two sites in dry forest (Nékoro and Mépouiri).

1.4 Thesis structure

The remainder of this thesis consists of nine chapters. Eight of these are written in the form of papers; the final chapter is a general discussion. While written as stand-alone papers, they have been designed to complement each other and collectively they address the stated aim of the thesis. This format means that there is inevitable repetition of some methods and study site details. Each chapter starts with a summary written in both English and French. This is to ensure that the key findings of the study are accessible to the widest possible readership within New Caledonia where French is the dominant language. References have been placed at the end of each chapter.

Chapter 2 reviews the literature relevant to the genus and the state of knowledge on New Caledonian *Placostylus*. It introduces the research questions of the thesis and also highlights the need for research directed at enhancing the conservation of New Caledonian *Placostylus*.

Chapter 3 assesses the influence human harvest has had on *Placostylus* population and tracks population density trends through time on the Isle of Pines.

Chapter 4 describes the demography of two species of *Placostylus* in New Caledonia, one in an evergreen forest, the other in dry forest.

The threats imposed by introduced species on *Placostylus* populations are investigated in the two following chapters. Chapter 5 aims to determine the abundance of introduced rodents in native dry forest and rainforest, and evaluates two abundance index techniques while chapter 6 investigates the impact of the little fire ant (*Wasmannia auropunctata*) on *Placostylus* snails.

In Chapter 7, data from previous chapters are used to develop a computer model that investigates the collective and independent effects of predation and human harvest on *Placostylus* snail population dynamics.

Two studies that focus on aspects of the conservation biology of the snails follow on the restoration of threatened *Placostylus* populations, first by controlling rodents by poisoning (Chapter 8), and second by supplementing a snail population with captive-bred snails (Chapter 9).

In Chapter 10, the significance of the results and conclusions from each chapter are outlined and specific management recommendations presented. Recommendations for further work and contribution of the study for the management and conservation of others exploited native fauna of New Caledonia are discussed.

Finally, there is an appendix with two additional papers, and two documents edited for a malacology conference, which are related annexe activities of the research. A published paper investigates the diversity and phylogeny of New Caledonian *Placostylus* snails (Trewick *et al.* 2008), and a research note describes the rearing method developing for *Placostylus*. Also two posters were presented at the World Conference of Malacology in Perth (Australia) in 2004.

1.5 Contribution of co-authors

My Supervisors, Assoc. Prof. Murray Potter and Assoc. Prof. Alastair Robertson are co-authors of all the papers combined to form the chapter manuscripts. Their assistance has been invaluable with experimental design and statistical analysis but also they have provided feedback on drafts of the papers and given discerning comments.

Dr Doug Armstrong, Professor of Conservation Biology, Massey University, provided assistance with data analysis in Chapter 4.

Dr Alasdair Noble, Senior Lecturer in Statistics, Institute of Fundamental Sciences at Massey University, provided valuable statistical advice on survey and sampling design for Chapter 3.

Associate Professor Ed Minot, Ecology Group Leader, Massey University, helped with Chapter 7 by providing advice on the use of STELLA[®] and on how to structure the model.

My local advisor, Dr Christine Pöllabauer, has made available her set of data on snail stock from 1993 to 2002, her experience and her observations on *Placostylus*, and provided valuable input into Chapters 1 and 4.

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CHAPTER 2

A REVIEW OF THE ECOLOGY AND CONSERVATION OF *PLACOSTYLUS* (MOLLUSCA: GASTROPODA: BULIMULIDAE) IN NEW CALEDONIA



*Morphological differences between the New Caledonian endemic snails *Placostylus fibratus* (bottom) and *Placostylus porphyrostomus* (middle), and the introduced snail *Achatina fulica* (top).*

Chapter reference:

Brescia F. M., Pöllabauer C. M., Potter M. A. & Robertson A. W. (2008) A review of the ecology and conservation of *Placostylus* (Mollusca: Gastropoda: Bulimulidae) in New Caledonia. *Molluscan Research* 28: 111-122.

Abstract

Land snails of the genus *Placostylus* Beck, 1837 are found only in the Western Pacific, from the Melanesian Plateau to New Zealand. While the ecology of the New Zealand *Placostylus* species is generally well known, having been studied for more than 20 years, and there is some published information on the one species of *Placostylus* from Lord Howe Island, there is very little published information on the six New Caledonian species. These New Caledonian taxa are all endangered, but their conservation is hampered by a lack of information about the life-history, biology and ecology especially relating to *Placostylus bondeensis*, *P. eddystonensis*, *P. scarabus* and *P. caledonicus*. The data that is available comes mostly from studies on the two remaining species - *P. fibratus* and *P. porphyrostomus*. Here we review what is known of the activity patterns, growth rates, life-histories, habitat use, nutrition, movement patterns and causes of population decline in these two species and collate the available information from the limited and mostly unpublished literature. The two species are threatened in different ways - *Placostylus fibratus* is favoured as food, and as a result, has been over-collected from the wild, while *P. porphyrostomus* is threatened by habitat modification and destruction and by predation by introduced rodents. We make several recommendations for the conservation of New Caledonian *Placostylus* which ultimately may depend on the work we describe here on captive breeding and management. Translocations to predator-free sanctuaries coupled with augmentation of existing populations may be necessary to maintain populations of these species in the wild.

Etat des connaissances sur l'écologie et la conservation des *Placostylus* (Mollusca: Gastropoda: Bulimulidae) de la Nouvelle-Calédonie

Résumé

Les escargots terrestres du genre *Placostylus* Beck, 1837 se rencontrent uniquement dans le Pacifique Sud-Ouest, depuis le Plateau Mélanésien jusqu'à la Nouvelle-Zélande. L'écologie des espèces de *Placostylus* de la Nouvelle-Zélande, étudiées depuis plus de 20 ans, est de relativement bien connue. Par contre, très peu de travaux ont été publiés sur les six espèces de la Nouvelle-Calédonie. La conservation de ces taxons, tous endémiques et menacés, est entravée par le manque de connaissances sur les traits d'histoire de vie, la biologie et l'écologie principalement pour *Placostylus bondeensis*, *P. eddystonensis*, *P. scarabus* et *P. caledonicus*. La plupart des informations disponibles proviennent des études réalisées sur les deux autres espèces, *P. fibratus* and *P. porphyrostomus*. Un état de la bibliographie récente sur plusieurs aspects de la biologie et de l'écologie de ces deux espèces (activité, croissance, reproduction, habitat, alimentation, mouvements et causes de disparition) est réalisé ici afin de compiler les connaissances à partir de la littérature disponible et non publiée de manière générale. *Placostylus fibratus*, très recherché pour la consommation humaine est collecté dans le milieu naturel, alors que *P. porphyrostomus* est menacé par la modification et la perte de son habitat naturel, et par la prédation par les rongeurs introduits. Enfin, différentes recommandations pour la conservation des *Placostylus* de la Nouvelle-Calédonie sont établies à partir des travaux d'élevage et des pistes de gestion discutés ici. La translocation d'espèces dans des réserves sans prédateurs, associée à l'augmentation des populations existantes peut être nécessaire à la survie des populations sauvages.

2.1 Introduction

The genus *Placostylus* Beck, 1837 belongs to the Bulimulidae (Gastropoda, Heterobranchia, Pulmonata), a widely dispersed snail family that is most numerous in South America and reaches its maximum diversity in Brazil (17 genera). A few genera extend north into the West Indies, Mexico, and the southern United States; others are found in Australia, New Zealand and Melanesia. The phylogeny of the Bulimulidae remains uncertain, but a South American radiation in the Mesozoic and Tertiary is suggested by the present distribution, comparative anatomy and fossil record (Solem 1959). *Placostylus* (subfamily Placostyliinae) is found only in the Western Pacific, extending northwards from the tip of the North Island in New Zealand to Lord Howe Island, Fiji, the Solomon Islands, Vanuatu and New Caledonia including the Loyalty Islands (Hedley 1892; Cockerell 1929; Solem 1959). The New Caledonian *Placostylus fibratus* (Martyn, 1789) is the type species of the genus (Chérel-Mora 1983). Molecular analysis suggests that the Lord Howe Island species and the New Zealand mainland taxa are sister groups, but that the Three Kings Islands taxon (off the northern tip of New Zealand) is independently derived, possibly from New Caledonian stock (Ponder *et al.* 2003). The New Caledonian species have typically been classified into two groups, namely *Leuchocharis* Pilsbry, 1900 and *Placostylus s. str.*, ranked as sections by Pilsbry (1901–1902) and as separate genera by Franc (1956).

The literature on the taxonomy of New Caledonian *Placostylus* abounds with more than 130 specific and infraspecific names (Crosse 1855a, 1855b, 1867, 1868, 1869, 1870, 1875, 1881, 1886, 1895; Gassies 1863, 1869, 1870, 1871, 1880; Brazier 1881, 1882; Pain 1955, 1958; Solem 1961). This multitude of taxa within New Caledonia is the result of the high degree of morphological variation in the shells (Solem 1959), and the tendency by early conchologists to describe taxa on the basis of just one or two individuals. Solem (1959) suggested that the New Caledonian species were monophyletic and all closely related, and that the shell divergences between the sections (or genera) represent minor habitat adaptations. More recent treatments have revised the species number downwards. Franc (1956) recognized 19 species, whereas Solem (1961) proposed 33 species. Starmühlner (1970) described the anatomy, the radula and the shell characteristics for seven species—*Placostylus albersi* Dautzenberg & Bouge, 1923, *P. caledonicus* (Petit, 1845), *P. duplex* (Gassies, 1871), *P. fibratus*, *P. goroensis* (Souverbie, 1870), *P. layardi* Kobelt, 1891 and *P. porphyrostomus* (Pfeffer,

1851). Using anatomical characteristics and analysis of shells from many populations collected all over New Caledonia and adjacent islands, Chérel-Mora (1982, 1983) recognized only four endemic species, each of them exhibiting very wide clinal geographic and ecological variation: *Placostylus fibratus*, *P. porphyrostomus*, *P. caledonicus* and *P. eddystonensis* (Pfeffer, 1855). Drs E. Neubert and P. Bouchet (MNHN, Paris; pers. comm. 2000; Neubert 2001) who are currently investigating the taxonomy and anatomy of New Caledonian *Placostylus*, suggest that six valid species and approximately twenty well defined geographic subspecies spread over the territory can be recognised in New Caledonia. In addition to the four species recognised by Chérel-Mora, *Placostylus scarabus* (Albers, 1854) and *Placostylus bondeensis* (Crosse & Souverbie, 1869), which were considered synonyms of *Placostylus caledonicus* by Chérel-Mora (1983), are recognized as valid species by Neubert (2001). Our observations in the New Caledonian dry forest since 1993, on *Placostylus porphyrostomus* in particular, show that further investigations on the systematics of New Caledonian *Placostylus* may still be warranted (Brescia and Pöllabauer 2004). Nevertheless, here we have adopted the classification of six species proposed by Neubert (2001).

The natural history of the New Caledonian *Placostylus* species remains poorly known and very little has been published on their behaviour, biology or ecology. In 1993, a study of the stock size and aspects of the biology and ecology of the two best known species of *Placostylus* (*P. fibratus* and *P. porphyrostomus*) was initiated (Pöllabauer 1994). This research is ongoing and is being expanded because all the New Caledonian species are considered at risk of extinction due to anthropogenic disturbances. Three species—*P. eddystonensis*, *P. fibratus* and *P. porphyrostomus*—are listed as vulnerable by IUCN (IUCN 2006). Very little is known of *P. caledonicus*; only one small population (estimated size ~200 individuals in 2004) is known from the North of New Caledonia (Koumac, “Three Creeks”), while *P. eddystonensis* seems to be the rarest species, with no living snails found in the last 10 years. The population status of *P. scarabus* and *P. bondeensis* has never been documented but our observations show that the populations of these species are very restricted and found only in the far north of the main island and only in small patches of remnant forest.

Placostylus fibratus is the most polymorphic species and is found throughout New Caledonia, including the Loyalty Islands where a dwarf form occurs. This edible

species is known as ‘the snail of the Isle of Pines’ (named after the coral island to the south of the mainland from which they are collected). Indeed, the only snails to be marketed commercially for consumption are those from this island. Control measures on the harvesting of these snails were imposed by the local authorities charged with environmental protection. In parallel, conservation strategies such as off-site preservation as well as developing farming methods have been explored by the Institut Agronomique néo-Calédonien (IAC) since 1997 and will be described below. *Placostylus porphyrostomus* is the most common species in sclerophyllous forests (Chérel-Mora 1983), which is the dominant vegetation type in dry areas on the west coast of the mainland (less than 1100 mm annual rainfall, mostly falling in three months of the year). This forest type is characterized by a high diversity of plant species.

Placostylus porphyrostomus is also found on the Isle of Pines where it is sympatric with *P. fibratus*. It is also collected by locals for their own daily consumption but it is not commercially marketed. The sclerophyllous forest is currently the most threatened of the Caledonian biomes due to deforestation and habitat modification by feral ungulates (Programme Forêt Sèche 2007). A conservation programme with ten international, national and local partners (‘Programme Forêt Sèche’) has been recently initiated in an attempt to try to save this highly endangered biome and its associated specialised fauna and flora.

In this paper, we use the available literature and our own observations on many populations of each species to summarise what is known of the biology and the ecology of *P. fibratus* and *P. porphyrostomus*. For more than 10 years these two species have been the subject of research in New Caledonia because of their importance as food, which provides an economic imperative for their study. We assume here that the study of their biology will be indicative of the New Caledonian species generally, although we recognise the differences in the relative abundances in the species. We also review causes of the decline of the New Caledonian *Placostylus* in the wild and summarise the results of a captive breeding programme. Recommendations for the conservation of these species are given.

2.2 General state of knowledge

2.2.1 Life History

Published information about the life-history of New Caledonian *Placostylus* is very sparse. However, in this review we bring together information presented in a series of unpublished technical reports to government authorities in New Caledonia, particularly those concerning *P. fibratus* (Pöllabauer 1994, 1995; Brescia 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2007) and *P. porphyrostomus* (Brescia and Pöllabauer 2004, 2005). Some additional inferences can be made from studies on the New Zealand endemic *Placostylus* species (Choat and Schiel 1980; Penniket 1981; Brook and Laurenson 1992; Sherley *et al.* 1998; Stringer *et al.* 2004) and on the one species of *Placostylus* on Lord Howe Island (Murphy and Nally 2004).

2.2.2 Distribution, habitat and diet

Placostylus fibratus, the most widespread species, inhabits all of the New Caledonian mainland, the Isle of Pines, and the Loyalty Islands. On the mainland, it is found in humid evergreen forests of the east coast; in the dry coastal forests of the west; and in the humid evergreen forests of the central mountain chain up to an altitude of 900 m from the north to the extreme south, where it occurs as a spectacular giant form weighing up to 100 g and measuring about 15 cm in shell height. *Placostylus porphyrostomus* is characteristic of the dry forests of New Caledonia (Chérel- Mora 1983). It is found in remnant patches of sclerophyllous forest along the west coast of the mainland, and does not occur in the wet forests of the island's interior. *Placostylus porphyrostomus* is sympatric with *P. fibratus* on the Isle of Pines. *Placostylus caledonicus*, occurs in the far north of the mainland, and inhabits dry coastal forests to an altitude of 500 to 600 m (Chérel-Mora 1983).

These snails appear to be relatively specific in their habitat requirements. *Placostylus fibratus* seems to be primarily associated with calcium-rich soil (Brescia 2001). On the Isle of Pines, opportunistic observations show that *P. fibratus* and *P. porphyrostomus* are attracted to and feed under trees with large canopies and/or with broad leaves such as fig and banyan trees (*Ficus* spp.), *Elaeocarpus hortensis* Guillaumin, 1931, *Meryta macrocarpa* Baillon, 1878, but also under the ferns *Asplenium nidus* Linnaeus, 1753 and *Microsorium punctatum* Copeland, 1929 (Pöllabauer 1995). Brescia (2000) found them preferentially under Pweu (*Ficus habrophylla* Bennett & Seeman, 1865) and Kohu (*Intsia bijuga* (Collebrooke) Kuntze,

1891). Indigenous snail collectors on the Isle of Pines search preferentially for *Placostylus* under these trees, and also under Buniê (*Manilkara dissecta* var. *pancheri* (Baillon) Maas Geesteranus 1941) as they are known to be favoured by the animals. Juveniles (up to 1.5 cm in shell height) are often found up to 2 m from the ground on the foliage of the Jaanyi (*Codiaeum variegatum* Blume, 1825) (pers. obs.). *Placostylus* show a tendency to hide during daylight: Brescia (1997) found *P. fibratus* to be hidden during the day under dead leaves of the litter, under roots, coral rocks or fallen wood (82% of snails found, n=53) and very few (18%) were under no protection.

Very little data are available on the diet of New Caledonian *Placostylus*, but they are known to consume both fresh and fallen leaves of the species listed above. Adults and juveniles have also been seen grazing on algae and lichens on leaves and coral rocks (Pöllabauer 1995; pers. obs. F.B., and knowledge of locals from the Isle of Pines). After snails have been collected and just before they are marketed, women often feed them with the green leaves of Trüü (*Rivina humilis* Linnaeus, 1753, the Coral Bay), and also leaves of *Asplenium nidus* Linnaeus, 1753. When she studied the anatomy of *Placostylus*, Pöllabauer (1995) also found soil in the intestine.

In the dry forests of the mainland, the favoured habitat and environmental conditions have been described for *P. porphyrostomus* by Brescia and Pöllabauer (2005). The snails appear to seek out areas with deep leaf litter, where the cover of understorey trees is high (> 75%). In general, they are found in shady places with low light levels (ca. 800 lux), and where environmental conditions are cooler (on average, 2–3°C less than points 1 m radius away from the snail). This suggests that snails use microhabitat variation to attain a more suitable environment (lower temperature and higher relative humidity) which may enable them to avoid desiccation during the drier daylight hours and during periods of low rainfall. Important components of the habitat of *Placostylus* of dry forests are the understorey trees of *Codiaeum peltatum* (Labillardière) Green (1986), *Carissa ovata* Brown 1810, and *Fontainea pancheri* (Baillon) Heckel 1870. In these forests the snails are generally found under leaf litter or close to fallen logs.

In New Zealand, Penniket (1981) found that the distribution and abundance of *P. ambagiosus* (Suter, 1906) and *P. hongii* (Lesson, 1830) in forest communities is also greatly influenced by the distribution of ground cover and local variation in leaf

litter depth, and that older juveniles and adult snails feed on fallen leaves from broadleaf trees and shrubs. According to Brook and Laurenson (1992), the principal factors determining the within-colony distribution of the other New Zealand species *P. bollonsi* are the presence of broadleaf food plants and/or of a sheltered microhabitat that occurs under broadleaf litter or groundcover plants. Penniket (1981) suggested that there might be a minimum sized leaf under which a snail may find such a favourable microclimate.

On Lord Howe Island, Murphy and Nally (2004) found *P. bivaricosus* (Gascoin, 1854) under well-developed, moisture-retaining leaf litter in evergreen closed forest, often, but not exclusively, in the vicinity of Banyan Figs (*Ficus macrophylla columnaris* Moore & Mueller 1874). These authors also observed that *P. bivaricosus* was sparse or absent in areas developed as palm plantations, but mixed palm and broad-leaf forest provided good habitat.

2.2.3 Activity

Like most pulmonate land snails including other *Placostylus* species (Penniket 1981, Brook and Laurenson 1992, Murphy and Nally 2004), the New Caledonian *Placostylus* are nocturnal. Pöllabauer (1995) observed activity of *P. fibratus* between 7:00 pm and 6:00 am during the cool season and between 12:00 and 4:00 am during the warm season. She found that the peak of activity was between 2:00 and 3:00 am whatever the season (Figure 2.1), and that activity is negatively related to temperature ($r = -0.75$) and positively to humidity ($r = 0.46$).

In observations of captive and wild populations over 24-hour periods during both the cool and warm seasons, Brescia *et al.* (1998) also found that *P. fibratus* is active between 7:00 pm and 6:00 am, but described two peaks of activity: one near 8:00 pm and another one between 3:00 am and 4:00 am. The intensity of activity appeared to be related to weather conditions, being greater during or following periods of rain. Overall, the activity levels were low—only 13 to 14% of the dark period of each 24 h comprised moving, feeding or sexual activities.

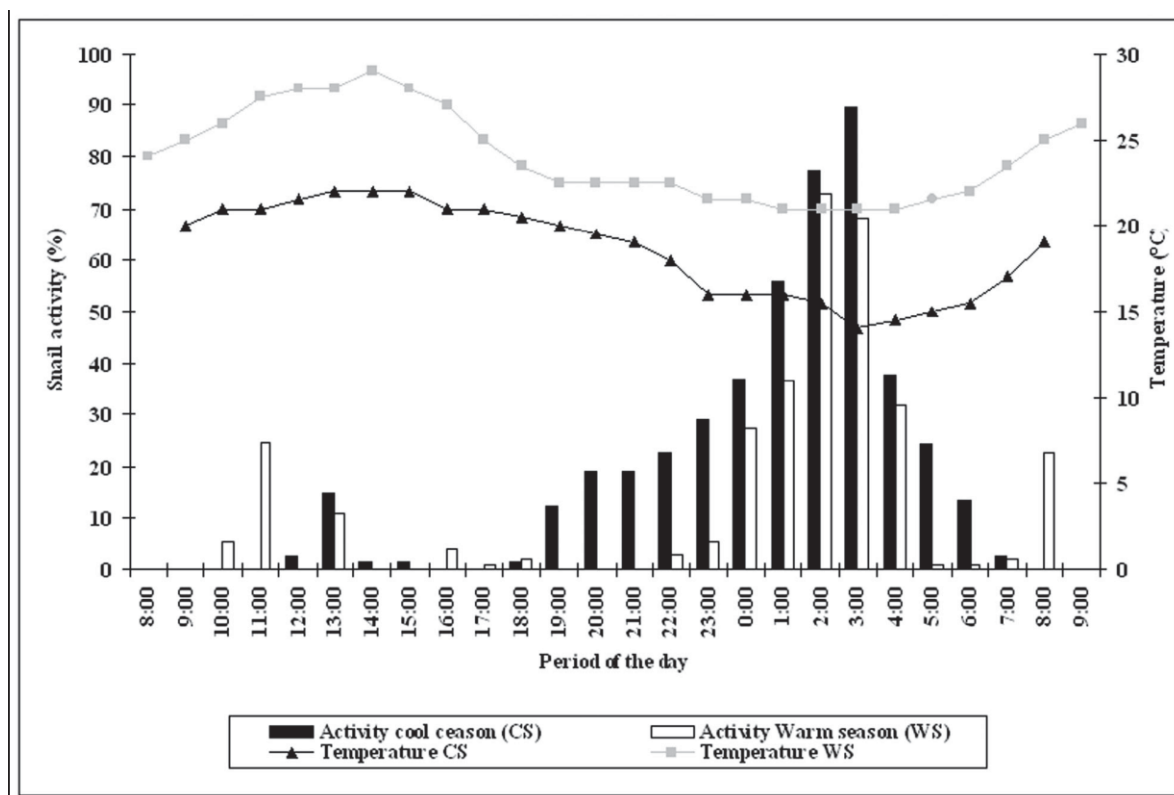


Figure 2.1: Daily activity patterns (defined as snails outside their shell showing locomotory and/or nutritional activities) of wild *Placostylus fibratus*, in Kaana, Isle of Pines, New Caledonia in the cool season (CS) ($n=79$) and warm season (WS) ($n=109$) (from Pöllabauer C. 1995).

Brescia (1997) found that during a week of observations in the field in July 1997, 19% ($n=194$) of snails showed no activity during that whole period. Salas *et al.* (1997) and Brescia *et al.* (1998) found that, in captivity, between 6 and 50% of snails under observation remained inactive each night despite variation in temperature, humidity and lighting regimes. Hatchlings and juveniles appear to be more active than sub-adults and adults (Pöllabauer 1995, pers. obs. F.B.).

Brescia (1997) observed *Placostylus* in captivity under controlled conditions by having the snails in a reverse light cycle - exposing them to light in their normal dark period - and showed that they appear fundamentally nocturnal and that a negative phototropism exists. Penniket (1981) suggested that the nocturnal behaviour of New Zealand *Placostylus* may serve as both a predator-avoidance mechanism and a strategy to avoid higher daytime temperatures and its drying effects.

Pöllabauer (1995) found seasonal differences in *P. fibratus* activity levels. At the beginning of the warm season (which runs from December to March), activity was found to be very low, with the majority of snails remaining inactive. When provided with a friable soil substrate during this season, the snails were found to burrow to cover their shell aperture, evidently as protection from desiccation. Even so, during extended dry periods, 30 to 45% loss of body weight due to desiccation was recorded. In the cool season (May to October), movement, reproduction and growth all resume.

2.2.4 Dispersal

Placostylus fibratus is a slow-moving animal and typically travels only about 1 m per night (Brescia 1997), although some adults have been observed to travel up to 20 m in a single night to lay eggs. The New Caledonian *Placostylus* tend not to disperse far: tagged *P. porphyrostomus* and *P. fibratus* are regularly relocated in the same 10 x 10 m quadrat and mostly under the same shrub or tree over a year or more (Pöllabauer 1995; F. Brescia, pers. obs.; Brescia and Pöllabauer 2005). Penniket (1981) found that the New Zealand *Placostylus* also exhibited a very low rate of dispersal of about 1 to 2.8 m after six months and suggested that the snails may exhibit a homing behaviour, since some snails remain for several months in the same crevice or under the same tree. Penniket (1981) suggested that this strategy of low dispersal may be of selective value to an organism dependent on patchily-distributed resources in a heterogeneous environment, i.e. where preferred food trees and ground shelter are scattered within a mixed-forest association. By comparison, the introduced giant African snail *Achatina fulica* (Bowdich, 1822) was observed traversing more than 50 m in a night (Van S. Greve 1981).

2.2.5 Life span and growth

Placostylus fibratus is a large snail and reaches 80–100 g when adult with a shell height of 9–15 cm. *Placostylus porphyrostomus* is smaller (7–8 cm in shell height, 45 g), and is characterised by the partial or total disappearance of the periostracum from the shell when adult.

Placostylus fibratus reaches maturity at five years and, based on a prediction of shell growth rates, it is suggested that they may live 15 years and attain 11.7 cm shell height (Pöllabauer 1995). Once maturity is reached, the increase in shell height stops, but thickening of the peristome continues (Pöllabauer 1995). This growth pattern is termed determinate in contrast to that of snails, such as *Achatina fulica*, with

indeterminate growth where the shell continues to increase in height after they become adult. Adult *P. fibratus* are thus characterised by a shell with a thickened apertural lip (more than 4 mm) which is also strongly correlated with the maturity of the genital tract ($r = 0.70$ for female organs and $r = 0.60$ for male organs) (Pöllabauer 1995).

The first study of growth rates of New Caledonian *Placostylus* in the wild used a Von Bertalanffy model fitted to mark-recapture data of 708 individuals of *P. fibratus* on the Isle of Pines (Pöllabauer 1995). The fitted model $H(1 - \exp^{-K(t-t_0)})$ predicts the height of the shell as a function of the animal's age (yr), where K is the rate of growth, set at 0.22 yr^{-1} and H , the maximal possible shell height, set to 11.7 cm. This model recognises that shell height growth slows as maturity is approached. *Placostylus fibratus* generally exhibited slow growth rates during this study. In the dry year of 1994, growth rates (shell height increments) were only in the order of 5 to 19 mm per annum. However, it appears that *P. fibratus* exhibits great plasticity in growth rates and is able to respond to favourable environmental conditions—one marked individual grew from a shell height of 2.4 cm to reach maturity at 9.6 cm over the course of a single year (Pöllabauer 1995).

In a comparative study of growth under natural and artificial conditions, Brescia (2004) estimated mean growth rates of 18 mm shell height per annum in 30 juveniles of *P. fibratus* monitored in forest habitat on the Isle of Pines between February and June 2004. In captivity over the same period, when snails were fed an artificial diet (see below), animals in the same age class had mean growth rates about 2.5 times higher (44 mm shell height per annum). No information exists on the longevity and growth rate in other New Caledonian *Placostylus*.

Parrish *et al.* (1995) re-captured alive in 1991 snails that had been first marked in 1979, and suggested that the New Zealand species *P. hongii* and *P. ambagiosus* may live to 20 years or more. *Placostylus hongii* have survived in captivity for more than five years (Penniket 1981), and in a recent growth study, Stringer *et al.* (2004) suggested that *P. hongii* may live at least 10 years and possibly more than 30 years, supporting the conclusions of Choat and Schiel (1980). In discussing New Zealand *Placostylus*, Penniket (1981) suggested that the long lifespan in these animals may be a strategy to compensate for living in environments where recruitment to the breeding population may be irregular and variable. The rate of increase in shell height for *P.*

hongii varied from 6 to 25 mm per year in juveniles with shells < 38 mm in height, but slowed when adults reached maturity. Subsequently, the lip thickness increased about 0.1 to 0.4 mm per year but this growth rate varied considerably between individuals. In a study of size-frequency of *Placostylus bollonsi caperatus* Powel, 1948 from Wet Bay on Great Island (Three Kings Islands), Brook and Laurenson (1992) indicated an increase in shell height of about 25–30 mm per year, and that snails attain adult size at about 3 years. The growth rate and lifespan of *P. bivaricosus* in Lord Howe Island are unknown (Murphy and Nally 2004).

2.2.6 Reproduction

Placostylus, like all pulmonates, are hermaphroditic and so all individuals are potentially capable of producing eggs. In the field, egg laying in New Caledonian species has been observed to occur primarily during the cool season, but the reproductive season of *P. fibratus* on the Isle of Pines can extend until October (Pöllabauer 1995). Clutches of 25 to 450 eggs are deposited in nests formed in depressions in the soil. These nests are generally located near coral blocks or close to tree roots in a friable humus-rich soil. Pöllabauer (1995) observed egg-laying at a rate of about 17 eggs per hour, followed by about 20 to 30 min of rest. The interval between laying and hatching was between 15 and 21 days. The egg-laying behaviour of *P. fibratus* kept in captivity, under semi-natural conditions, was similar to the field behaviour noted above, though here it was possible to observe that individuals can produce eggs several times per year (observed range 1 to 4 clutches). Eggs were produced at similar times of the year to snails in the wild (Brescia 1999 to 2005). Clutches averaged 205 eggs (SD=84; n=103, range 13 to 515). The eggs are oval and off-white, with a thin calcareous shell. Egg size varies from 3.6 to 4.4 mm × 5.5 to 6.7 mm, and their weight varies from 0.8 to 100 mg (67.7 mg on average, n=164). Brescia (2002) found no consistent variation in egg size or numbers of eggs per clutch among snails from different geographic origins on the Isle of Pines. However, as seems general for pulmonates (Tompa 1984; Heller 2001), egg size varies according to animal size—the larger the parent, the larger the egg and the larger the hatchling.

The interval between laying and hatching varies from 10 to 45 days in captivity (average 22 days), and is strongly dependent on ambient temperature—high temperatures (25°C) hasten hatching to about 10 days. The hatching success in captivity is now in the order of 70% and at emergence, shell height varies between 4.4

and 7.2 mm, and the weight of the living animal between 23 and 94 mg. Hatchlings have been observed to stay within or near the nest for several days but after that exhibit a strong tendency to climb on the walls of the enclosures. This behaviour can be reduced by the addition of a thick layer of leaf litter to the soil surface. In the wild, on Isle of Pines, hatchlings and juveniles (up to 15 mm in shell height) are often found climbing on shrubs and small trees such as the juvenile form of *Meryta* sp. (2 m high) or the fern *Asplenium nidus* (pers. obs.).

Mating has rarely been observed in New Caledonian *Placostylus*. One case involving *P. fibratus* was observed in June 2002 (F. Brescia & C. Pöllabauer, pers. obs.), with copulation lasting eight hours.

The reproductive biology of the New Zealand taxa appears similar to that of *P. fibratus*. *Placostylus hongii* and *P. ambagiosus* reach sexual maturity at 3–5 years. Mating appears to be triggered by climatic conditions in these species, and probably occurs every year except in periods of drought. Mating can last 10 hours or more and snails may mate several times with several different mates. Twenty to thirty eggs are laid in a nest and egg size varies from 5.7 mm long by 5.3 mm wide to 6.6 mm by 5.4 mm (Penniket 1981). Brook and Laurenson (1992) mentioned that *P. bollonsi* lays a smaller number of relatively large eggs (12.5–18.0 mm long). The temporal variability in abundance of eggs observed suggests that egg laying by *P. bollonsi* is seasonal, occurring in spring and/or early summer, with most eggs hatching by late summer (Brook and Laurenson 1992; Penniket 1981; Parrish *et al.* 1995). Hatching occurs after 6–15 weeks in these species, and the hatchlings spend an unknown period living in trees and shrubs up to 4 m above the ground where they are believed to graze on algae on leaf surfaces. The development of this arboreal behaviour by *Placostylus* hatchling snails may be a response to environmental (temperature) gradients by which snails seek lower temperatures at higher elevations (Penniket 1981).

On Lord Howe Island, *P. bivaricosus* lays small clutches of eggs in the soil beneath leaf litter, probably during the warmer months. Hatchling snails possess shells about 6.7 mm in height and 5 mm in width. Hatchling and juvenile mortality is high (Murphy and Nally 2004).

2.2.7 Population structure and population decline

All the species of New Caledonian *Placostylus* appear to have previously been more abundant and widespread than they are today, judging by historical records and by the frequent presence of old shells in forests, indicating former populations where no living snails exist today (Pisier 1985; Pöllabauer 1995; Brescia and Pöllabauer 2005; Philippe Bouchet, pers. comm. 1999).

Few data are available on the population structure of New Caledonian *Placostylus*. Density estimates have been made for *P. fibratus* on the Isle of Pines for the period 1995 to 2004 (Pöllabauer 1995, 2002; Brescia 2004, 2005), and for *P. porphyrostomus* in a few patches of dry forest on the mainland (Brescia and Pöllabauer 2004, 2005). The populations of *P. porphyrostomus* that remain appear far more scattered and isolated than populations of *P. fibratus*; this situation is largely due to the high level of fragmentation of dry forest compared to the situation of the humid forests of the Isle of Pines (see below). Densities of live snails and empty shells vary from 0.025 to 0.18 per m² (live) and 0.15 to 0.18 per m² (empty shells) for *P. fibratus* on the Isle of Pines (Brescia 2004), and from 0.009 to 0.115 per m² (live) and 0.073 to 0.74 per m² (empty) for *P. porphyrostomus* in mainland dry forests (Brescia and Pöllabauer 2005). Generally empty shells are more common (66% for *P. fibratus* and 85% for *P. porphyrostomus*) than live snails since empty shells can persist for many years on the forest floor. Adult-sized animals predominate amongst both the live snails (62% for *P. fibratus* and 78% for *P. porphyrostomus*) and the empty shells (94% for *P. fibratus* and 82% for *P. porphyrostomus*). For both species, recently-hatched or juvenile snails are rarely found in the field. Moreover, when they are found, a high proportion of hatchlings and non-hatched eggs are usually dead, suggesting that the eggs and hatchlings are very susceptible to desiccation or predation.

The populations of New Caledonian *Placostylus* species show a similar structure to those of the New Zealand taxa shown by Choat and Schiel (1980); Penniket (1981), and Stringer *et al.* (2004). In New Zealand, *Placostylus* occur primarily as small and widely isolated populations. These populations appear to be maintained by a pool of large and long lived adults (Choat and Schiel 1980) which produce many juveniles each with a low expectancy of reaching adult size. For *P. bollonsi*, Brook and Laurenson (1992) show that at least 60% of hatchlings fail to attain adulthood. This high juvenile mortality may be a natural feature of the

population dynamics of *Placostylus* and one that is not conducive to rapid population recovery, but it is possible that it is the result of a novel additional source of mortality that may have driven the populations into decline. Brook and Laurenson (1992) suggest that recruitment to the adult population, which is always uncertain, depends on favourable conditions of climate and habitat. The long life of adults may provide some buffering against this uncertainty. Penniket (1981) suggests that a low proportion of empty adult shells relative to live snails would be the first indication that a population is recovering.

According to the criteria of Molloy *et al.* (2002), the New Zealand *P. hongii* is classified as ‘Range Restricted’, and *P. ambagiosus* is classified as either ‘Nationally Critical’ or ‘Nationally Endangered’, depending on the subspecies (Hitchmough *et al.* 2007). These rankings reflect range and population sizes and vulnerability to decline. In terms of density estimates, New Zealand and Lord Howe Island *Placostylus* are evidently much more abundant than seen in New Caledonian populations of *P. fibratus* and *P. porphyrostomus*. Mean densities of live adults and juveniles of *P. hongii* on the Poor Knights Islands was variously estimated at 0.78/m² (Stringer *et al.* 2004), 1.9/m² (Choat and Schiel 1980) and 8.1/m² (Penniket 1981). For *P. bollonsi*, Brook and Laurenson (1992) recorded densities of between 2–6/m² in local patches, but overall mean densities ranged from 0.15 to 0.35 /m². On Lord Howe Island, *P. bivaricosus* occurred at an average density of 0.24 live adults and 0.33 live juveniles per square metre, with localised densities of up to two live animals per square metre in patches of good microhabitat (Murphy and Nally 2004). These figures are around 5 to 10 times higher than densities found for either *P. fibratus* or *P. porphyrostomus* in New Caledonia.

2.2.8 Reasons for the decline of New Caledonian *Placostylus*

The reasons for the decline of New Caledonian *Placostylus* snails are now fairly clear. Habitat destruction or modification, human harvesting for consumption, and predation by introduced species are all contributing factors.

2.2.8.1 Habitat modification and destruction

Since the New Caledonian *Placostylus* are found only in native forests, their range and abundance are strongly influenced by the removal and degradation of this vegetation type. The vegetation of New Caledonia has been considerably modified

since human arrival ca. 3,500 years ago, with over 50% of the original vegetation cover lost through deforestation. Losses have been acute for humid forest with only 30% (3,900 km²) remaining (Jaffré *et al.* 1997). Nonetheless, it is the dry sclerophyllous forests that have been most severely deforested with the current distribution of this vegetation only a relic of its original extent: 4,500 km² of dry forest once occupied the western coast, whereas today barely 45 km² (1%) remains (Programme Forêt Sèche 2007). Forest clearance for agriculture, mining, urbanisation, and losses through bush fires are the main reasons for this serious decline in forest cover. Accentuating the problem is the heavy fragmentation of the remainder which now comprises 238 small and isolated patches ranging from 0.25 ha to 200 ha. In addition, these forests are heavily infested with invasive plants such as the autochthonous Gaïac (*Acacia spiroides* Labillardière 1825) and the allochthonous Lantana (*Lantana camara* Linnaeus 1753). This phenomenon has seriously jeopardised the regeneration and indigenous composition of the forest. Moreover, the forests are severely affected by ungulates such as the introduced rusa deer (*Cervus timorensis russa* Blainville, 1822), feral pigs (*Sus scrofa* Linnaeus, 1758), cattle (*Bos primigenius taurus* Bojanus, 1827) and to a lesser extent goats (*Capra aegagrus* Erxleben, 1777), which browse the understorey and leaf litter. The activity of these animals destroys or highly modifies the habitat of native taxa such as *Placostylus* by reducing litter mass and changing the microclimate at ground level (raising temperatures, decreasing humidity, and increasing exposure to light). Forest destruction and its modification are thus considered the main factors contributing to the decline in New Caledonian *Placostylus*. Some populations are already extinct, others on the verge of extinction. The risk of extinction is particularly acute for *P. porphyrostomus* which inhabits the sclerophyllous forests. Among rainforest inhabitants, *P. caledonicus* is known only from one extant population, and *P. eddystonensis* is thought to be already extinct.

2.2.8.2 Over-collection for human consumption

Placostylus are an important part of the Melanesian culture and tradition on the Isle of Pines, and are used for various purposes including food and jewellery as well as for their medicinal properties (e.g. a snail stock is drunk by pregnant women to improve lactation). It is also a traditional food: today in some families, boiled snails are still eaten two or three times a week and represent an important source of protein. *Placostylus fibratus* and the sympatric species *P. porphyrostomus* are both collected

and consumed by Kuniés (Pöllabauer 1994; Lepoutre 1999; Brescia 2004, 2005). *Placostylus fibratus*, the largest and most widely distributed of the New Caledonia *Placostylus*, is the species most favoured for human consumption. However, only those populations on the Isle of Pines are sufficiently abundant to sustain harvesting, primarily by the Kunié people. The smaller *P. porphyrostomus* is only consumed by locals and is not marketed commercially.

Placostylus fibratus progressed from a gastronomic speciality in the Isle of Pines to a delicacy in Nouméa (the New Caledonian capital) around 1950 (Pisier 1985). The export to Nouméan restaurants and supermarkets continued until 2000 when the sale of *P. fibratus* on the mainland was prohibited by the authority in charge of the environment in a bid to reduce the number harvested. Snail-harvesting for consumption from the natural populations on the Isle of Pines progressively increased and reached 48 tonnes (about 700,000 snails) in 1993 (Pöllabauer 1995) and the export of the snails became an important economic activity for the island inhabitants, assessed at US \$180,000 annually. About 70 Kunié families representing approximately 250 people were involved in harvesting the resource (Lepoutre 1999). Snails were collected mainly by local women. They were then bought from the collectors by two main preparers of the snails (ca. US\$ 0.30 per snail), and cooked like European snails ‘à la Bourguignonne’ (with butter, garlic and parsley). Only adult *Placostylus* were collected for consumption, that is to say, snails with a thick aperture lip (> 4 mm).

During the last decade, at the request of Kuniés worried about the growing scarcity of the resource, a variety of scientific studies have been undertaken to improve the knowledge of *Placostylus* and to develop a sustainable management regime (Pöllabauer 1995, 2002; Brescia 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005; Brescia et al. 1998). A survey on the Isle of Pines was conducted from 1995 to 2004 to estimate the status of the *Placostylus* resource in the wild. Each year, *Placostylus* were searched for in about 140 randomly located, 100 m² quadrats. New quadrats were established for each survey and searched only once. In 2004, the total population of *P. fibratus* (adults and juveniles) on Isle of Pines was estimated at 4.6 ± 0.6 million (Brescia 2004). Snails of marketable size represented nearly 60% of the population; the remainder were mainly subadults. Preliminary results show that the population remained quite stable between 1993 and 2004 (Brescia 2005). Thus, the different control measures adopted during the period, such as setting-up of a collection period

outside of which harvest was prohibited, and the prohibition of export out of Isle of Pines from 2001, appeared to have been effective at reducing the number of snails collected annually and thus stabilising the populations.

To assess the annual harvest of adult *Placostylus* from the Isle of Pines, regular surveys of Kunié families, restaurants, and the two main snail processors have been conducted regularly since 1993 (Pöllabauer 2002; Brescia 2004, 2005). The results suggest that since the 2001 prohibition of export, the number of *Placostylus* collected from the forests on the Isle of Pines has been only about half of that collected during the period 1995–2000 which Pöllabauer (2002) estimated as 200,000 to 250,000 snails harvested annually. Harvesting from the natural populations since 2003 is estimated to be around 120 000 adult *P. fibratus* per annum. In 2003, 60,200 snails were marketed in restaurants of Isle of Pines. The annual collection by Kuniés for their own use was about 50,000 snails, with *P. fibratus* accounting for about 99% of the harvest and *P. porphyrostomus* making up the remaining 1%.

Thirty to fifty years ago *P. porphyrostomus* were also harvested from sclerophyllous forests on the mainland, largely for consumption, but this has now largely ceased. However, recently (2002), during a two day search, more than 200 *P. porphyrostomus* were collected for food by local residents from a 270 ha patch of sclerophyllous forest (a classified priority area), where the total snail population is evaluated at about 60,000 (Brescia and Pöllabauer 2005). The collectors were unaware of the status of the species on the mainland. Every now and then, reports of collections of the giant form of *P. fibratus* from the south of the mainland, and of the dwarf form of *P. fibratus* on the Loyalty Islands (particularly from Maré) are made (F. Brescia pers. obs.). On these occasions, the snails appeared in the local markets.

2.2.8.3 Pig and rodent predation

Introduced mammals such as feral pigs and rodents appear to also contribute to the decline of New Caledonian *Placostylus* populations. As well as destroying native vegetation and disturbing the leaf litter, feral pigs are predators of *Placostylus* (Pöllabauer 1995; Brescia 2004, 2005; Brescia and Pöllabauer 2005). They eat both large juveniles and adults. On the Isle of Pines, Brescia (2001) observed that in areas where pigs are present, *Placostylus* abundance was only half that of areas without pigs. Pigs are locally abundant on the Isle of Pines but their effects are even more important

in sclerophyllous forests of the mainland since *Placostylus* populations there are restricted to small and isolated patches and therefore more vulnerable to this pressure.

In sclerophyllous forests, it has been found that rodents (Polynesian rats *Rattus exulans* (Peale, 1848), ship rats *R. rattus* (Linnaeus, 1758), and house mice *Mus musculus* (Linnaeus, 1758) also eat juvenile *Placostylus* up to 5 cm shell height (Brescia and Pöllabauer 2005). Rodent-damaged *Placostylus* shells are easily identified as rodents typically remove a broad spiral band of shell from one or more whorls starting from the aperture lip (Figure 2.2).



Figure 2.2: Rodent-damaged *Placostylus* shells are easily identified by the broad spiral band of shell removed from one or more whorls.

Pig-damaged shells are also usually easily recognised since they typically break the shells into several large pieces. In 2004, during a search of thirty two 10 m x 10 m quadrats in three patches of sclerophyllous forest, 17 adults of *P. porphyrostomus* and 12 large juveniles and sub-adults were found along with 130 empty shells that showed evidence of rodent predation (Brescia and Pöllabauer, 2005). Similarly, Brescia (2007) found that in a mark-recapture study in sclerophyllous forests, up to 81% of shells on the ground in 20 m x 20 m permanent quadrats had been eaten by rodents. On both the Isle of Pines and in the sclerophyllous forests, piles of up to 100 empty rodent-damaged shells are frequently found in rat caches. Rodent damaged *Placostylus* shells are often more abundant than similarly damaged shells of the invasive giant African snail *Achatina fulica* suggesting a possible preference for the native snails. Mice have

been recorded eating entire *Placostylus* egg clutches under semi-natural captive conditions on the Isle of Pines (Brescia 2004). Thus rodents appear to be potentially very harmful to *Placostylus* populations as they systematically eat eggs, hatchlings and juveniles compounding the already high natural mortality rates of hatchling and juvenile size classes. The combined effect may greatly reduce recruitment to adult size. In New Zealand, predation by introduced pigs, rodents, and birds has also been implicated in the decline of the *Placostylus* species there, along with habitat destruction and modification by farming and burning (Penniket 1981; Parish *et al.* 1995; Sherley *et al.* 1998).

2.2.8.4 Other threats

In 1972 the herbivorous giant African snail *Achatina fulica* (Achatinidae) was introduced to New Caledonia. Since then, it has become a pest in agricultural areas and a potential competitor of *Placostylus* in native forests. In response, as has occurred elsewhere in the Pacific, two carnivorous land snails, *Euglandina rosea* (Férussac, 1821) and *Gonaxis quadrilateris* Preston, 1910, were introduced in 1974 as biological control agents for African snails. Only *E. rosea* has established in New Caledonia but its distribution remains very localised (Maré Island and some northern areas of the mainland). Neither *E. rosea* nor *G. quadrilateris* are specialist predators of the African snail (Clarke *et al.* 1984; Griffiths *et al.* 1993), and in Hawaii their introduction was blamed for the extinction of several arboreal native snail species (Hadfield and Miller 1992). Gargominy *et al.* (1996) consider that these two species are likely to be significant threats to the native New Caledonian malacofauna. *E. rosea* may already have been responsible for the decline of some *Placostylus* populations in the far north of New Caledonia and Maré Island since where *E. rosea* has established the *Placostylus* populations have become locally extinct (pers. obs.).

Since the giant African snail and *Placostylus* share the same microhabitat, it is also possible that competition may also adversely affect *Placostylus* populations, but this hypothesis has not yet been directly tested.

Pöllabauer (1995) suggests that on the Isle of Pines, the presence of an indigenous carnivorous snail *Ouagapia inaequalis* (Pfeiffer, 1854) may further threaten *Placostylus* recruitment. She frequently observed up to 2–3 of these egg predators within *Placostylus* egg clutches, and noted that they have the potential to

destroy all the eggs in a clutch. Brescia (2001) recorded a predation rate on clutches of 56% (n=42) on the Isle of Pines. On average, 4.6 ± 2.7 *O. inaequalis* were present per clutch in this survey. The little fire ant, *Wasmannia auropunctata* (Roger, 1863), was recorded for the first time in New Caledonia in 1972 and has subsequently spread rapidly and invaded a wide array of habitats on the mainland, the Isle of Pines, and the Loyalty Islands. It is now found in both rainforest and sclerophyllous forest. It was shown that when the little fire ant is present, a disruption of the native litter ant fauna and herpetofauna occurs in both types of New Caledonian forest (Jourdan *et al.* 2001). Nevertheless, as far as *Placostylus* are concerned, observations in the field on the Isle of Pines and in sclerophyllous forest suggest that little fire ant may have a net positive impact by controlling ground beetle (Carabidae) populations which are known predators of landsnails, or by influencing the spatial distribution of rodents. As evidence, we have generally found juvenile *Placostylus* in higher abundance where these ants are also present, though it is possible that little fire ants and juvenile *Placostylus* have similar habitat preferences and this positive association is an incidental consequence.

2.3 Conservation

2.3.1 Legal aspects

In 1994, a law was passed by the South Province Assembly of New Caledonia (Délibération 50–94/APS) that regulated the collection and the transportation of *P. fibratus* on the Isle of Pines. It became illegal to collect snails from 1st May to 30th September (during the breeding season), and illegal to transport live snails out of the Isle of Pines at any time (only cooked snails could be sent to restaurants and supermarkets on the mainland).

In 2000, the Assembly revised the law (Délibération 26-2000/APS), adding an amendment that allowed the collection of *Placostylus* throughout the year on the Isle of Pines but the prohibition of export to the mainland became applicable to both live and cooked snails. Cooked snails from the Isle of Pines thus could only be eaten in restaurants and by locals on the island but not at all on the mainland. As noted previously, this reduced the number of adult *Placostylus* collected on the island two-fold (to around 100,000 snails per year). No restrictions currently exist on the collection of *Placostylus* on the New Caledonian mainland.

2.3.2 Captive breeding

In parallel with passing of laws that control the numbers of *Placostylus* harvested from the wild, the Institut Agronomique Néo-Calédonien (IAC) has been actively developing farming methods. Captive breeding of snails may help to allow the exploitation of the resource to continue (a topic of great concern for inhabitants of Isle of Pines) by supplementing or replacing the harvest from the wild, as well as facilitating the preservation of natural populations. Successful farming of snails may also enable the re-stocking of small populations of *Placostylus* in areas where they are now rare or extinct.

A successful farming method has now been developed for *P. fibratus* following many years of trials (Brescia, 1997, 1998, 1999, 2000, 2001; Brescia *et al.* 1998). The initial attempts were not encouraging and it appeared that these snails were going to be very difficult to maintain in captivity. Salas *et al.* (1997) recorded a 90% mortality rate of hatchling snails, a very slow growth rate of juveniles, a very high mortality rate (nearly 70 %), and almost no breeding in captive snails. However, studies of *Placostylus* ecology and behaviour in natural conditions and further studies in captivity under semi-natural and regulated conditions enabled us to significantly improve our understanding of the snail's needs. This led to refined handling methods through systematic testing of alternative farming methods.

Placostylus are now maintained in plastic boxes with an artificial substrate of coco fibre compost supplemented with calcium carbonate. Humidity is maintained by daily watering. A thick layer of leaves (papaya, banana) is used as a cover to maintain moisture, to reduce the light reaching the snails, and to limit the climbing behaviour of hatchlings. An artificial diet has been developed as a substitute to the natural diet of decaying forest leaves. Different artificial diets were tested and the growth and reproduction performance measured. Eventually, we decided to vary the diet to suit the different age classes of snails. Adult and juvenile snails are fed a dry mix of cereal flour (80% of dry weight) supplemented with calcium carbonate (20%). Hatchlings are fed a more energy-rich powder of cereal flour (50%) and calcium carbonate (20%) supplemented with milk powder (30%). A large number of feeding dishes and water-troughs are set out in different areas of the enclosures to improve access for these relatively sedentary snails.

To maximise the reproductive productivity, adult snails are collected from the forest during the breeding season and maintained in captivity under the conditions described above, with a stocking rate limit of 5 kg/m². At the start of these trials in 1995, only about 0.16 egg clutches per adult per year was obtained. Now, we achieve more than 10 times this (1.5 to 2.7 egg clutches per adult per year). About 72% of adult snails lay at least one clutch per year in captivity. Each day, egg clutches are collected from the enclosures and placed in a nursery on a substrate of humid coco-fibre/soil mix. Hatching under these conditions occurs after 10 to 45 days. Survival of the hatchlings to one month in the nursery now approaches 70% (in earlier farming attempts it was only 10%); and 68% of juveniles now survive to eight months. The best growth rates of juveniles are obtained when the stocking rates are maintained at a low level, around 1.5 to 2.0 kg/m². Adult size (and sexual maturity) in captivity is reached in two years under these conditions, compared with five years in the wild (Pöllabauer 1995).

In New Zealand, the techniques needed for successful captive breeding have not yet been developed (Parrish *et al.* 1995). However, researchers at Massey University have managed to keep a small number of *Placostylus* adults in captivity until they laid eggs which were then successfully raised to adulthood (Stringer and Grant 1992).

2.3.3 Utility for conservation

It is now possible to produce New Caledonian *P. fibratus* and *P. porphyrostomus* en masse in captivity. This farming method has also been shown to work for several other New Caledonian *Placostylus* species (Brescia and Pöllabauer 2004, 2005). Growth rates have doubled since the earlier rearing trials but the relatively high cost of this method of production needs to be reduced in order for commercial farming to be viable. The next step in achieving this economy may be to develop extensive or semi-extensive methods with enclosures set directly in the forest. We are currently trialling the transfer of the farming method to local Kuniés and adapting it to suit the sociological and economic realities of the Isle of Pines.

The supplementation of threatened New Caledonian *Placostylus* populations using captive rearing is now feasible and this may provide some security against extinction. Accordingly, snails from some of the most threatened populations of the

sclerophyllous forests are now being maintained in captivity to complement the ongoing management of natural populations. Conservation trials on re-introduction, supplementation and translocation are now conceivable using animals from captive breeding programmes. However, there is a need to demonstrate the subsequent survival of released snails in the wild. Equally important, is the development of a strategy and operational plan that addresses and maintains the genetic integrity of wild populations. Caution must be exercised before snails are released into the wild to make sure that the existing genotypes are not swamped with new introduction of potentially unsuited genotypes sourced from elsewhere.

2.3.4 Research needs and conservation recommendations

Since 1994, three New Caledonian *Placostylus* species -*P. eddystonensis*, *P. fibratus* and *P. porphyrostomus*- have been registered as Vulnerable on the Red List of IUCN (IUCN 2006) but a revision now seems warranted. *Placostylus bondeensis* and *P. scarabus* have never been evaluated and thus are not listed. Taking into account the small geographic range of these species (less than 100 km², in some cases restricted to a single locality), the population declines evident due to loss of native forests (99% for dry forest and more than 70 % for humid forest), and the severe fragmentation of many of these populations, *P. caledonicus*, *P. bondeensis*, *P. scarabus* and *P. eddystonensis* should be revised to Critically Endangered. The status of *P. fibratus* should also be changed to Endangered, given the estimated population decline due to the habitat degradation and the levels of exploitation and other factors implicated in the population decline.

No recovery plan currently exists for any New Caledonian *Placostylus*. To develop such a plan, further research on the predation, population dynamics and genetic differentiation between populations and species is a priority. The management of *Placostylus* in sclerophyllous forests to prevent further extinction of the most distinctive races or morphs is urgently needed. The conservation of existing colonies in the wild will require fencing to protect the snails from pigs and the habitat from browsing by introduced rusa deer. Some re-vegetation and restoration of dry forests to enhance the habitat for snails will also be helpful. The maintenance and amplification of the most threatened races in captivity must also be pursued and investigations into the possibility of translocations and population supplementation should continue. The

monitoring of population trends of selected populations will then be needed to assess the success of these different management strategies.

There is a need for further research to expand our knowledge on the status of extant populations, and enable the identification of suitable habitat for the establishment of new populations to enhance protection of critical areas. Rodent control programmes at priority key locations should assist the persistence and recruitment rates of remnant snail populations. Research into competition for food and habitat with the introduced giant African snail would also be useful, especially in areas where rodents are being controlled.

Further scientific collaboration between New Zealand and New Caledonia will be of great value for the conservation of the genus in both countries and on neighbouring islands. On the Isle of Pines, the monitoring of natural population stocks of *P. fibratus* over the whole island should be continued. The total annual harvest of adult snails for local consumption by Kuniés and for the market should continue to be measured and depending on the results, further regulation may be necessary. The ecological studies initiated by Brescia and Pöllabauer (Brescia 2004, 2005; Brescia and Pöllabauer 2004, 2005) on population dynamics through the recording of recruitment, fecundity, longevity and mortality and the loss of snails from rodent and pig predation will enhance our understanding of population trajectories. The ultimate plan for the conservation of *Placostylus* on the Isle of Pines will depend on the integration of all these data in a Population Viability Analysis (PVA), allowing predictions to be made of whether the population will remain viable under various harvesting scenarios. This is a high priority for the agencies in charge of the environment in their quest to develop regulatory measures that will achieve a sustainable use of the resource and to protect the species and the economic potential for Kuniés.

Environmental education aimed at Kuniés on the Isle of Pines, and land owners on the mainland where patches of dry forest remain should continue, advocating the necessity of protecting *Placostylus* snails as part of a natural heritage and/ or an economic resource. Demonstrating the cultural meaning and economic importance of *Placostylus* to local communities would probably be more successful if the Kuniés were directly involved in recovery planning and actions. This kind of community-led

action, if successful, could provide an exemplary case and stimulate further recovery efforts for other threatened New Caledonian invertebrates.

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**STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS**

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

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Name of Candidate: Fabrice Brescia

Name/Title of Principal Supervisor: Assoc. Prof. Murray Potter

Name of Published Paper: Brescia F. M., Pöllabauer C. M., Potter M. A. & Robertson A. W. (2008)
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CHAPTER 3

THE INFLUENCE OF HUMAN HARVEST OF THE ENDEMIC NEW CALEDONIA SNAILS *PLACOSTYLUS FIBRATUS* (MOLLUSCA: GASTROPODA: BULIMULIDAE) ON POPULATION TRENDS



Preparation of snails and cooked Placostylus snails marketed in the restaurants of Isle of Pines

Abstract

Placostylus fibratus snails have been harvested by the local Kunié people as a traditional food source for many years, but harvest intensity has increased considerably since the 1950s when snails started to be collected for commercial purposes and marketed in Nouméa. The intensity of human harvest was investigated by surveying restaurants and inhabitants on the Isle of Pines: in 2003, 52,986 snails were collected for marketing from the wild, 56,897 snails in 2005 and in 2006 it was 66,227 snails. Also, $42,624 \pm 26,208$ snails are estimated to be eaten annually by Kuniés. Thus the actual annual harvest represents approximately 6% of the estimated wild adult stock (ca. 2,471,857 snails for the period 2001-2008). The sustainability of this harvest, in the actual context of significant decline of populations, needs seriously to be regulated. Repeated harvests for decades on certain districts of Isle of Pines may have led to local population extinction or population reduction to unsustainably low densities.

We explore the population consequences of the sustained commercial and domestic harvesting of an endemic New Caledonian land snail *Placostylus fibratus* on the Isle of Pines. We analysed data from 15 years of snail surveys obtained from 1,056 random 100-m² quadrats within local forests in which 8,758 snails were found and measured during the period. Population trends showed a significant decline in both adult ($r^2 = 0.50$; $F = 11.8$; $p < 0.001$) and juvenile ($r^2 = 0.25$; $F = 4.1$; $p < 0.05$) snail abundance from 1993 to 2008. The number of adults found in 1993 was high compared to following years (equivalent to a total population of 4,810,000 snails) and suggests a relatively steep decline since then. However, if the counts from 1993 and 1994 are excluded a less alarmist scenario is suggested, with no evidence of adult population decline since 1995 ($r^2 = 0.11$; $F = 2.1$; $p > 0.05$). However, even with these exclusions, the juvenile population continued to decline markedly over the same period ($r^2 = 0.3$; $F = 5.8$; $p < 0.05$), raising concerns about the long term viability of this population.

Being of commercial value, it is of great concern to the local authorities and to Kuniés that the snails of Isle of Pines are subject to rational and sustainable exploitation. To this end, we recommended that management strategies are required to monitor population trends in the future, to establish a more rigorous collection plan including “no-take areas”, to facilitate development and coordination of the local snail

industry and to develop captive breeding capability. The development of a sustainable harvest will require on-going monitoring and research.

Impact de l'exploitation des escargots endémiques de la Nouvelle-Calédonie *Placostylus fibratus* (Mollusques; Gastropodes: Bulimulidae) sur l'évolution des populations

Résumé

Les conséquences de la collecte répétée des escargots terrestres de la Nouvelle-Calédonie, *Placostylus fibratus*, sur l'île des Pins à des fins commerciales et pour la consommation locale des ménages ont été étudiées. Les données recueillies au cours des 15 dernières années (1993 à 2008), obtenues à partir de la réalisation de 1056 quadrats aléatoires de 100m² dans les forêts de l'île des Pins et de 8756 escargots collectés et mesurés durant la période, ont été analysées. La tendance évolutive des populations est à un déclin significatif de l'abondance des escargots adultes ($r^2= 0.50$; $F=11.8$; $p<0.001$) et juvéniles ($r^2= 0.25$; $F=4.1$; $p<0.05$) entre 1993 et 2008. En 1993, l'estimation du nombre d'escargots adultes était importante (4 810 000 escargots) et la tendance suggère ainsi un déclin sérieux depuis cette période. Cependant, si les estimations de 1993 et 1994 sont écartées des analyses afin de se positionner dans un scénario moins alarmiste, la diminution de la population adulte depuis 1995 n'est pas avérée ($r^2= 0.11$; $F=2.1$; $p>0.05$) alors que le stock d'escargots juvéniles a fortement décliné au cours de la même période ($r^2=0.3$; $F=5.8$; $p<0.05$), ce qui constitue une menace sérieuse pour la viabilité à long terme de la population. Les escargots de l'île des Pins sont collectés et consommés traditionnellement par les habitants de l'île (Kuniés) depuis de nombreuses années, mais la collecte s'est intensifiée de manière considérable depuis les années 50 lorsque les bulimes ont été collectés à des fins commerciales pour être vendus à Nouméa. Le nombre d'escargots collectés a été estimé par enquêtes auprès des restaurateurs, des deux principales préparatrices et des habitants de l'île des Pins : en 2003, 52 986 escargots ont été collectés en forêt pour être vendus, 56 897 en 2005 et 66 227 en 2006. Aussi, le nombre d'escargots collectés pour la consommation des ménages Kuniés a été estimé à $42,624 \pm 26,208$ escargots à l'année. En conséquence, le nombre de bulimes prélevés annuellement représente 6% de la population d'escargots adultes estimée à 2 471 857 individus pour la période 2001-2008. Afin d'être maintenue, l'activité de collecte dans ce contexte avéré de déclin des populations nécessite d'être encadrée. La collecte de manière répétée depuis de nombreuses années dans certaines tribus de l'île des Pins pourrait conduire à l'extinction localisée de la population d'escargots ou à diminuer les effectifs à un

niveau tel qu'ils deviendraient non compatibles avec la poursuite de la collecte. La valeur commerciale de l'escargot de l'Ile des Pins, fait qu'il est dans l'intérêt des autorités en charge de l'environnement et des Kuniés eux-mêmes que soient prises des mesures afin de rationaliser et rendre durable la collecte. Pour ce faire, des recommandations pour la gestion de l'espèce ont été formulées: poursuite du suivi de l'évolution des stocks, établissement d'un plan de prélèvement plus rigoureux instaurant éventuellement des zones de non-collecte, développement et structuration de la filière escargot sur l'Ile des Pins et développement de l'élevage. Le maintien de l'activité de collecte nécessite la poursuite des actions de recherche et de suivi.

3.1 Introduction

The genus *Placostylus* Beck, 1837 (Gastropoda, Heterobranchia, Pulmonata, Bulimulidae), is found only in the Western Pacific, extending northwards from the tip of the North Island of New Zealand to Lord Howe Island, Fiji, the Solomon Islands, Vanuatu and New Caledonia including the Loyalty Islands (Hedley 1892; Cockerell 1929, Solem 1959).

The six species found in New Caledonia (*Placostylus fibratus*, *P. porphyrostomus*, *P. caledonicus*, *P. eddystonenis*, *P. bondeensis* and *P. scarabus* (Neubert & Bouchet 2009)) are all endemic and are either threatened or endangered (Brescia *et al.* 2008). These snails appear to be relatively specific in their habitat requirements. *Placostylus* seems to be primarily associated with calcium-rich soil, and inhabits exclusively native dry or evergreen forests where they are generally found under leaf litter (Brescia *et al.* 2008).

Placostylus fibratus and the sympatric species *P. porphyrostomus* are both collected and consumed by Kuniés (the local inhabitants of Isle of Pines) (Pöllabauer 1994; Lepoutre 1999; Brescia 2004, 2005). *Placostylus fibratus*, the largest (60-100 g when adult) and most widely distributed of the New Caledonia *Placostylus*, is the species most favoured for human consumption. However, only those populations on the Isle of Pines are sufficiently abundant to sustain harvesting, primarily by the Kunié people. *Placostylus* are an important part of the Melanesian culture and tradition on the Isle of Pines, and are used for various purposes including food and jewellery as well as for their medicinal properties (e.g. pregnant women drink a snail stock to improve lactation). It is also a traditional food and an important source of protein. The smaller *P. porphyrostomus* is only consumed by locals and is not marketed commercially. *Placostylus fibratus* progressed from a gastronomic speciality on the Isle of Pines to a delicacy in Nouméa (the New Caledonian capital) around 1950 (Pisier 1971). The export of these snails to Nouméan restaurants and supermarkets continued until 2000 when the sale of *P. fibratus* on the mainland was prohibited by the authority in charge of the environment in a bid to reduce the number harvested. From 1950, snail-harvesting for consumption from the natural populations on the Isle of Pines had increased progressively, reaching 48 tonnes (about 700,000 snails) in 1993 (Pöllabauer 1995), and the export of the snails became an important economic activity for the island inhabitants, assessed at US \$180,000 annually. In 1994, a law was passed by the

South Province Assembly of New Caledonia (Délibération 50–94/APS) that regulated the collection and the transportation of *P. fibratus* on the Isle of Pines. It became illegal both to collect snails between 1 May and 30 September (during the breeding season), and to remove live snails from the Isle of Pines at any time (only cooked snails could be sent to restaurants and supermarkets on the mainland). As a result of these legislative changes, the number of snails collected annually dropped from 700,000 before 1993 to around 300,000 from 1994 to 2001, and then to 120,000 since 2001.

During the height of the harvesting era, around 70 Kunié families representing approximately 250 people were involved in harvesting the resource (Lepoutre 1999). Snails were collected mainly by local women. They were bought from the collectors by two main preparers of the snails (ca. US\$ 0.30 per snail), and cooked like European snails ‘à la Bourguignonne’ (with butter, garlic and parsley). Only adult *Placostylus* were collected for consumption; i.e. snails with a thick aperture lip (> 4 mm). Over the last decade, at the request of Kuniés worried about the growing scarcity of the resource, a variety of scientific studies have been undertaken to improve knowledge of *Placostylus* with the aim of developing a sustainable management regime (Pöllabauer 1995, 2002; Brescia 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005; Brescia *et al.* 1998). In 2000, the South Province Assembly revised the law (Délibération 26-2000/APS), adding an amendment that allowed the collection of *Placostylus* throughout the year on the Isle of Pines but the prohibition of export to the mainland was expanded to include both live and cooked snails. Cooked snails from the Isle of Pines thus could only be eaten in restaurants and by locals on the island but not at all on the mainland.

We explore here the consequences of this human harvest of adult *Placostylus* on snail populations on the Isle of Pines and discuss management options for sustainable exploitation of the resource. The aims of the study were i) to analyse population trends through time from 1993 to 2008 to assess the status of wild populations of *Placostylus* on Isle of Pines, ii) to increase knowledge of human harvest practices and the quantities of snails collected, and iii) to establish recommendations for better management of the resource.

3.2 Methods

3.2.1 Study area

The study was conducted in New Caledonia which has three major seasons: a hot wet season (mid November-mid May; mid April-mid May is a transition period); a cool dry season (mid May-mid September); and a hot dry season (mid September-mid November) (ORSTOM 1981). Snails were surveyed over the whole of the Isle of Pines (152 km²), an island 50 km south of the New Caledonian mainland. The local Kuniés are organized in eight tribes that compose the eight districts of the island.

The centre of the island is an arid iron-rich plateau surrounded by a ring of uplifted coral (Figure 3.1). Although the vegetation of much of the island has been disrupted by plantations and clearings, a large belt of native rain forest remains on the coral soils (Morat *et al.* 1984). The island as a whole receives on average 1200-1300 mm of rain per year. The west coast, which is slightly drier, is characterized by a closed-canopy forest dominated by *Intsia bijuga* Kuntze (Fabaceae). The wetter east coastal forests are similar in species composition but are more extensive. The column pines *Araucaria columnaris* (Forster) Hooker that give the island its name, are distributed patchily throughout the island, and coconut palms (*Cocos nucifera* Linnaeus) are typical of most beachfront areas.

3.2.2 Survey of snail stock and sampling design

3.2.2.1 1993 to 2004

A survey on the Isle of Pines was initiated in 1993 to estimate the status of the *Placostylus* resource on the island. The survey consisted of a series of five systematically placed 10 x 10 m quadrats spaced 150 m apart arranged along a randomly chosen azimuth and a random starting position within each of the eight tribal districts.

The original plan was to survey these five quadrats in each district four times a year, but financial constraints dictated that the number of quadrats and seasons sampled varied from year-to-year. In addition, new non-permanent quadrats, randomly distributed across the whole of the Isle of Pines, were established for each survey and searched only once (Table 3.2). Also, the snails in one district (Comwagna) are small and are not marketed, so this district was surveyed less frequently. No quadrats were searched at all in 1995 and 2005.

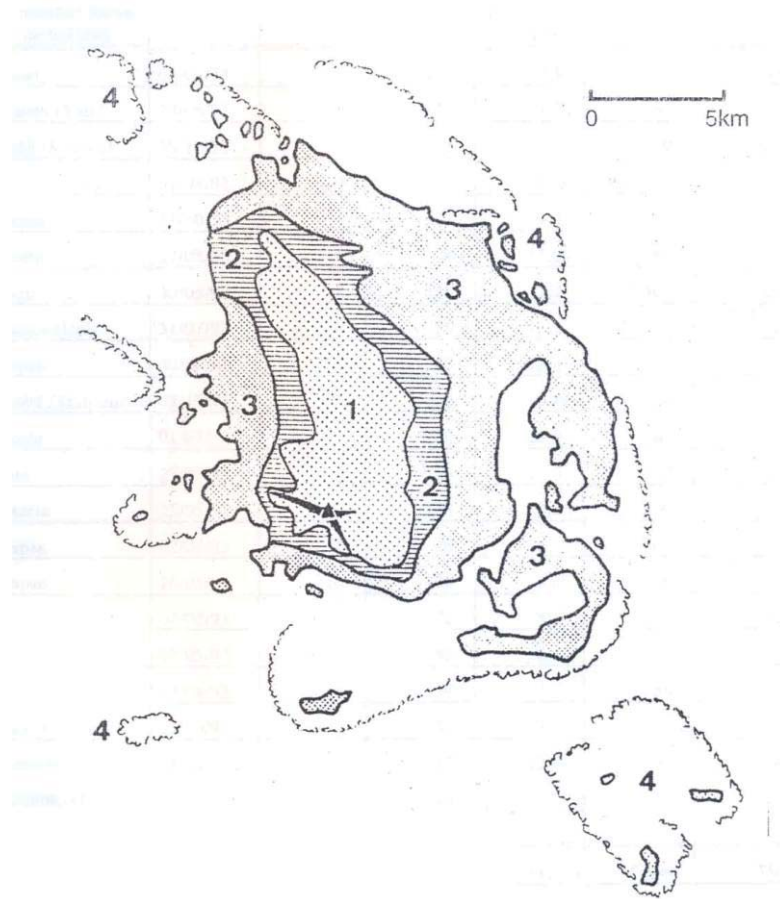


Figure 3.1: Map of the Isle of Pines (from Pisier 1971). 1: the central ferrallitic plateau; 2: edges of the plateau with culture areas; 3: native forest on coral soil; 4: coasts, islets and reef.

3.2.2.2 2006 to 2008

To reduce sampling effort further, a different sampling strategy was imposed from 2006 to 2008. Surveys were conducted every three months (i.e. four times a year) on a rotational basis across five districts in the following manner: session 1: survey districts 1, 2, 3, 4, 5; session 2: survey districts 6, 7, 1, 2, 3; session 3: survey districts 3, 4, 5, 6, 7, and so forth.

3.2.2.3 Information collected during snail surveys

In each quadrat, snails were searched for on the ground by at least three people for about one hour. The number of live snails found per quadrat was noted and, for each snail, weight was measured with a portable HAUS balance (± 2 g) and height and thickness of the lip aperture of the shell were measured to 0.01 mm with a digital calliper. These measurements were used to classify snails into adult, juvenile, or

newborn. Pöllabauer (1995) considered that adult *P. fibratus* are those characterized by a shell with a thickened aperture lip (more than 4 mm); however, our observations in captivity indicated that snails with an apertural lip of 3.5 mm were sexually mature and capable of laying eggs. Thus, snails were classified as adults when the aperture lip was ≥ 3.5 mm, as juveniles when the lip thickness was < 3.5 mm but the snail was > 10 mm long, and newborns when the aperture lip thickness was equal to 0 and the snail was ≤ 10 mm.

3.2.2.4 Social survey: number of snails collected on Isle of Pines for consumption

Regular surveys of Kunié families, restaurants, and the two main snail processors were conducted to assess the annual harvest of wild adult *Placostylus* from the forests of the Isle of Pines for human consumption.

3.2.2.5 Survey of the number of snails collected for daily consumption by Kuniés

About 1100 Kuniés live on Isle of Pines representing 261 households (Table 3.1 from ITSEE, 1998). During four chosen months between December 2003 and May 2004, ten different families were randomly selected each month and asked to keep in a bag the shells of snails they consumed during that month. At the end of the month, we counted the shells collected of each species to calculate household daily indigenous consumption.

3.2.2.6 Survey of the numbers of snails collected for commercial marketing

The two main preparers of snails for the restaurants on Isle of Pines buy snails from collectors. We supplied the preparers with a notebook calendar and asked them to enter monthly records of the number of snails purchased from collectors, the name of the collector, and the district where snails were collected. This gave us a very accurate assessment of the number of snails collected per year for consumption in restaurants on the Isle of Pines (the marketed snails). In 2003, when this survey was initiated, we also surveyed all restaurants on the island to validate the quantities of snails sold to restaurants as reported by the preparers of the snails.

Table 3.1: Distribution of Kunie families by district on the Isle of Pines (ITSEE, 1998).

Districts	Number of resident Kuniés	% of the island's population	Number of households	% of island's households
Comwagna	229	21	57	22
Gadgi	96	9	24	9
Kéré	92	9	23	9
Ouatchia	13	1	8	3
Touété	131	12	37	14
Vao	435	40	89	34
Wapan	37	3	9	3
Youati	43	4	14	5
Total	1076	100	261	100

3.3 Results

3.3.1 Snail population trends

From 1993 to 2008, a total of 1,056 random 100-m² quadrats were surveyed and 8,758 snails were found and measured (Table 3.2). For each year, the mean number of snails within each of three age-classes (adults, juveniles and newborns) per 100 m² was calculated (Table 3.3). Due to their arboreal behaviour, very few newborns were found during quadrat searches. We only started to detect young snails on the ground when their shell reached around 10 mm. Extrapolating these counts to the 6,000 ha of primary forest on the Isle of Pines using the method of Pöllabauer (1993 to 2002) allowed an estimate of the total number of snails of each age-class on the whole island (Figure 3.2).

Regression analyses of the change in the estimated stock of both adult and juvenile *P. fibratus* on Isle of Pines from 1993 to 2008 are shown in Figure 3.3. For both stages, the linear regression indicated a significant decline ($r^2 = 0.50$; $F = 11.8$; $p < 0.001$ for adults and $r^2 = 0.25$; $F = 4.1$; $p < 0.05$ for juveniles) during the 15-year survey.

Table 3.2: Annual number of random 100 m² quadrats surveyed from 1993 to 2008, and annual number of *Placostylus fibratus* snails of each stage (newborns, juveniles and adults) recorded in the seven districts of Isle of Pines (Comwagna excluded).

	1993	1994	1996	1997	1998	1999	2000	2001	2002	2003	2004	2006	2007	2008
No. quadrats	119	76	47	70	139	70	71	94	35	70	70	70	80	45
No. newborns	3	1	2	0	10	4	1	3	0	5	5	0	0	0
No. juveniles	395	324	192	253	418	314	370	390	203	196	239	137	187	61
No. adults	954	499	251	398	445	308	273	365	146	294	333	288	329	162

Table 3.3: Mean number (and SD) of adult and juvenile *Placostylus fibratus* snails per 100 m² and per year from 1993 to 2008 on Isle of Pines.

Year	mean juveniles per 100 m ² (SD)	mean adults per 100 m ² (SD)	mean total snails per 100 m ² (SD)
1993	3.5 (2.3)	8.1 (1.8)	11.6 (3.5)
1994	4.3 (2.1)	6.6 (2.0)	10.8 (3.2)
1996	5.9 (10.9)	5.6 (1.9)	11.6 (13.2)
1997	4.4 (9.9)	5.9 (3.2)	10.3 (12.7)
1998	3.1 (3.8)	3.3 (2.6)	6.5 (6.2)
1999	4.5 (3.0)	4.4 (2.7)	8.9 (3.4)
2000	5.2 (3.3)	3.8 (1.3)	9.1 (3.9)
2001	4.5 (3.7)	4.6 (5.4)	9.2 (8.1)
2002	6.9 (6.1)	4.4 (1.6)	11.3 (7.3)
2003	2.8 (1.2)	4.2 (2.2)	7.1 (2.7)
2004	3.6 (2.3)	5.4 (5.6)	9.0 (7.2)
2006	1.8 (1.9)	3.8 (1.9)	5.7 (3.0)
2007	3.1 (2.3)	4.1 (2.2)	7.1 (3.5)
2008	2.2 (3.1)	3.7 (2.2)	5.9 (4.0)

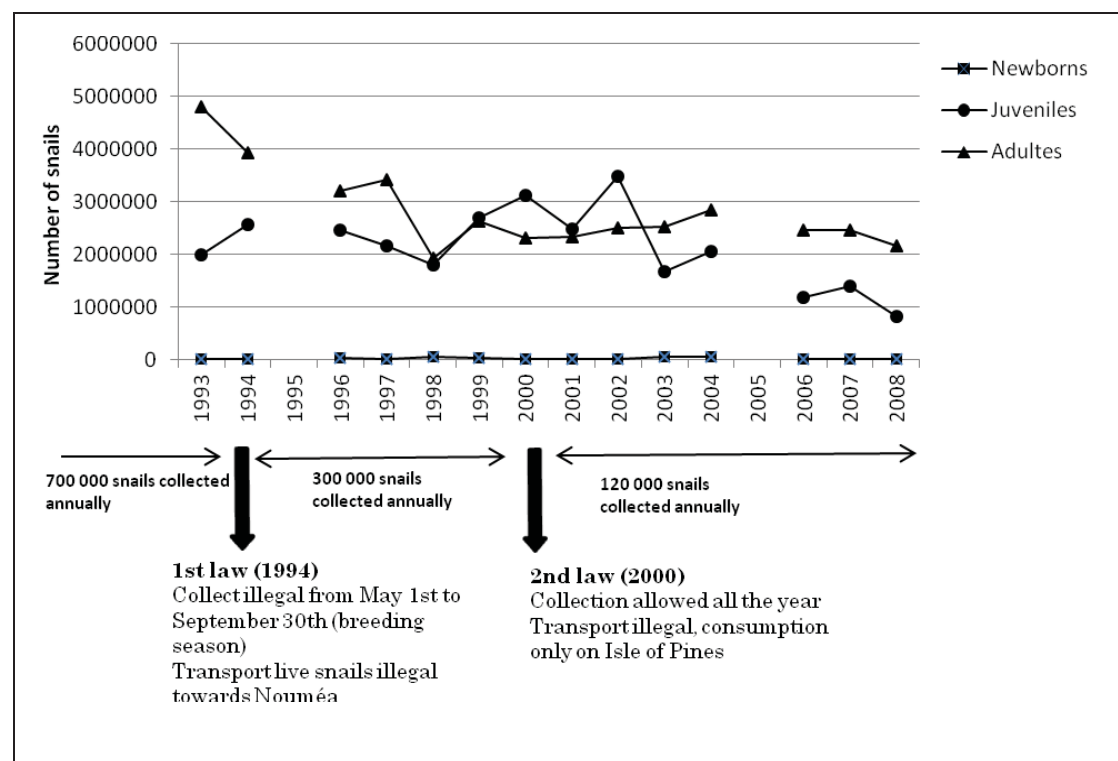
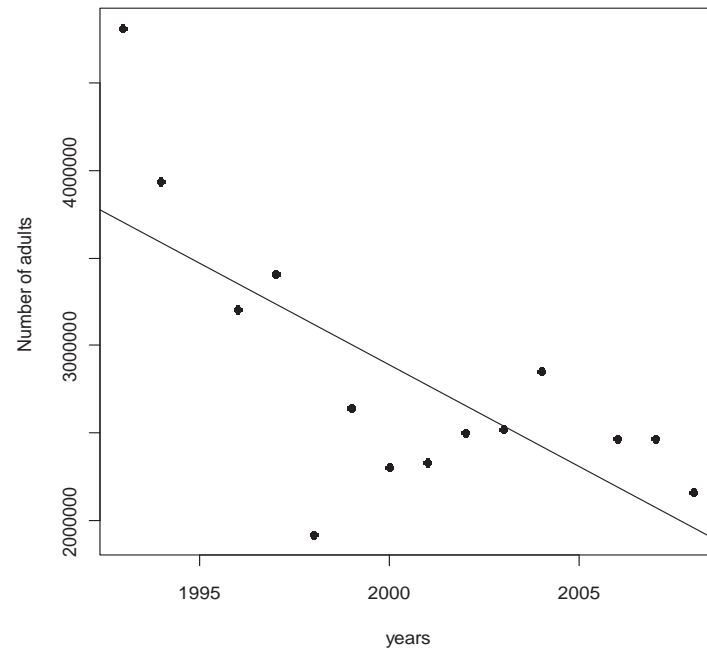
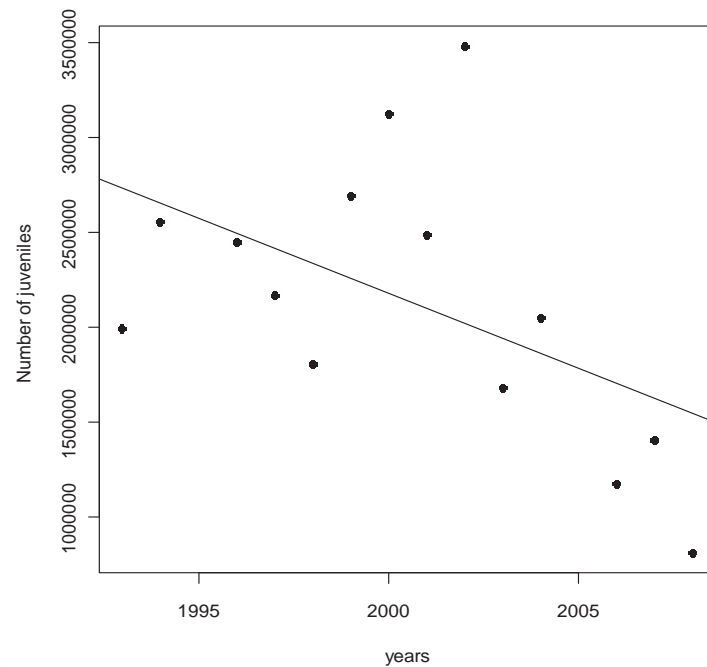


Figure 3.2: *Placostylus fibratus* population changes through time on Isle of Pines from 1993 to 2008.



A



B

Figure 3.3: Changes in the adult (a) and juvenile (b) *Placostylus fibratus* population on Isle of Pines from 1993 to 2008. The simple linear regression is given by the line.

Adults ($Y = 236150115 - 116630 X$) ($R^2 = 0.50$; $F = 11.8$; $p < 0.005$)

Juveniles ($Y = 160554708 - 79188 X$) ($R^2 = 0.25$; $F = 4.1$; $p < 0.05$)

The number of adults found in 1993 was high (equivalent to a total population of 4,810,000 snails) and suggests a relatively steep decline since then. However, if the counts from 1993 and 1994 are excluded a less alarmist scenario is suggested (Figure 3.4), with no evidence of adult population decline since 1995 ($r^2 = 0.11$; $F = 2.1$; $p > 0.05$). However, even with these exclusions, the juvenile population continued to decline significantly over the same period ($r^2 = 0.3$; $F = 5.8$; $p < 0.05$).

Given the changes in harvest regulations during the 15-year survey period and the resulting drop in snail collection, analyses were undertaken to consider two periods separately. Linear regressions on the snail stock between 1996 and 2000 indicated that neither the adults nor the juveniles declined during this period (Figure 3.5A and 3.5B), while between 2001 and 2008, the number of juveniles declined significantly (Figure 3.6B) while the number of adults remained stable (Figure 3.6A). From 1993 to 2008, the juvenile and adult stock changed differently among the districts (Table 3.4), with a significant decline in adult populations occurring in Touete, Ouatchia and Youaty, but no significant change in the remaining districts. Juveniles declined in Wapan district for the same period while their numbers remained stable in other districts.

Table 3.4: Summary of linear regressions on the juvenile and adult *Placostylus fibratus* stock changes by district from 1993 to 2008.

Districts	JUVENILES			ADULTS		
	R^2	F	P	R^2	F	P
Gadgi	0.3	1.263	>0.05	0.07	0.96	>0.05
Kéré	0.002	0.018	>0.05	0.10	1.36	>0.05
Touété	0.15	2.21	>0.05	0.63	20.19	$=0.01^*$
Vao	0.001	0.15	>0.05	0.18	2.55	>0.05
Ouatchia	0.31	5.56	<0.05	0.36	6.59	$<0.05^*$
Wapan	0.61	18.99	$<0.01^*$	0.05	0.61	>0.05
Youaty	0.37	7.20	<0.05	0.50	11.85	$<0.01^*$

*significant at $P < 0.05$

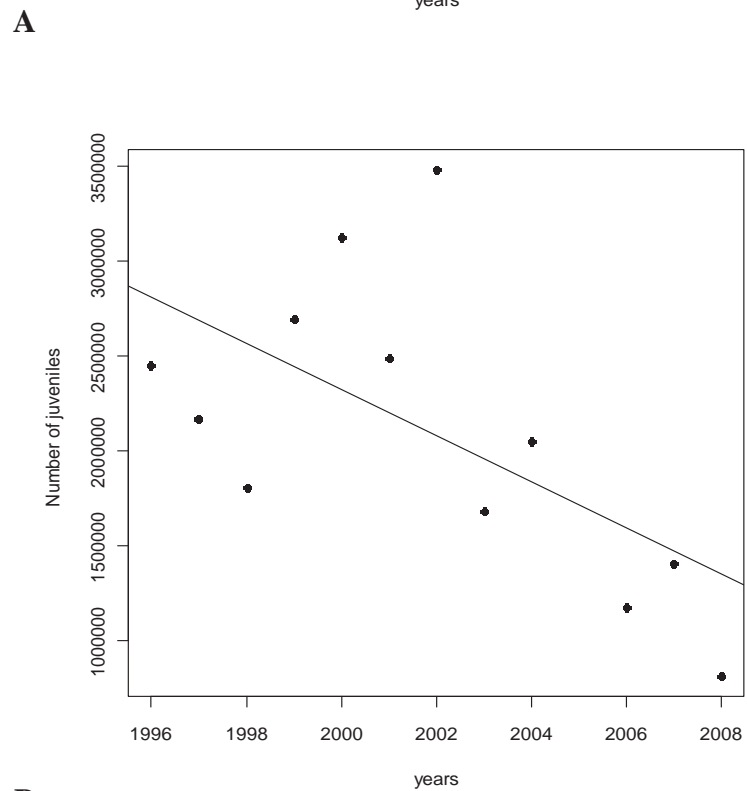
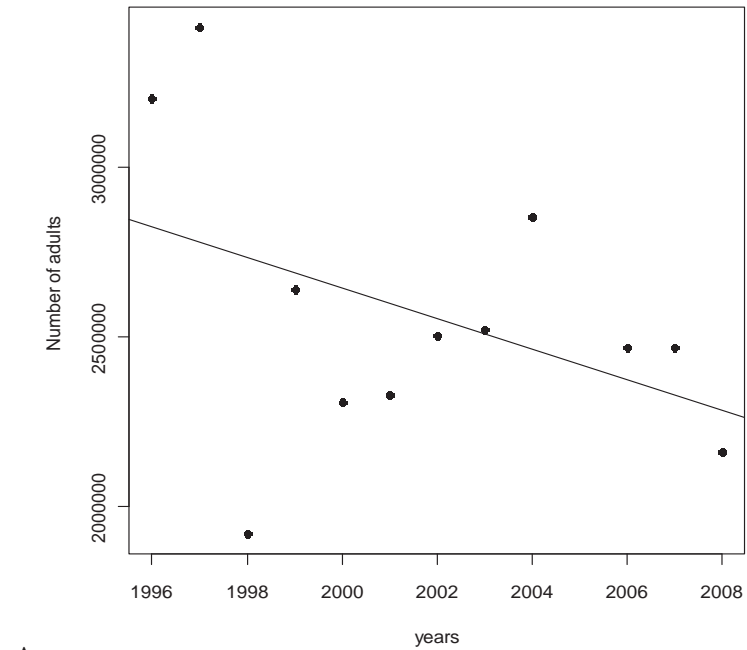
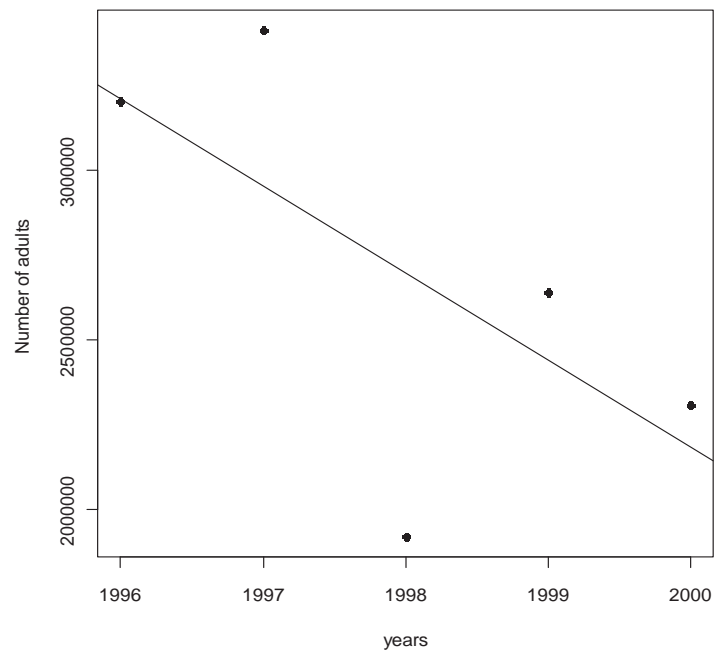


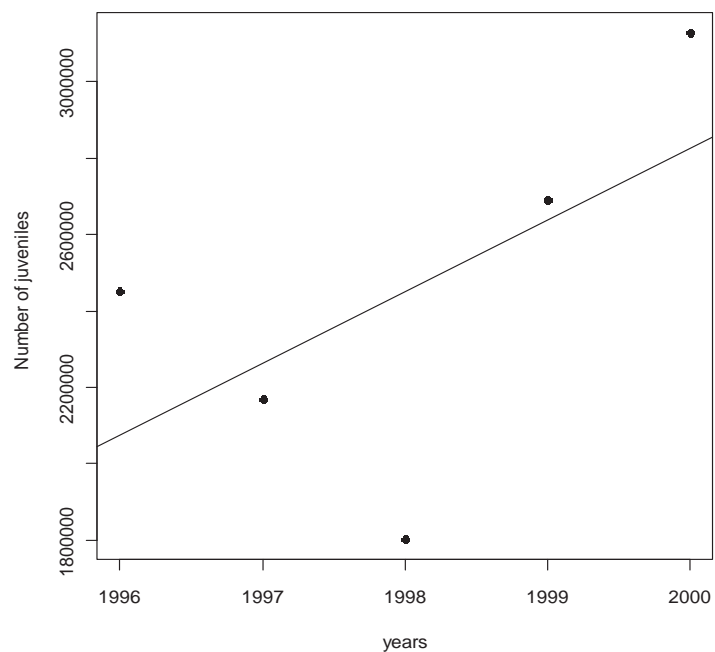
Figure 3.4: Changes in adult (a) and juvenile (b) *Placostylus fibratus* population on Isle of Pines from 1996 to 2008. The simple linear regression is given by the lines.

Adults ($Y = 92432149 - 44894 X$) ($R^2 = 0.1$; $F = 2.1$; $p > 0.05$)

Juveniles ($Y = 244811799 - 121244 X$) ($R^2 = 0.3$; $F = 5.8$; $p < 0.05$)



A



B

Figure 3.5: Changes in adult (a) and juvenile (b) *Placostylus fibratus* population on Isle of Pines from 1996 to 2000. The simple linear regression is given by the line.

Adults ($Y = 515354488 - 256586 X$) ($R^2 = 0.4$; $F = 2.2$; $p > 0.05$)

Juveniles ($Y = -372026844 + 187425 X$) ($R^2 = 0.3$; $F = 1.6$; $p > 0.05$)

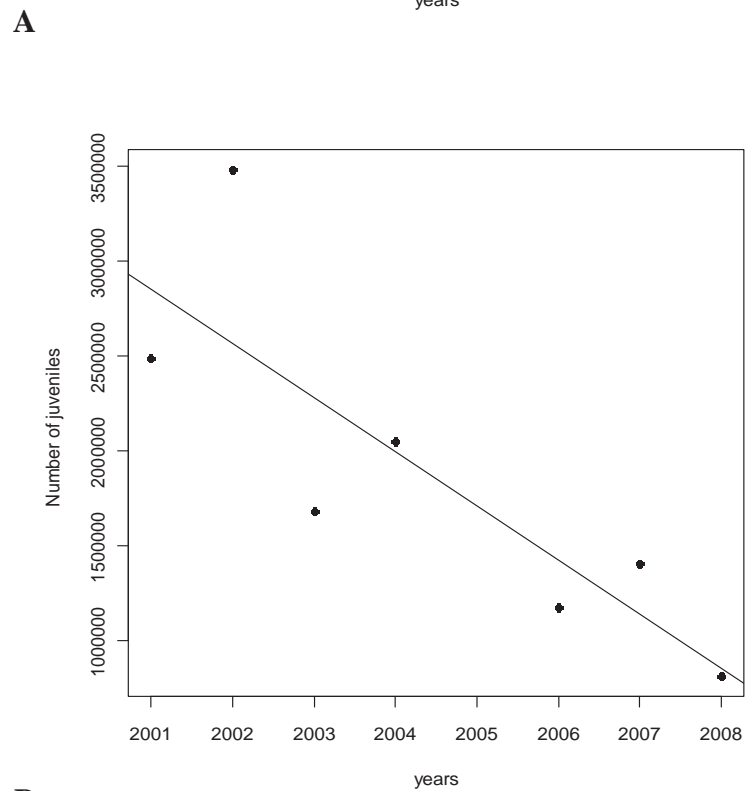
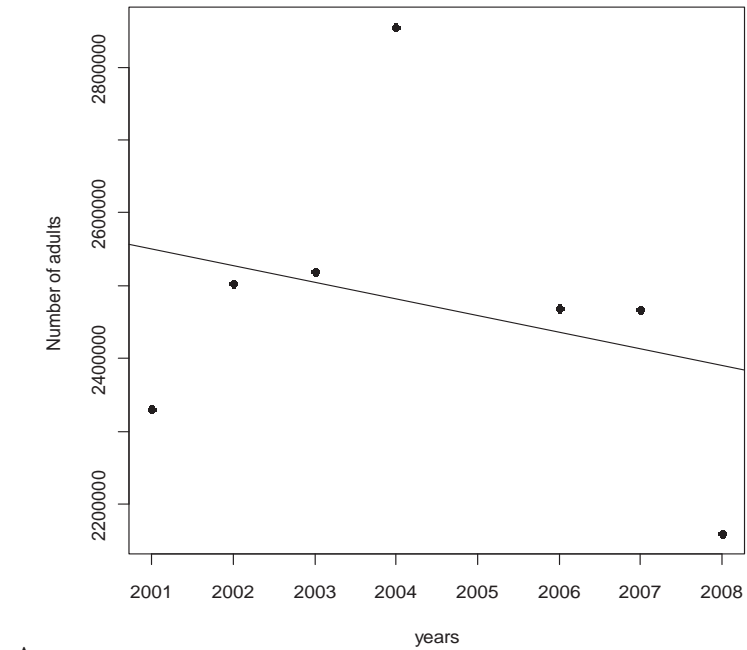


Figure 3.6: Changes in adult (a) and juvenile (b) *Placostylus fibratus* population on Isle of Pines from 2001 to 2008. The simple linear regression is given by the line.

Adults ($Y = 48168961 - 22798 X$) ($R^2 = 0.08$; $F = 0.4$; $p > 0.05$)

Juveniles ($Y = 574058013 - 285462 X$) ($R^2 = 0.7$; $F = 11.6$; $p = 0.01$)

3.3.2 Human harvest of snails

3.3.2.1 Snails collected for marketed

In 2003, the numbers of harvested snails declared by preparers and restaurants were very similar: 52,896 (preparers) versus 47,573 snails (restaurants) (Table 3.5). One restaurant also prepared snails by buying them directly from collectors; this represented only 13% of the total number of snails prepared on the whole island (52,896 snails for 2003). Preparers also sold snails directly to locals and tourists (7,704), for consumption on the island. Some collectors may illegally market snails to people on the Mainland but the quantities involved are probably negligible, but because the trade is illegal it is difficult to evaluate.

Table 3.5: Declared quantities of Placostylus fibratus snails on Isle of Pines harvested in 2003 by the different protagonists during the snail preparation phase.

	Volume declared in 2003	Total
By preparers (n=2)	45,282 (restaurants) + 7,704 (locals and tourists)	52,986
By restaurants (n=8)	40,443	40,443
By restaurants preparers (n=1)*	7,130	7,130
Total marketed in 2003		60,116

**One restaurant buys directly live snails from collectors*

Due to the close agreement between the numbers of snails declared by preparers and by restaurants in 2003, only the preparers were surveyed in 2005. From 2003 to 2006, the number of snails collected and marketed on Isle of Pines varied across the year (Figure 3.7) becoming higher during the tourist season (September to December) and at end-of-year feasts. In 2003, 52,986 snails were collected for marketing from the wild, in 2005 the count was 56,897 snails, and in 2006 it was 66,227 snails. The district of heaviest harvest also varied during this period (Figure 3.8). On average, 34.8% of the snails collected in 2003, 2005 and 2006 were from Touété, 29.9% came from Kéré, 20.3 % from Gadgi and 10.4% from Wapan.

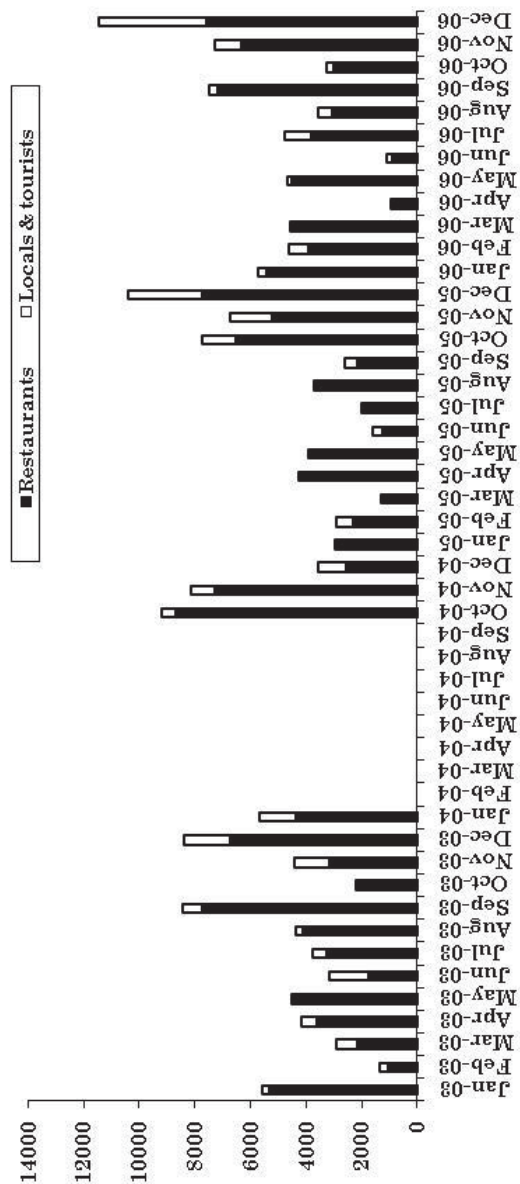


Figure 3.7: Monthly number of *Placostylus fibratus* snails collected and marketed on Isle of Pines from January 2003 to December 2006.

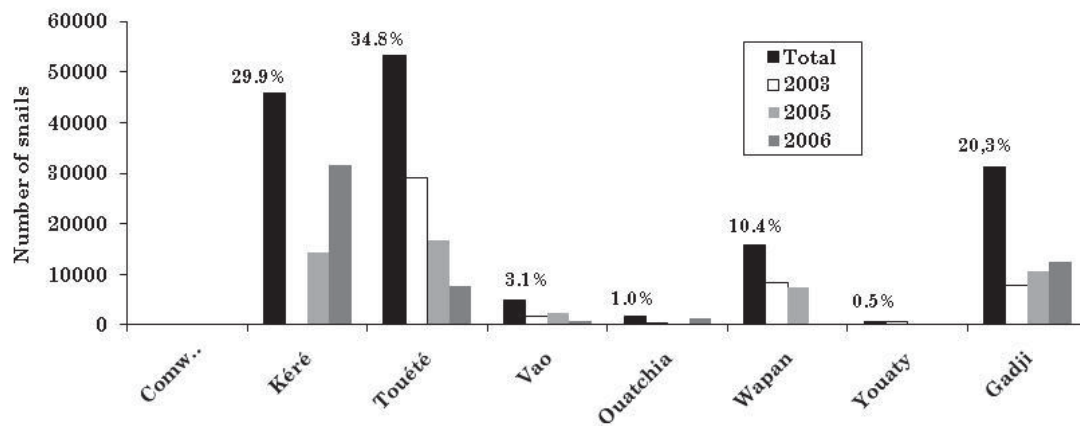


Figure 3.8: Number of *Placostylus fibratus* snails collected on Isle of Pines in each district in 2003, 2005 and 2006.

3.3.2.2 Snails collected for personal consumption

From December 2003 to May 2004 the discarded shells of 27 households were surveyed (four households chosen at the beginning of the study subsequently decided not to participate). The main species collected and eaten was *P. fibratus* and 99% were adult snails (lip >3.5 mm); *P. porphyrostomus* represented only 1% of this consumption. Consumption varied across months (Figure 3.9), being higher during special feasts like Christmas and New Year's Eve and during the peak tourist season in December, and the cultural event in May. During this period from May to January, mean consumption was 37 ± 3 snails per household per month. During the less festive period from February to April, mean consumption was 7 ± 1 snails per household per month. Snail consumption also varied across districts (Figure 3.10), being higher in Youaty and Touete averaging 50 and 30 snails per household per month respectively. Given the distribution of household per districts (Table 3.1), and their monthly number of snails eaten, $42,624 \pm 26,208$ snails are estimated to be eaten annually by Kuniés.

3.3.2.3 Total annual harvest

Based on the survey data from restaurants and households, the estimated total number of snails collected from forests on the Isle of Pines was 120,000 per annum. This represented 6% of the mean estimated adult wild stock of 2,471,000 snails for the period 2001-2008 (2,160,000 snails for the year 2008). In comparison, before 1993 about 700,000 snails were collected annually, representing about 16% of the mean adult stock (4,375,000) and from 1995 to 2000, approximately 300,000 snails were collected annually represented 11% of the estimated stock (2,696,717).

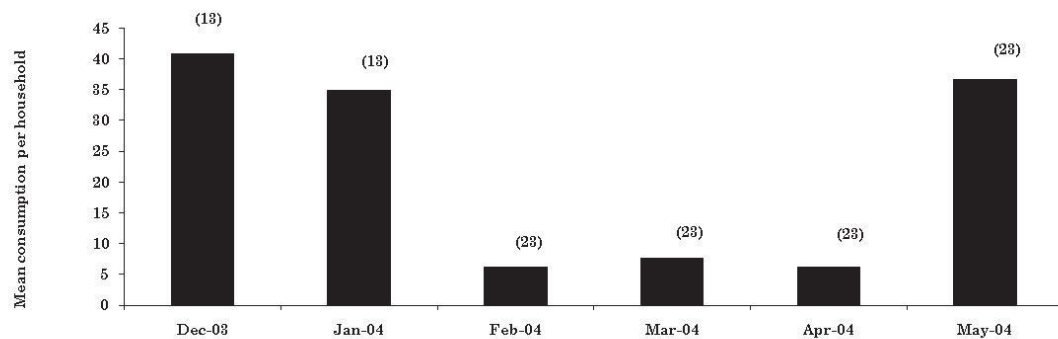


Figure 3.9: Monthly mean number of *Placostylus fibratus* snails eaten by households on Isle of Pines in 2003 from December 2003 to Mai 2004. The number of surveyed households is mentioned in brackets.

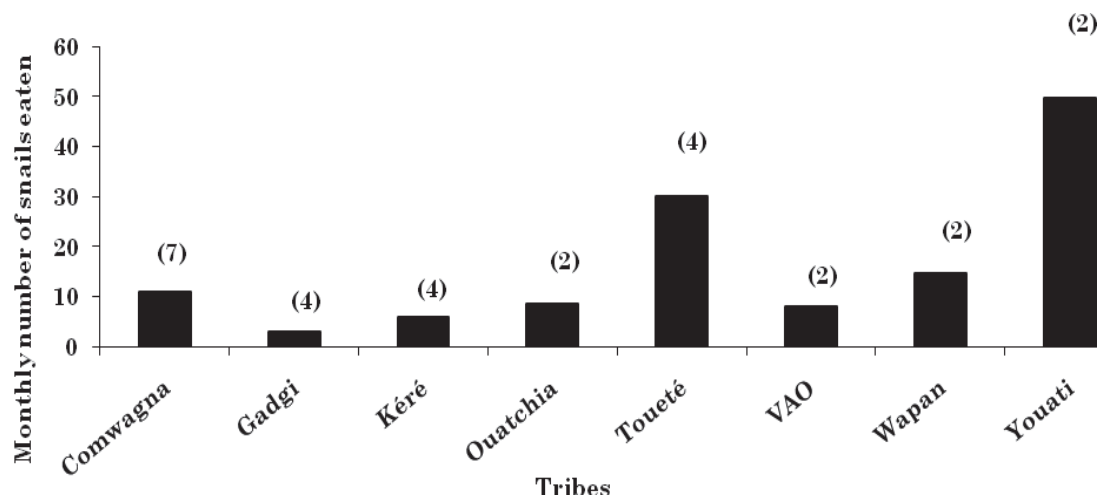


Figure 3.10: Monthly mean number of *Placostylus fibratus* snails eaten by households on Isle of Pines in 2003 by district. The number of surveyed households is mentioned in brackets.

3.4 Discussion

3.4.1 Population changes through time

Evidence for change in the total population of *Placostylus fibratus* snails on the Isle of Pines between 1993 and 2008 depends upon the period selected. Analysis of the data across the entire 15 years suggests that there has been a significant decline in both adults and juveniles, with an average rate of decline of $6.2 \pm 13.2\%$ per annum. When data from 1993 and 1994 are excluded, evidence for a decline is less convincing. More compelling is the apparent decline in the population of juveniles from 2001 to 2008. *P. fibratus* are long-lived (15+ years), and reach maturity at 3-5 years (Chapter 4). Thus these snails are likely to be vulnerable to a diminishing rate of recruitment that at some critical point could trigger a population collapse.

Placostylus snails on the Isle of Pines had always been collected for traditional consumption but exploitation for commercial purposes began in the 1950s (Pöllabauer, 1994). Before 1993, and probably for a short period after commercial harvest started in 1950, around 700,000 snails were collected for consumption annually (Pöllabauer, 1995). Thus, repeated intensive collection started decades before the survey of snails was initiated; the effective population size was once thus likely to have been substantially higher than today. This assertion is supported by the fact that the monitoring programme was initiated following concerns raised by the women who were collecting the snails that they were becoming increasingly difficult to find.

The apparent decline in the population estimates for *P. fibratus* over the 15 years surveyed is strongly dependent upon the high population estimates obtained from the 1993 and 1994 surveys, especially for adults. One interpretation would be that the legislation imposed in 1994 to reduce snail harvest had immediate benefits in halting an earlier decline, but this seems improbable. There is no compelling evidence that the further tightening of the legislation regulating snail harvesting that was imposed in 2000 led to a subsequent increase in snail numbers. But both of the two legislations reducing significantly the number of snails harvested compared to 1993 and previously, would certainly have contributed to maintain snail number by limiting the decrease.

While there was no apparent change in the number of adult snails over the twelve year period from 1996 to 2008, it seems probable that the removal of large numbers of adult snails over several decades before 1993 will have affected the

potential for natural recovery and to a certain extend may possibly have started to reduce local genetic diversity via genetic drift in areas where snails have been especially over-collected. According to Bishop *et al.* 2009, processes driving the loss of genetic diversity may be buffered by intrinsic biological traits; specifically long generation times in age-structured species can result in remnant populations that appear genetically diverse despite periods of substantial decline. Retention of genetic variation in partially recovered populations may be deceptive, as it masks the reality of a significant decline in the population's effective size, and even if the current effective size is maintained, both allelic diversity and heterozygosity may decline.

Aspects of the life history traits of the New Caledonian *Placostylus* snails make them prone to overexploitation. First, these are long-lived invertebrates – almost 15 years (Pöllabauer, 1995) and possibly more than 30 years (Stringer *et al.* 2004) – that show a natural high mortality among newborns and juveniles. This vulnerability is heightened by the impacts of introduced rodents on these stages. Second, sexual maturity is reached after 3-5 years so recruitment of new adults into the population is slow (Brescia *et al.* 2008). Exploitation of adult snails in wild populations in forests on the Isle of Pines must further erode the breeding population. Third, repeated collection for decades in same areas may led to local population extinction or the reduction to low densities which retards the natural recovery of the population (Hobday *et al.* 2001). Dispersal and mobility are low for these snails (Brescia *et al.* 2008) and as a result, snails may have difficulties in finding partners (Allee effect). A similar problem was highlighted by Andreev (2006) studying the effects of exploitation of wild populations of the land snail *Helix pomatia* in Moldova.

3.4.2 Prospects for management

Our study demonstrates a significant impact of the repeated collecting of adult snails on wild populations, especially on juvenile recruitment. Being of commercial value, it is of great concern to the local authorities and to Kuniés that the snails of Isle of Pines are subject to rational and sustainable exploitation. To this end, we make the following recommendations:

3.4.2.1 Continue monitoring population trends

The monitoring of snail abundance on Isle of Pines started in 1993 and has continued almost annually till now. We recommend that annual surveys continue so as

to assess how the snail population responds to management measures imposed in the future.

The optimal survey effort (number of quadrats that must be done per year) will depend to some extent on political decisions and financial support from local authorities. Nevertheless, we recommend the continuation of the survey methods used between 2006 and 2008. During these years a more cost-effective survey strategy was used whereby quadrat surveys were done every three months (four times a year) with five districts being sampled on an alternated basis (see section 2. Methods). This requires about 100 quadrats to be surveyed annually (compared to 140 prescribed in the original 2003 design), yet this design still gives a good representation of seasons and districts. Reducing the frequency of surveys to every two years would further reduce costs and help assure the long-term continuity of the monitoring programme.

3.4.2.2 Involve the local people

Involvement of local people in management of collecting would facilitate more responsible approaches to resource use. Kuniés could also be involved in the monitoring programme that could be eventually devolved to them by local authorities.

3.4.2.3 Establish a systematic harvesting plan

The management of *Placostylus* snail collection would benefit from a more rigorously organised regime in the spatial variation of harvesting to avoid depletion. The current system has allowed repeated collecting in the same districts for decades rather than spreading harvests more evenly. To enable populations to recover, alternating the collection in specific areas would be an efficient way to use the resource more sustainably as well as facilitating a more equitable income in each district. The establishment of “no-take areas” – a concept developed for protecting marine environments from extractive activities such as fishing (Kelleher *et al.* 1995; Hughes *et al.* 2003) – could also be implemented to maintain a source population for recruitment into the surrounding area. Adhesion of the local population would be required due to traditional property owners; techniques for sustainable harvesting and monitoring should be taught beforehand to the Kuniés.

3.4.2.4 Organisation of the snail industry

It may be necessary to restructure the economic basis of the snail industry on the Isle of Pines. The price paid to collectors has remained the same for around 20

years now. This unit price was fixed arbitrarily by traditional authorities but is very low (US\$0.34 per live snail) while the price of cooked snails varies between preparers but is much higher (around US\$1.40 for a cooked snail); and the price paid by tourists also varies but is often more than twice the price paid to preparers at around US\$3.90 per snail. The price of snails ought to be rationalised and adjusted to take account of the scarcity of snails, their endemic status, and the real costs of their preparation for sale. Inevitably there will be trade-offs between the aspirations of collectors expecting to earn a reasonable return for their efforts, customers expecting to pay for the quality, and conservationists expecting measures to protect a rare endemic snail. The price of a dozen snails ideally would incorporate a levy that is reinvested into conservation actions, including monitoring of the snail populations. Where possible, local community participation should be involved in the active management of the resource.

3.4.2.5 Exploited snails from captivity

The Institut Agronomique Néo-Calédonien (IAC) has been actively developing farming methods for snails to reduce the reliance on the wild population for harvest and to provide source for restocking wild populations. Captive breeding of snails may help to allow the exploitation of the resource to continue by supplementing or replacing those harvested from the wild, as well as facilitating the preservation of natural populations. Successful farming of snails may also enable the re-stocking of small populations of *Placostylus* in areas where they are now rare or extinct. A successful farming method has now been developed for *P. fibratus* following many years of trials (Brescia, 1997, 1998, 1999, 2000, 2001; Brescia *et al.* 1998).

3.4.2.6 Sustainable use of the resource

Human harvest represents nowadays about 6% of the estimated adult stock. Snails have been collected frequently and repeatedly from the same locations over many years, especially in four districts (Kéré, Touété, Gadgi and Wapan). For economic reasons, Kuniés exert pressure on authorities to allow more snails to be collected. Sustainable exploitation will only occur when the extraction rate does not exceed that of animals born into the population (Lyashenko, 2001). In this context, studies of sustainability are essential to allow prediction of population trends, to ensure long-term resource use and to accompany effective management strategies.

The development of a snail collection model based on the information available on the life history of *Placostylus* snails predicting snail population trends under

different levels of allowable harvest would constitute a valuable tool for future management strategies.

3.5 Acknowledgements

All the work on *Placostylus* snails on Isle of Pines reported here was funded by the Direction de l'Environnement de la Province Sud (DENV), the Institut Agronomique Néo- Calédonien (IAC) and Agence ERBIO (Etudes et Recherches Biologiques). We thank the Grand Chef de l'Ile des Pins Hilarion Vandegou and all the clans for accepting the study on their island, and also all the Kuniés for helping with fieldwork, especially the Koteureu family (Catherine, Stéphanie, Véronique, Etienne and Vincent). We also thank all the restaurants on Isle of Pines for their participation to enquiries and also the two main snail preparers, Madeleine and Bernadette Vakié, and Maggy and Marcellin Douepere.

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CHAPTER 4

POPULATION STRUCTURE, GROWTH, LONGEVITY AND MORTALITY IN TWO SPECIES OF *PLACOSTYLUS* SNAILS (MOLLUSCA: GASTROPODA: BULIMULIDAE) IN EVERGREEN AND DRY FORESTS IN NEW CALEDONIA



Searching for snails in fixed quadrats in dry and evergreen forests of New Caledonia

Abstract

Mark-recapture over four years (2005-2009) in 20 x 20 m permanent quadrats was used to study the population structure, growth, longevity and mortality of the exploited New Caledonian endemic land snail *Placostylus fibratus* and of *P. porphyrostomus* in three sites in an evergreen forest on Isle of Pines and in two sites in a dry forest on the mainland of New Caledonia. Additional data on the competing invasive African Snail *Achatina fulica* were also recorded from all sites. Surveys of the snail stock was also conducted from 2006 to 2008 in the Isle of Pines sites using 224 random 10 × 10 m non-permanent quadrats to further examine the population structure of the same three species. Overall, more than 100 *P. porphyrostomus* and just under 1000 *P. fibratus* were found in the mark-recapture study. The number of live adult and juvenile snails was highly variable among and within the five sites. Empty shells were more common than live snails for each species at each site. For both *P. fibratus* and *P. porphyrostomus*, adults predominated amongst both live snails (62% in *P. fibratus* and 89% in *P. porphyrostomus*) and empty shells (73% in *P. fibratus* and 91% in *P. porphyrostomus*). Based on the rates of shell accumulation in the fixed quadrats from 2005 to 2009, the maximum persistence of empty shells of each species was estimated to be 37 years for *P. fibratus*, 80 years for *P. porphyrostomus* and two years for *A. fulica* on Isle of Pines. In dry forest, the maximum persistence of empty shells was estimated to be nine years for *P. porphyrostomus* and one year for *A. fulica*.

For *P. fibratus* on the Isle of Pines, the estimated annual survival rate for juveniles was 59.0% and 70.0% for adults. Rodent predation appeared to be the major cause of juvenile deaths, both for *P. fibratus* juveniles on Isle of Pines (73.2% of empty shells showed signs of rat predation) and for *P. porphyrostomus* in dry forest (87.6%). The high level of rodent predation in these forests seriously jeopardises recruitment. If snails survive this predation it appears to take approximately four years from hatching for *P. fibratus* to reach maturity (an aperture lip thickness of 3.5 mm). Mean fecundity over six months was 0.73 young per adult (95% CI= 0.24-1.20) for *P. fibratus* on Isle of Pines and 0.27 young per adult (95% CI= 0.11-0.45) for *P. porphyrostomus* in dry forests.

Structure de population, croissance, longévité et mortalité chez deux espèces d'escargots du genre *Placostylus* (Mollusca: Gasotropoda: Bulimulidae) en forêt humide et forêt sèche de la Nouvelle-Calédonie

Résumé

La structure de population, la croissance, la longévité et la mortalité de *Placostylus fibratus*, escargot endémique à la Nouvelle-Calédonie et exploité sur l'Ile des Pins, et de *Placostylus porphyrostomus*, espèce caractéristique de forêt sèche sur la Grande-Terre (mais aussi sympatrique à *P. fibratus* sur l'Ile des Pins) ont été étudiées au cours d'une étude de capture-marquage-recapture (CMR) durant quatre années (2005-2009). Des informations sur l'escargot géant Africain *Achatina fulica* ont aussi été enregistrées. Des données complémentaires issues de l'évaluation du stock de *P. fibratus* sur l'Ile des Pins (224 quadrats aléatoires de 10x10m réalisés de 2006 à 2008) ont également été analysées afin d'améliorer les connaissances sur la structure de population des trois espèces. Tous sites confondus, une centaine de *P. porphyrostomus* et un millier de *P. fibratus* ont été identifiés au cours de l'étude de CMR. Des variations inter et intra sites pour le nombre d'escargots vivants et morts ont été relevées. Les coquilles vides sont plus communes que les escargots vivants pour chacune des espèces dans chacun des sites. Pour *P. fibratus* et *P. porphyrostomus*, le stade adulte prédomine parmi les escargots vivants (62% pour *P. fibratus* et 89% pour *P. porphyrostomus*) mais aussi parmi les coquilles vides (73% pour *P. fibratus* et 91% pour *P. porphyrostomus*). L'observation de l'accumulation des coquilles vides au sein des quadrats permanents de 2005 à 2009 a permis d'estimer la persistance maximale des coquilles vides au sol à 37 ans pour *P. fibratus*, 80 ans pour *P. porphyrostomus* et 2 ans pour *A. fulica* sur l'Ile des Pins, et à 9 ans pour *P. porphyrostomus* et 1 an pour *A. fulica* en forêt sèche.

Le taux annuel de survie pour *P. fibratus* à l'Ile des Pins est de 59.0% pour les juvéniles et 70.0% pour les adultes. La prédation par les rongeurs introduits constitue la première cause de mortalité chez les escargots juvéniles de *P. fibratus* sur l'Ile des Pins (73.2% des coquilles vides présentent des signes de prédation) et chez *P. porphyrostomus* en forêt sèche (87,6%); ce haut niveau de prédation dans ces forêts met sérieusement en péril le recrutement au sein des populations. Lorsque les escargots survivent, quatre années environ sont nécessaires pour qu'un nouveau-né atteigne la maturité (une lèvre coquillière épaisse de 3.5 mm). Le taux de fécondité moyen par

période de 6 mois est de 0.73 jeune par adulte (95% CI= 0.24-1.20) pour *P. fibratus* à l'Ile des Pins et de 0.27 jeune par adulte (95% CI= 0.11-0.45) pour *P. porphyrostomus* en forêt sèche.

4.1 Introduction

Placostylus land snails (subfamily Placostylinae) are found only in the Western Pacific, extending northwards from the tip of the North Island in New Zealand to Lord Howe Island, Fiji, the Solomon Islands, Vanuatu and New Caledonia including the Loyalty Islands (Hedley 1892; Cockerell 1929; Solem 1959). The six species found in New Caledonia (*Placostylus fibratus*, *P. porphyrostomus*, *P. caledonicus*, *P. eddystonenis*, *P. bondeensis* and *P. scarabus* (Neubert *et al.* 2009)) are all endemic and are either threatened or endangered (Brescia *et al.* 2008). Three species - *P. eddystonensis*, *P. fibratus* and *P. porphyrostomus* are listed as vulnerable by IUCN (IUCN 2006). Habitat destruction or modification by introduced ungulates, human harvesting for consumption, and predation by introduced species are all factors contributing to their decline (Brescia *et al.* 2008).

These large, slow moving, slow developing and long-lived land snails appear to be relatively specific in their habitat requirements and are primarily associated with calcium-rich soil, and are restricted to native dry or evergreen forest where they are generally found under leaf litter (Brescia *et al.* 2008).

Placostylus fibratus is the most polymorphic species and is found throughout New Caledonia, including the Loyalty Islands where a dwarf form occurs. This edible species is known as “the snail of the Isle of Pines” (named after the coral island to the south of the mainland from which they are collected). Indeed, the only snails to be marketed commercially for consumption are those from this island. Control measures on the harvesting of these snails have been imposed by the local authorities charged with environmental protection (Délibération 26-2000/APS). In parallel, conservation strategies such as off-site preservation as well as developing farming methods have been explored (Chapters 8 & 9 and Appendix 2; Brescia *et al.* 2008).

Placostylus porphyrostomus is the most common species in sclerophyllous forests (Chérel-Mora 1983) which dominate the dry west coast of the mainland where there is less than 1100 mm annual rainfall. This forest type is characterized by a high diversity of plant species (Bouchet *et al.* 1995) but it is currently the most threatened of the Caledonian biomes (only 1% remains) due to deforestation and habitat modification by feral ungulates (Programme Forêt Sèche 2007). *P. porphyrostomus* is also found on the Isle of Pines where it is sympatric with *P. fibratus*. It is also

collected there by locals for their own daily consumption but it is not sold commercially.

To date, there has been very little information available on the demographics and population structure of New Caledonian *Placostylus* despite the importance of such information for the management of these species. Studies of this type have been undertaken to inform conservation and management strategies for the congeneric species *Placostylus hongii* in New Zealand (Stringer *et al.* 2004) and for the endangered tree snails *Partulina proxima* (Hadfield *et al.* 1989) and *Achatinella lila* (Severns 1981) in Hawaii, and to enhance strategies for the control of the pestiferous *Achatina fulica* in India (Raut 1991). The only relevant data available from New Caledonia are density estimates for *P. fibratus* on the Isle of Pines for the period 1995 to 2008 (Chapter 3), and for *P. porphyrostomus* from just a few patches of dry forest on the mainland (Brescia & Pöllabauer 2004, 2005).

This chapter describes the results of a four-year mark-recapture study of natural populations of *P. fibratus* and *P. porphyrostomus* in evergreen and dry forests of New Caledonia. We report on their population structure, growth, longevity and rates and causes of mortality. Data on the introduced and invasive competitor, the African snail *Achatina fulica* are also provided here.

4.2 Methods

4.2.1 Study areas

The work was conducted in New Caledonia which has three major seasons: a hot wet season (mid November-mid May; mid April-mid May is a transition period); a cool dry season (mid May-mid September); and a hot dry season (mid September-mid November) (ORSTOM 1981).

Five sites with two contrasting vegetation types were selected (Figure 4.1). Two sites in native sclerophyllous forest, Nékoro and Mèpouri, near Poya, are privately-owned ranches located on the western coast of “Grande-Terre” (altitude 0-100 m asl). Nékoro is one of the last remaining moderately large remnant patches of dry forest (272 ha) with about 150 ha of forest recently fenced in 2007 to exclude rusa deer (*Cervus timorensis*) and cattle (*Bos taurus*). The forest contains a small remnant snail population of *P. porphyrostomus*, with a mean density of 2.3 snails / 100 m² (SD

= 2.8) (Brescia & Pöllabauer 2004, 2005). In Mèpouiri, about 10 km from Nékoro, is a patch of dry forest (99 ha) in which 8 ha was fenced in 1994 and an additional patch of 6 ha was fenced in 2000. This fence excludes rusa deer and cattle, but also feral pigs (*Sus scrofa*). Here, *P. porphyrostomus* is rare, with a mean density of 0.9 snails / 100 m² (SD= 0.6), and the population was only rediscovered in 2003 (Brescia & Pöllabauer 2004, 2005).

The three other sites were located in the Gadgi, Youaty and Kéré districts on the Isle of Pines (152 km²) which is 50 km south of the New Caledonian mainland and in total comprises eight tribal districts. The vegetation here is a native evergreen humid forest on coral soil, 15-20 m high, composed principally of Kohu trees *Intsia bijuga*, Buni *Manilkara dissecta* and columnar pine trees *Araucaria columnaris*. These sites have a relatively high density of *Placostylus fibratus* snails (6.2, 3.7 and 5.8 snails / 100 m² for each district respectively in 2008 (Chapter 3) and they are regularly collected for sale to local restaurants (Brescia *et al.* 2008). *P. porphyrostomus* lives here in sympatry with *P. fibratus* but is far less abundant. In both dry and evergreen forest, the introduced African snail (*Achatina fulica*) is also found.

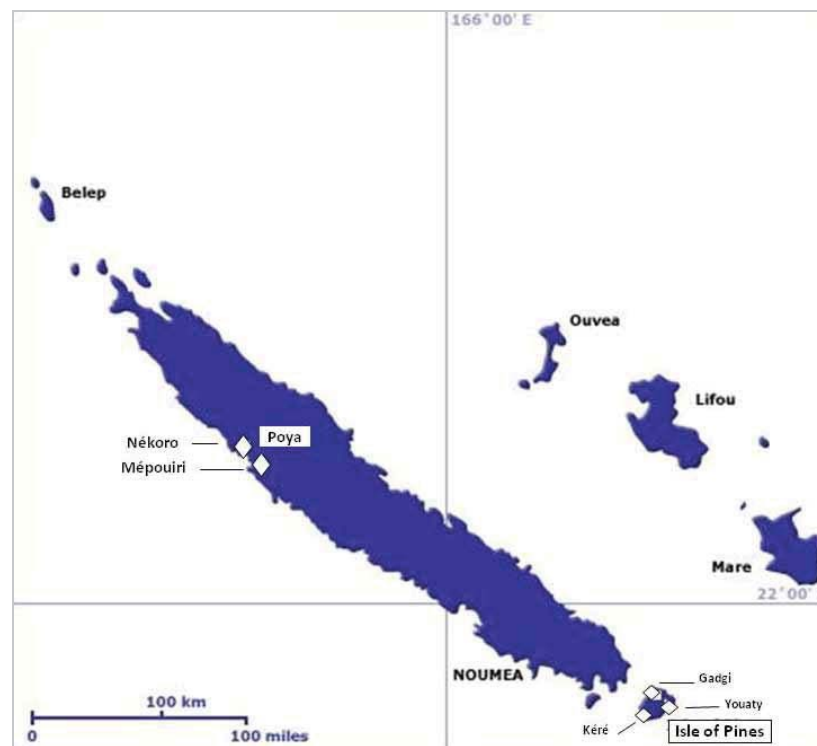


Figure 4.1: Map of New Caledonia and the five study sites: Gadgi, Youaty and Kéré districts in the rainforest on the Isle of Pines and Nékoro and Mèpouiri (Poya) in dry forests on the west coast of the mainland.

4.2.2 Mark recapture study

To assess recruitment, longevity, mortality and growth parameters, a mark-recapture study was initiated. Two 20 x 20 m permanent quadrats were established in each of the five forests with each pair separated by at least 150 m. The quadrats were positioned where live snails had been recorded during previous pilot surveys. On Isle of Pines, quadrats were established in January (Gadgi) and February (Kéré and Youaty) 2005, and in dry forests in May 2005. To facilitate the search, each 20 x 20 m quadrat was divided into four 10 x 10 m sub-quadrats. Snails were searched for on the ground in each sub-quadrat by at least three people for about one hour every six months. The number of live snails found per quadrat was noted and for each snail, weight, height and thickness of the lip aperture of the shell were recorded, the latter being used to determine whether a snail was an adult or a juvenile. Pöllabauer (1995) considered that adult *P. fibratus* are those characterized by a shell with a thickened aperture lip (more than 4 mm); however, my observations in captivity indicated that snails with an aperture lip of 3.5 mm can be sexually mature (laying eggs). Thus, snails were classified as adults when the aperture lip was ≥ 3.5 mm, as juveniles when the lip thickness was < 3.5 mm but the snail was > 10 mm long, and infants (newborns) when there was no thickening of the aperture lip and the snail was ≤ 10 mm long.

Individual identifying numbers were engraved on the shells of live snails > 15 mm long by carefully grinding the periostracum using a portable engraver. To help relocate these snails in subsequent surveys, harmonic radar transponders were attached to the middle of the shell on live sub-adult and adult snails, and to the apex of the shell of juveniles where it would not interfere with growth as the shell enlarged. The transponders were built according to the design of Stringer *et al.* (2004) and consisted of an aerial of thin copper (about 7 mm wide and 0.25 mm thick) folded into the shape of an open triangle with a 5082-2800 Schottky diode (Farnell InOne, UK) soldered across the ends. Transponders were fixed to the shells with neoprene glue Sader (Bostik S.A.) after the shells had been cleaned and dried with tissue paper and lightly buffed with fine carborundum paper. A hand-held harmonic radar unit (Type R5P1, Recco AB, Sweden) was used to locate snails. The detection range was about 3 to 5 m. These searches were done rigorously inside each sub-quadrat but also in an extended area of 15-30 m beyond each quadrat to find snails that had moved out of the quadrats.

Every *Placostylus* snail was measured by recording the maximum height of shell for live snails and empty shells, the age class (newborn, juvenile or adult), whether it was live or dead (whole undamaged empty and predator-damaged shells) and, where appropriate, the predator concerned. Empty shells were discarded outside the quadrats so they were not included in subsequent samples. The same data was recorded for *A. fulica* but in the absence of reliable criteria to characterize sexual maturity (I often observed snails of different sizes laying eggs and in this species the lip does not thicken), I did not distinguish adult or juvenile African snails. Empty shells were also discarded away from the quadrats.

4.2.3 Survey of snail stock from 2006 to 2008 on the Isle of Pines

Additional information on population structure of *Placostylus* snails in evergreen forest was obtained from a survey of *Placostylus* abundance on the Isle of Pines conducted from 2006 to 2008 (Chapter 3). Every three months, *Placostylus* were searched for in randomly located 100 m² non-permanent quadrats. A survey consisted of exploring one of the eight tribal districts, establishing a first quadrat in the forest using a tape and compass, walking a distance of 150 m following an azimuth using a compass and then establishing a new quadrat. This was repeated until five quadrats were established per district. In each quadrat, snails were searched for on the ground by at least three people for about one hour. The numbers of dead and live snails found per quadrat were noted and the following details were recorded for each snail: the weight, height and thickness of the lip aperture of the shell of live and dead snails as described above.

4.2.4 Caged rodent trial

In order to enhance our knowledge of the impact of the three introduced rodents (the Polynesian rat *Rattus exulans*, the Ship rat *Rattus rattus* and the mouse *Mus musculus*) on New Caledonian *Placostylus* snails, I set up a caged-rodent trial in captivity to determine the vulnerability of different snail size classes to each rodent species. The Norway rat *R. norvegicus* was not included in this study because I have never found this species in previous rodent surveys on the Isle of Pines or in dry forests (Chapter 5). The rodents were captured in an 11 ha patch of dry forest in Nouméa (Koumourou, Ducos), which is one of the last sites near the New Caledonia capital known to host a remnant *Placostylus* population, using 25 Rat Cage Traps (Pest Management Service, NZ) placed at 25 m intervals along a transect. The traps were

baited with cheese and peanut butter, and were checked daily until five specimens of each species had been captured. The rodents were transported to Païta where they were held in a captive facility.

Each of the 10 rats was housed individually in a 100 x 50 x 75 cm cage with 5 mm wire mesh and each mouse was held individually in a 42 x 25 x 15 cm solid stainless steel cage. Both rat and mouse cages contained a shelter, a manger and a drinking trough. Cages were cleaned daily and water was provided *ad libitum*.

On the first day of the experiment, each rodent was individually presented with five specimens of one of the following classes of snail: eggs, newborns (<5 mm in height), juvenile stage 1 (height ≤ 22 mm, lip = 0 mm), juvenile stage 2 (height ≤ 47 mm, lip = 0 mm), sub-adult (height ≤ 65 mm, lip = 0 mm), and adult (height ≥ 85 mm, lip = 0 mm). The experiment was monitored for the three days and the number of snails each rodent ate was noted. During the trials, eaten snails were not replaced. The trial was repeated until each rodent had been presented with all of the size-classes of snails. The entire trial was run twice; first when the rodents had only snails to eat, and second, when they had access to alternative food (commercial dry dog food).

4.2.5 Data analysis

To estimate survival and site fidelity of the marked *P. fibratus* snails, Burnham's (1993) approach of combining dead recovery and live encounter data into a single analysis was employed in Program MARK 5.1 (White and Burnham 1999). Six-monthly survival rates (S), recapture rates (P) and fidelity (F = the probability that the animal remains on the study area) were estimated. Due to the limited number of *P. porphyrostomus* snails found in both regions, survival was evaluated for each age-class of snail by calculating re-detection probability and known minimum survival times. Transpondered snails enabled determination of an estimate detection probability $p = m_1/m_2$ where m_1 is the number of transpondered snails re-detected during hand searches and m_2 is the number confirmed after radar searches in the 400 m² surrounding each quadrat. I then estimated the number of snails in each size class (juvenile and adult) based on the number found and the estimated detection probability ($N = n_x/P_x$ where n_x is the number of snails in class x and p_x the estimate detection probability for that age-class). Survival of each class for each survey and for each of the two quadrats was calculated using the above estimates as $S_x = N_{x+1, t+1} / N_{x,t}$ where S_x is the estimated survival, $N_{x+1, t+1}$ is the number of snails in an age class at time $t+1$,

and $N_{x,t}$ is the number of snails in the previous survey. For both *P. fibratus* and *P. porphyrostomus*, fecundity at each survey of the two quadrats was estimated as $N_{1,t+1} / N_{a,t}$ where $N_{1,t+1}$ is the number of snails in first age class at time $t+1$ and $N_{a,t}$ is the estimated number of breeding-age snails present in the quadrat at the last survey.

Comparisons of snail densities were performed using a repeated-measures ANOVA in SPSS 15.0 after log transformation of data to improve homogeneity of variance (Mauchly's Test of Sphericity).

Binomial analysis of variance was performed on the proportion of empty shells found in the fixed quadrats to partition the variance in predation rates among and within sites.

4.3 Results

4.3.1 Snail abundance

During the seven (dry forest) or eight successive searches (Isle of Pines) conducted between 2005 and 2009, 27 *P. porphyrostomus* were found and marked in the dry forests of in Mépouri and 42 in Nékoro, while on the Isle of Pines, 10 *P. porphyrostomus* were found in Kéré, and 52 in Youaty. Three hundred and forty one *P. fibratus* were found in Gadgi, 233 in Kéré, and 422 in Youaty. The number of both adult and juvenile snails were often quite different in the two quadrats surveyed in each of the five sites (4.7 Appendix 1) but, overall, there were marked differences in abundances of all the three species and snail category (adult or juvenile) among the sites surveyed (Table 4.1).

There were no significant differences in the total numbers of *P. fibratus* snails found in quadrats during successive searches conducted between 2005 to 2009 on Isle of Pines (Repeated Measures ANOVA, $F_{6,36}=0.55$, $p>0.05$), but there was a significant within-tribe effect ($F_{12,36}=3.27$, $p<0.01$) and a significant three-way interaction between successive searches, snail category (juveniles or adults) and tribe ($F_{12,36}=2.34$, $p<0.05$).

Table 4.1: Average number \pm s.e. of live snails of each species found in the two monitored permanent 400 m² quadrats combined at each site of the Isle of Pines and in dry forest for all surveys between 2005 and 2009.

(a) adults

	Gadgi	Kéré	Youaty	Mépouiri	Nékoro
<i>P. fibratus</i>	44.2 \pm 6.5	23.2 \pm 3.6	13.2 \pm 3.1	-	-
<i>P. porphyrostomus</i>	-	0.8 \pm 0.4	5.3 \pm 1.9	3.4 \pm 1.0	9.8 \pm 4.3
<i>A. fulica</i> *	15.5 \pm 3.5	1.0 \pm 0.6	52.3 \pm 13.0	29.9 \pm 13.8	28.4 \pm 19.8

(b) juveniles

	Gadgi	Kéré	Youaty	Mépouiri	Nékoro
<i>P. fibratus</i>	13.3 \pm 2.4	7.7 \pm 1.7	28.7 \pm 5.6	-	-
<i>P. porphyrostomus</i>	-	0.1 \pm 0.1	1.0 \pm 0.5	1.0 \pm 0.6	1.1 \pm 1.1

* Adults and juveniles cannot be distinguished in this species, so snails of all sizes were included in this table.

There was a significant difference in the number of snails for each category ($F_{12, 1}=7.8$, $p<0.05$) and in the interaction of snail category and tribe ($F_{12, 2}=20.0$, $p<0.01$). Thus, adult *P. fibratus* density in Gadgi was relatively high (44.2 snails per 400 m²) and was significantly different (Bonferroni post-hoc analysis, $SE=0.16$, $p<0.01$) from densities observed in Kéré and Youaty, which were also significantly different from each other (Bonferroni post-hoc analysis, $SE=0.16$, $p<0.01$). Juvenile density was higher in Youaty than in Gadgi (Bonferroni post-hoc analysis, $SE=0.15$, $p<0.01$) and in Kéré (Bonferroni post-hoc analysis, $SE=0.15$, $p<0.01$). Gadgi and Kéré were significantly different for the number of juveniles (Bonferroni post-hoc analysis, $SE=0.15$, $p<0.001$).

On the Isle of Pines, the density of adult *P. porphyrostomus* was significantly higher in Youaty compared to that observed in Kéré (non-normality in the data even after transformation, Mann-Whitney test $U=22.0$, $p<0.001$). No *P. porphyrostomus* were found in Gadgi. Densities of adult *P. porphyrostomus* were higher in the dry forest in Nékoro than on the Isle of Pines (Mann-Whitney test $U=263.5$, $p<0.01$) but densities in Nékoro and Mépouiri were not significantly different (Mann-Whitney test $U=72.5$, $p>0.05$). No significant difference existed between juvenile densities among sites (Mann-Whitney tests, $p>0.05$), but the number of snails found in this category

was very low. Nevertheless, in Youaty, the mean number of juvenile *P. fibratus*, 28.7 per 400 m², was twice that recorded in Gadgi and four times more than in Kéré.

In the dry forest, the density of the African snail was similar in Nékoro and Mèpouri (Mann-Whitney test $U=77.0$, $p>0.05$) and the Isle of Pines and dry forests were also similar (Mann-Whitney test $U=584.5$, $p>0.05$) when the sites within each region were combined. In the dry forest, *A. fulica* was far more abundant than adult *P. porphyrostomus* (Mann-Whitney test $U=323.0$, $p=0.001$).

4.3.2 Snail population structure from the survey of stock on the Isle of Pines

During the survey of the snail stock from 2006 to 2008 on the Isle of Pines, 224 non-permanent quadrats representing a total of 2.24 ha of forest were searched. Consistently, more empty shells than live snails of each species were found in the quadrats (Table 4.2, Paired t-tests, all $p<0.001$). The mean number of live snails observed differed significantly among the species (Table 4.2; one-way ANOVA, $F=35.6$, $df=671$, $p<0.001$) with more live *P. fibratus* than *P. porphyrostomus* and *A. fulica* (Bonferroni test, both $p<0.001$) but there was no significant difference between *A. fulica* and *P. porphyrostomus* density (Bonferroni test, $p>0.05$). *P. fibratus* represented 53.8% ($n=1404$) of the total number of the live snails found, while *P. porphyrostomus* accounted for 20.9% ($n=544$) and *A. fulica* for 25.4% ($n=664$).

Table 4.2: Mean number of snails (number per 100 m² \pm 95 % CI) of each species found in the 224 non-permanent quadrats on the Isle of Pines from 2006 to 2008.

Live	Dead	Live	Dead	Live	Dead
<i>P. fibratus</i>	<i>P. fibratus</i>	<i>P. porphyrostomus</i>	<i>P. porphyrostomus</i>	<i>A. fulica</i>	<i>A. fulica</i>
6.3 \pm 0.7	18.0 \pm 2.6	2.4 \pm 0.6	7.8 \pm 1.7	3.0 \pm 0.8	15.6 \pm 4.7

Large juveniles of *P. fibratus* (> 50 mm) represented 91% of the snails found in the quadrats, and with a thickened shell aperture < 3.5 mm thick could be considered as sub-adults rather than juveniles.

Empty shells were more common than live snails for each species (67.1% (95% CI= 64.3-69.9%) versus 32.9% (95% CI= 30.1-35.7%) for *P. fibratus*; 69.3% (95% CI= 64.6-74.0%) versus 30.7% (95% CI= 24.2-33.6%) for *P. porphyrostomus* and 71.1% (95% CI= 66.4-75.8%) versus 28.9% (95% CI= 24.2-33.6%) for *A. fulica*). *P.*

fibratus predominated among the whole live snails found in the 224 quadrats (61.2%; 95% CI= 57-65.4%) followed by *A. fulica* (14.0%; 95% CI= 8.8-19.2%) and then *P. porphyrostomus* (10.2%; 95% CI= 6.7-13.7%). Empty shells of *P. fibratus* were the most abundant: 55.1 %; 95% CI= 51.2-59.0%) followed by *A. fulica* (26.0%; 95% CI= 22.5-29.5%) and then *P. porphyrostomus* (18.8%; 95% CI= 16.4-21.2%). For both *P. fibratus* and *P. porphyrostomus*, adults predominated amongst both live (62% for *P. fibratus* and 89% for *P. porphyrostomus*) and empty shells (73% for *P. fibratus* and 91% for *P. porphyrostomus*).

The distribution of shell height of live snails and empty shells found during the 2006 to 2008 surveys were remarkably similar within each species (Figure 4.2), except for a small difference in *A. fulica* where the proportion of live snails was higher than empty shells in the 60 to 90 mm range and in *P. fibratus* where 30-40 mm live shells were significantly less common than empty shells of the same size ($\chi^2=24.5$; $df=1$; $p<0.001$).

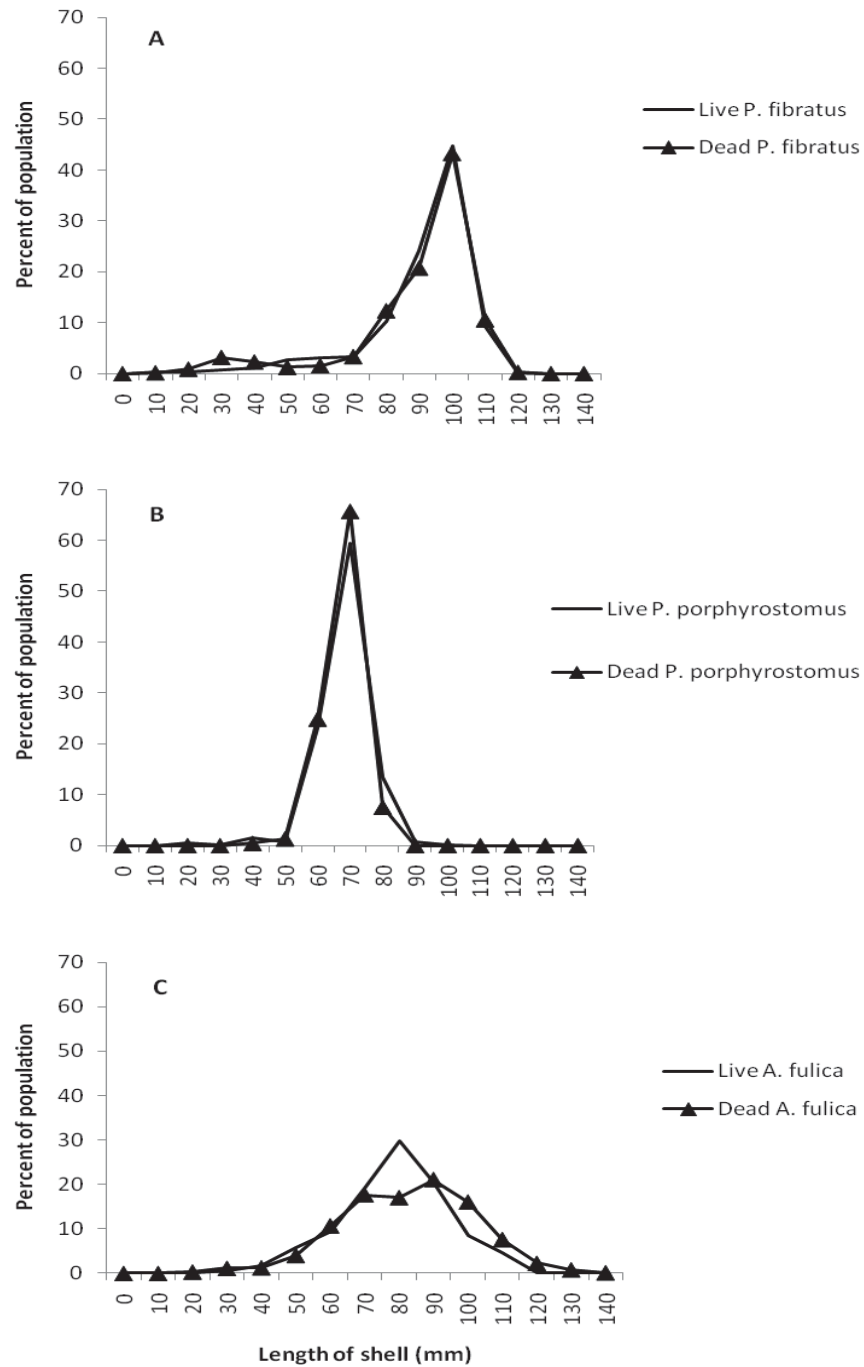


Figure 4.2: Frequency distributions of the total shell height of live and empty shells observed in the 224 quadrats of 100 m² on the Isle of Pines from 2006 to 2008. A: *P. fibratus*, B: *P. porphyrostomus* and C: *A. fulica*

The frequency distributions based on the aperture lip thickness (Figure 4.3) showed a higher proportion of empty shells in the 3-4 mm to 7-8 mm thickness range than live snails for *P. fibratus*, and in the 4-5 mm to 6-7 mm thickness range for *P. porphyrostomus*. The mean aperture thickness was significantly higher for dead shells than for live individuals for both *P. fibratus* (Mann-Whitney test, $p < 0.001$) and *P. porphyrostomus* (Mann-Whitney test, $p < 0.05$). In both species the proportion of snails with an aperture lip of zero was consistently higher in live snails ($X^2 = 181.9$, $DF = 1$, $p < 0.0001$ for *P. fibratus* and $X^2 = 27.2$, $DF = 1$, $p < 0.0001$ for *P. porphyrostomus*).

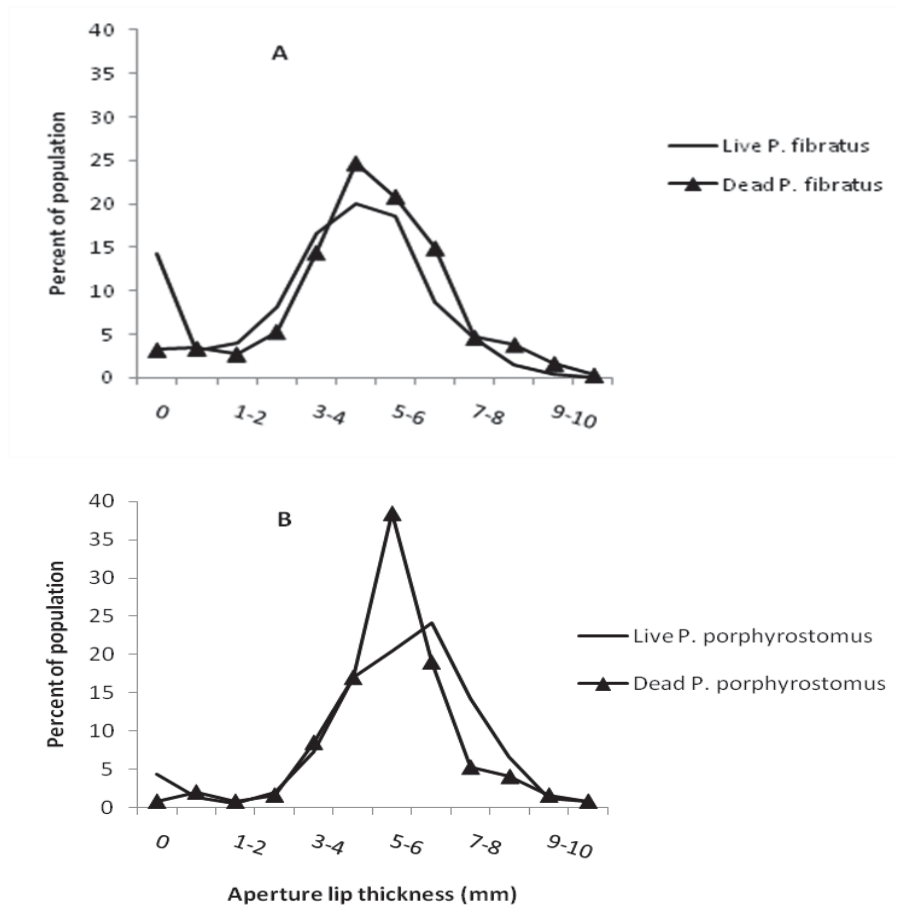


Figure 4.3: Frequency distributions of the aperture lip thickness of live and empty shells observed on the 224 quadrats of 100 m² on the Isle of Pines from 2006 to 2008. A: *P. fibratus*, B: *P. porphyrostomus*.

The number of dead and live snails across the 224 quadrats were significantly but weakly correlated (Figure 4.4) for each species: Pearson correlation coefficient= 0.4 ($p < 0.0001$); 0.3 ($P < 0.001$) and 0.2 ($p < 0.001$) respectively for *P. fibratus*, *P. porphyrostomus* and *A. fulica*.

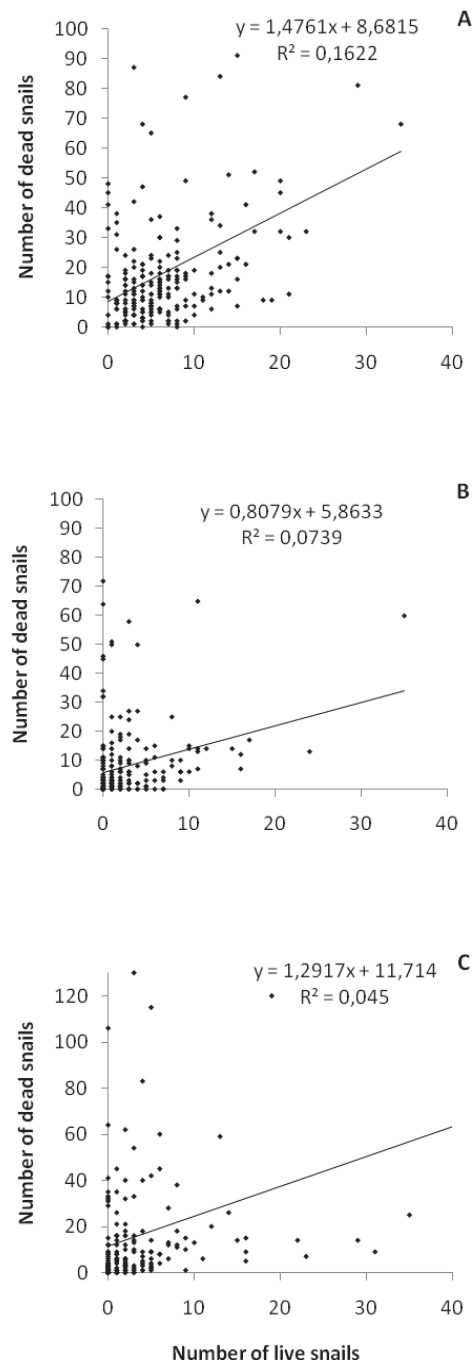


Figure 4.4: Number of live snails plotted against the number of dead snails for the 224 quadrats of 100 m² on the Isle of Pines from 2006 to 2008. A: *P. fibratus*; B: *P. porphyrostomus*; C: *A. fulica*.

4.3.3 Empty shell accumulation

For each species on the two permanent 400 m² quadrats at each site, a steady accumulation of dead shells was recorded from 2005 to 2009 (Figure 4.5). The number of empty shells varied for each of the five sites. Empty shell accumulation (number of newly dead shells found) since the quadrats were first searched in 2005 varied across quadrats and sites for each species (Table 4.3). When the two very first surveys in 2005 were excluded (because lots of empty shells of unknown age were present), the accumulation rate of shells on the Isle of Pines varied from 1.3 to 27.2 shells per six month survey in 400 m² for *P. fibratus*, 0 to 10.8 shells for *P. porphyrostomus* and 0 to 76.6 shells for *A. fulica*. Similarly, in dry forest, the accumulation rate of shells varied from 0.6 to 12.8 shells per six month survey in 400 m² for *P. porphyrostomus* and 5.2 to 149.1 shells for *A. fulica*.

Given these accumulation rates and the maximum number of empty shells found in quadrats when they were first searched in 2005 (Table 4.4) and assuming that the recruitment of newly dead shells has remained constant, the maximum persistence of empty shells of each species would be 37 years for *P. fibratus*, 80 years for *P. porphyrostomus* and two years for *A. fulica* on Isle of Pines. In dry forest, the maximum persistence of empty shells would be nine years for *P. porphyrostomus* and one year for *A. fulica*.

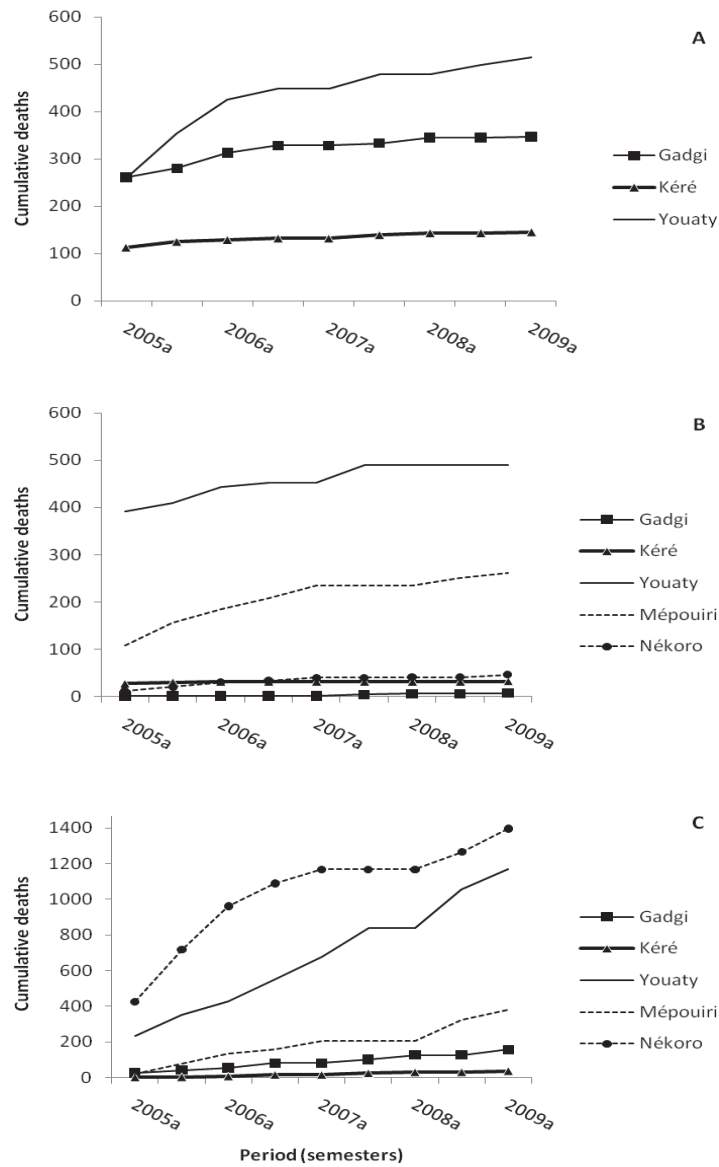


Figure 4.5: Cumulative counts of the numbers of new empty shells of each species found in the two 400 m² quadrats on the Isle of Pines (in Gadgi, Kéré and Youaty districts) and dry forest (Mépouiri and Nékoro) by 6-monthly period for each species (a: first semester from January to June and b: second semester from July to December) from 2005 and 2009 in the mark-recapture study)

A- For *P. fibratus* in Gadgi ($Y=10.133X+269.33$; $R^2=0.83$); Kéré ($Y=3.6167X+115.36$; $R^2=0.91$) and Youaty ($Y=26.383X+301.97$; $R^2=0.81$)

B- For *P. porphyrostomus* in Gadgi ($Y=0.8667X-1.2222$; $R^2=0.82$); Kéré ($Y=3.3833X+28.639$; $R^2=0.54$); Youaty ($Y=12.6X+393.22$; $R^2=0.88$); Mépouiri ($Y=17.033X+122.94$; $R^2=0.87$) and Nékoro ($Y=3.8X+14.667$; $R^2=0.86$)

C- For *A. fulica* in Gadgi ($Y=15.767X+9.3839$; $R^2=0.98$); Kéré ($Y=4.8167X-6.4167$; $R^2=0.97$); Youaty ($Y=115.93X+102.33$; $R^2=0.99$); Mépouiri ($Y=39.183X-5.9167$; $R^2=0.93$) and Nékoro ($Y=100.3X+538.83$; $R^2=0.84$)

Table 4.3: Mean shell accumulation (number of dead shells found per six-month period) by site and species in the two 400 m² quadrats combined on the Isle of Pines and in dry forest from 2005 to 2009 in the mark-recapture study

	Gadgi	Kéré	Youaty	Mépouiri	Nékoro
<i>P. fibratus</i>	5.4 ±1.7	2.0 ±0.7	15.9 ±11.3	-	-
<i>P. porphyrostomus</i>	0.4 ±0.2	0.3 ±0.6	6.1 ±4.7	9.6 ±3.2	2.1 ±1.5
<i>A. fulica</i>	8.2 ±3.5	2.3 ±2.5	58.4 ±18.2	22.4 ±17.2	60.8 ±88.3

Table 4.4: Number of empty shells of each species found in the two 400 m² quadrats (quadrat 1 / quadrat 2) on the Isle of Pines and in dry forest the first time they were searched in the mark-recapture study

	Gadgi	Kéré	Youaty	Mépouiri	Nékoro
<i>P. fibratus</i>	140/121	96/17	221/39	-	-
<i>P. porphyrostomus</i>	0/1	10/17	224/168	64/44	11/1
<i>A. fulica</i>	7/18	0/0	60/173	12/9	78/348

4.3.4 Causes of mortality

The identified causes of snail deaths based on empty shells found for *P. fibratus*, *P. porphyrostomus* and *A. fulica* by age (adult or juvenile) (Tables 4.5, 4.6 & 4.7) were natural mortality (i.e. undamaged empty shells), rodent predation, pig predation and trampling by feral cattle on the Isle of Pines, and natural mortality and rodent predation in dry forests.

Juvenile P. porphyrostomus and P. fibratus

Rodent predation was the main cause of juvenile death both for *P. fibratus* on Isle of Pines and for *P. porphyrostomus* in dry forest during the four year survey. In the dry forest, 87.6% of all of the empty juvenile shells of *P. porphyrostomus* appeared to have died from rodent predation (Table 4.5a) and 73.2% of *P. fibratus* on Isle of Pines (Table 4.6a).

Rodent predation on juvenile *P. fibratus* were significantly different within sites on Isle of Pines (Binomial ANOVA, $F_{2,3}=13.258$, $p<0.001$). The mean overall annual rodent predation rate on juvenile *P. fibratus* in the two quadrats was 67.1 % (95% CI= 46.9-87.1%) [59.2% (95% CI= 33.7-84.7%) in Gadgi, 47.6% (95% CI= 0-100 %) in Kéré and 86.0% (95% CI= 66.4-100%) in Youaty]. The mean height of

rodent damaged shells was 34.2 ± 3.2 mm ($n=131$; min=12.8 mm; max=80 mm) in *P. fibratus* and 29.6 ± 1.4 mm ($n=110$; min=15 mm; max=50 mm) in *P. porphyrostomus*.

In dry forest, the mean overall annual rodent predation rate on juvenile *P. porphyrostomus* was 87.2% (95% CI= 87.3-87.1%) and predation rates were not significantly different between the two sites (Binomial ANOVA, $F_{1,2}=0.0002$, $p=0.989$) [93.5% (95% CI= 93.4-93.5%) in Mépouiri, 81.9% (95% CI= 66.3-97.5%) in Nékoro]. We could not identify the causes of mortality on juvenile *P. porphyrostomus* on the Isle of Pines. On the Isle of Pines, 27% of empty juvenile shells found for *P. fibratus* were caused by natural death (Table 4.6a).

Table 4.5: Total numbers of (a) juvenile and (b) adult *P. porphyrostomus* snails found dead and causes of mortality in the two 400 m² quadrats for each of five sites in the mark recapture study from 2005 to 2009 in dry forest and on the Isle of Pines. Note that no dead juvenile *P. porphyrostomus* were positively identified on the Isle of Pines, hence no data are presented for them.

(a) Juveniles

		Rat Predation	Natural Mortality
Dry forest	Mépouiri	141	20
	Nékoro	78	11

(b) Adults

		Rat and pig predation	Natural Mortality
Isle of Pines	Gadgi	0	7
	Kere	0	32
	Youaty	0	489
Dry forest	Mépouiri	0	101
	Nékoro	0	48

Table 4.6: Total numbers of (a) juvenile and (b) adult *P. fibratus* snails found dead and causes of mortality in the two 400 m² quadrats for each of five sites in the mark recapture study from 2005 to 2009 in dry forest and on the Isle of Pines.

(a) Juveniles

		Rat Predation	Natural Mortality
Isle of Pines	Gadgi	20	28
	Kere	58	12
	Youaty	151	44

(b) Adults

		Pig predation	Cattle Crush	Natural Mortality
Isle of Pines	Gadgi	61	0	238
	Kere	6	6	69
	Youaty	339	0	117

Adult *P. porphyrostomus* and *P. fibratus*

In both the Isle of Pines and dry forest, natural mortality was the only cause of death of adult *P. porphyrostomus* (100% of all of the empty adult shells found during the four year survey appeared to have died from natural causes (Table 4.5b)), and it was also common in adult *P. fibratus* (50.7% of all the empty shells found) on Isle of Pines (Table 4.6b). Pig predation (evident in 48.6% of all empty adult shells found during the four year survey) was recorded in localized areas on the Isle of Pines, namely in Gadgi and, most commonly, in Youaty; the differences between these sites were significant (Binomial ANOVA, $F_{2,3}=146.8$, $p<0.001$). The two patches of dry forest on the mainland were fenced and therefore pig-proof. Similarly, the only place where adult snails were found crushed by cattle was on the Isle of Pines, and then only in Kéré district. This was responsible of 0.7% of the whole deaths for adults on the whole Isle of Pines.

Achatina fulica

In dry forest and on Isle of Pines respectively, 49.7% and 97.3% of all of the empty *A. fulica* shells found during the four year survey appeared to have died from natural causes (Table 4.7). Rats were the other source of deaths and were responsible for 2.7% of the mortality of *Achatina fulica* on the Isle of Pines and 50.3% in dry

forest on the mainland (Table 4.7). The rodent predation rates were significantly different between all five sites (Binomial ANOVA, $F_{4,5}=280.38$, $p<0.001$), and also differed between the Isle of Pines and the dry forest areas (Binomial ANOVA, $F_{1,8}=1011.1$, $p<0.001$). No difference on rodent predation within sites on Isle of Pines existed (Binomial ANOVA, $F_{2,3}=1.84$, $p=0.1581$), but there was a significant difference between the two sites on dry forest (Binomial ANOVA, $F_{1,2}=106.7$, $p<0.001$).

Table 4.7: Total number of *Achatina fulica* found dead and causes of mortality in the two 400 m² quadrats for each site in the mark recapture study from 2005 to 2009 on the Isle of Pines and in dry forest.

		Rat Predation	Natural Mortality
Isle of Pines	Gadgi	7	149
	Kere	0	37
	Youaty	30	1138
Dry forest	Mépouiri	103	277
	Nékoro	790	607

4.3.5 Snail vulnerability to predation by rodents

The caged rodent trial conducted in captivity showed that rodents did not eat significantly more snails when this was their only available food resource (T test $T_{30,28} = -1.08$, $P>0.05$) (Figure 4.6). Mice were able to eat eggs, newborns (< 5 mm in height), and juvenile stage 1 (height ≤ 22 mm, lip= 0 mm). *Rattus rattus* and *R. exulans* also ate eggs and newborns in the same proportions as mice (Kruskall Wallis tests, $P>0.05$), but they consumed four times more juvenile stage 1 than mice did (Kruskall Wallis tests, $P<0.05$) and they were also able to eat juvenile stage 2 (height ≤ 47 mm, lip= 0 mm) and sub-adult (height ≤ 65 mm, lip= 0 mm) snails. Adults (height ≥ 85 mm, lip= 0 mm) were not eaten by any of the rodents.

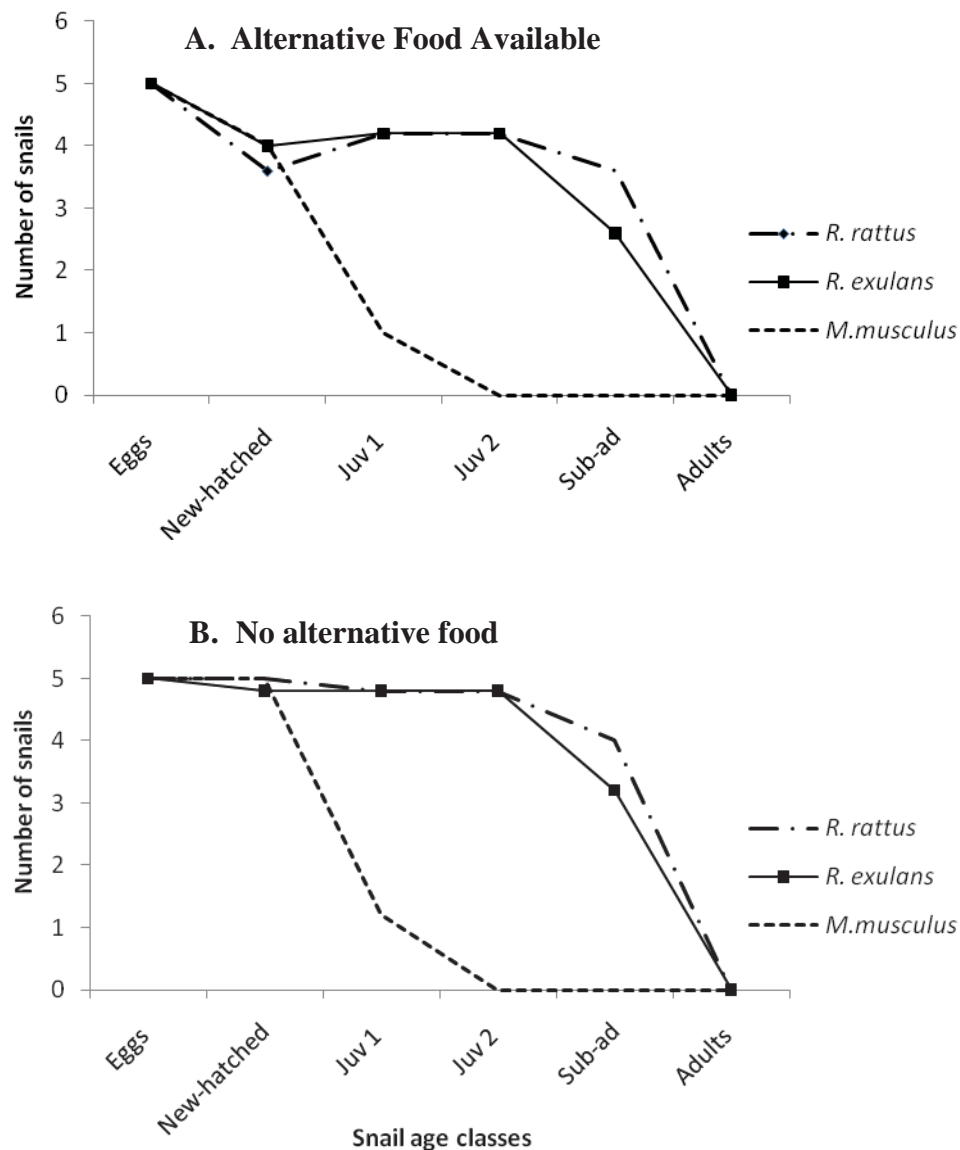


Figure 4.6: Mean number of *Placostylus* snails of each age class (eggs, new-hatched, juveniles 1 (height ≤ 22 mm, lip = 0 mm), juveniles 2 (height ≤ 47 mm, lip = 0 mm), sub-adults and adults) eaten after three nights in captivity by the three species of caged rodents caught in a dry forest (A) when an alternative food source was available for the rodents and (B) when rodents had only snails to eat.

4.3.6 Survival and fecundity

Large numbers of *P. fibratus* snails were found during the mark-recapture study on the Isle of Pines, but very few *P. porphyrostomus* were found either here or in the dry forest, and only a single dead *P. porphyrostomus* was found at each of these sites (Table 4.8). Thus, there were insufficient data to estimate survival rates for *P. porphyrostomus* at either site using MARK software.

Table 4.8: Numbers of snails by species on Isle of Pines and in dry forest that were marked during the four-year mark-recapture study, and the numbers of marked snails found dead over this period.

Sites	Species	Stages	Number of marked	Number found
			snails	dead
Dry Forests	<i>P. porphyrostomus</i>	Juvenile	0	0
		Sub-adult	19	1
		Adult	51	0
Isle of Pines	<i>P. fibratus</i>	Juvenile	13	0
		Sub-adult	450	18
		Adult	635	45
Isle of Pines	<i>P. porphyrostomus</i>	Juvenile	0	0
		Sub-adult	11	0
		Adult	55	1

For all Isle of Pines quadrats combined, survival, recapture, recovery and fidelity estimates for *P. fibratus* obtained with MARK per six months periods are presented Table 4.9. Annual survival rates were 59.0% for juveniles and 70.0% for adults. The probability of recapture was assumed to be equal for juveniles and adults and was 22% per annum; the recovery rate (probability of being found dead during surveys) was also assumed to be the same for both snail category and was 0.8%. The probabilities of fidelity to the sampling region were high for both adults (100%) and juveniles (98%).

Table 4.9: Real function parameters (survival, recapture, recovery, and fidelity rates) for *P. fibratus* on Isle of Pines for all sites combined obtained with MARK for six-month periods.

Parameters	95% confidence interval			
	Mean	SE	Lower	Upper
<i>Adult survival</i>	0.84	0.009	0.82	0.86
<i>Juvenile survival</i>	0.77	0.02	0.73	0.81
<i>Probability of recapture</i>	0.47	0.01	0.45	0.48
<i>Probability of recovery if dead</i>	0.09	0.009	0.07	0.10
<i>Adult fidelity</i>	1.00	0.34 ^{E-6}	0.99	1.00
<i>Juvenile fidelity</i>	0.99	0.03	0.26 ^{E-3}	1.00

For *P. porphyrostomus* in dry forests, based on the number of transpondered snails detected during each search session every six months, I calculated an estimate for mean adult and juvenile survival rates (Table 4.10). On average, adult survival was 75.7% per six month period (95% CI= 66.2-85.2%) for *P. porphyrostomus* in dry forest from 2005 and 2009 (i.e. annual survival rate of about 57%). Average juvenile survival rate for six month periods was 33.3% (95% CI= 6.4-60.2%) for *P. porphyrostomus* in dry forests (i.e. annual survival rate of about 11%). On Isle of Pines, adult survival for *P. porphyrostomus* was about 36% per six month period (i.e. annual survival rate of about 13%) and juvenile survival was estimated only in Youaty (52% per six month period, or 27% per annum).

Table 4.10: Mean ($\pm 95\%$ CI) six-monthly adult and juveniles survival rates (in %) recorded on the Isle of Pines and dry forests for *P. porphyrostomus* on each site (two 400 m² quadrats combined) from 2005 to 2009. No live *P. porphyrostomus* were present in Gadgi.

	Isle of Pines		Dry forest	
	Kere	Youaty	Mépouiri	Nékoro
Adult Survival (%)	39.6 \pm 43.4	33.3 \pm 14.8	72.2 \pm 16.7	82.6 \pm 15.6
Juvenile Survival (%)	-	52.2 \pm 43.3	29.2 \pm 33.0	50.0 \pm 97.9

The mean fecundity rates for each species in each pair of 400 m² quadrats are presented in Table 4.11. For each six-month survey, these estimates are based on the number of new juvenile snails found in a survey divided by the estimated number of breeding-age snails present in the quadrat in the previous survey. Mean fecundity was 0.73 young per adult across all six-monthly samples from 2005 to 2009 (95% CI= 0.24-1.2) for *P. fibratus* and 0.28 young per adult (95% CI= 0.11-0.45) for *P. porphyrostomus* in dry forests.

Table 4.11: Mean ($\pm 95\%$ CI) six-monthly fecundity (in number of young per adults) recorded on the Isle of Pines and dry forests for each species and each site (two 400 m² quadrats combined) from 2005 to 2009.

	Fecundity				
	Isle of Pines			Dry forest	
	Gadgi	Kere	Youaty	Mépouiri	Nékoro
<i>P. fibratus</i>	0.26 \pm 0.08	0.27 \pm 0.08	1.67 \pm 1.18	-	-
<i>P. porphyrostomus</i>	-	0	0.25 \pm 0.32	0.41 \pm 0.34	0.27 \pm 0.02

The indigenous egg predator - the snail *Ouagapia inaequalis* (Pfeiffer, 1854) (Rhytidae) was frequently found on the egg clutches. Of the 25 *P. fibratus* egg clutches found on the Isle of Pines and two *P. porphyrostomus* clutches found in dry forest) we recorded a *Ouagapia* predation rate of 68% for *P. fibratus* with 1.56 ± 0.66 *O. inaequalis* per clutch, and of 100% for *P. porphyrostomus* in dry forest with on average 1.5 *O. inaequalis* per clutch. 75% of the eggs of one clutch in dry forest had already been destroyed by this predator when I found it and there were three *O. inaequalis* present.

4.3.7 Growth and lifespan

Data on the growth rates of marked snails were limited by the fact that the marked snail population mainly comprised adults since it was difficult to find and recapture juveniles presumably due to their arboreal behaviour and the high rates of mortality in young life stages. Changes in the maximum shell height of the *P. porphyrostomus* in Mépouiri and Nékoro and *P. fibratus* on Isle of Pines that were marked and re-measured in the mark-recapture study are shown in Figure 4.7.

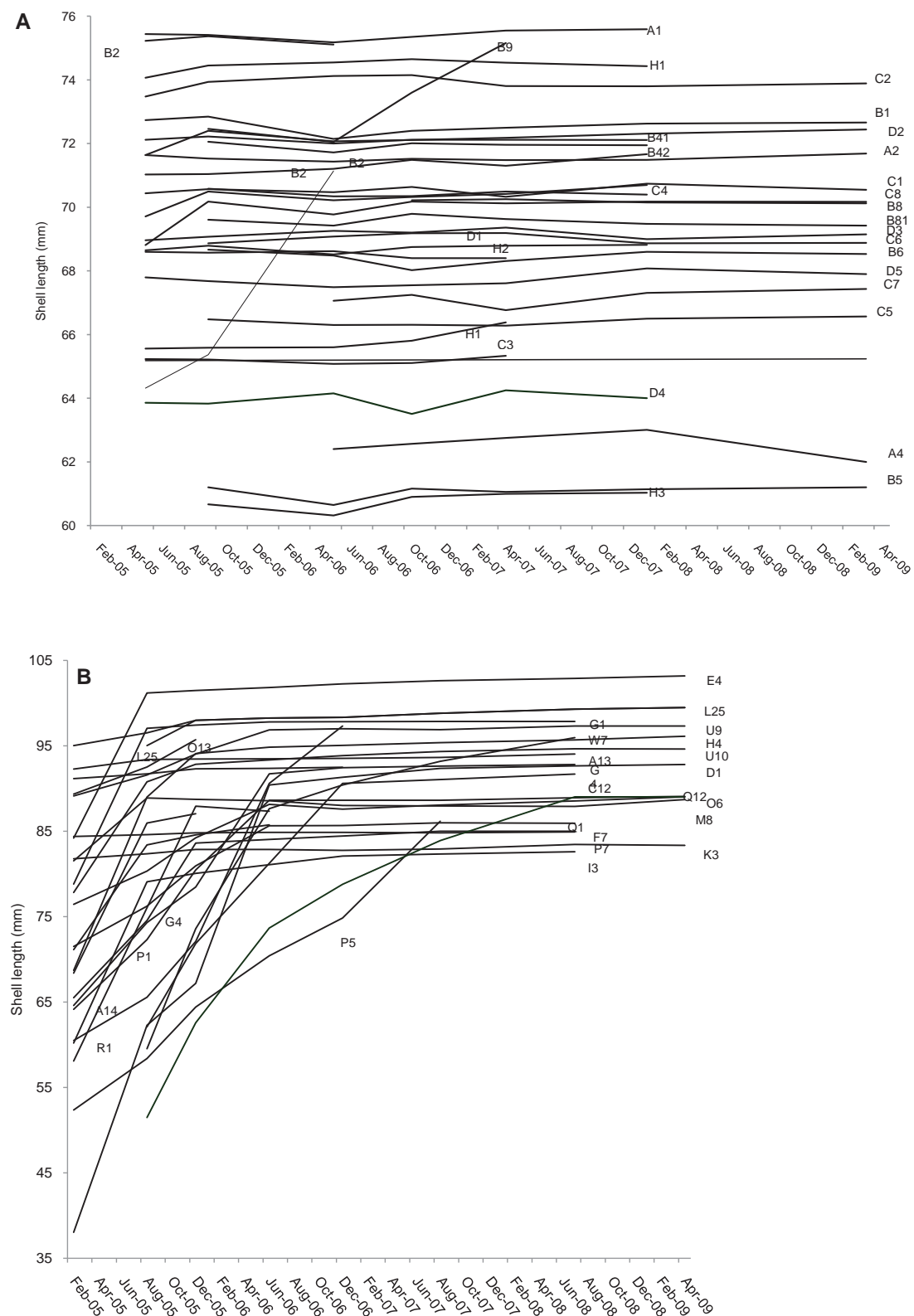


Figure 4.7: Changes in maximum shell height of (A) *Placostylus porphyrostomus* in dry forests, and (B) *P. fibratus* on the Isle of Pines recorded in the mark-recapture study.

The rate of increase in shell height reduced and approached an asymptote when graphed as the snails approached maturity and little further increase in height occurred once they were adult. The rate at which individuals reached this asymptote also varied considerably (Fig. 4.7). On average, juveniles grow at between 6 and 8 mm in height per year (Table 4.12). The lip thickness continues to increase in adult snails and the annual gain in lip thickness was not significantly different between adults and juveniles for either *P. porphyrostomus* in dry forest (Mann-Whitney test $U=78.0$, $p>0.05$) or *P. fibratus* on Isle of Pines (Mann-Whitney test $U=132.0$; $P>0.05$). The increase in height was significantly greater for juveniles than for adults for *P. fibratus* on Isle of Pines (Mann-Whitney test $U=58.9$; $P<0.01$) and for *P. porphyrostomus* in dry forest (Mann-Whitney test $U=5.0$; $p<0.001$). There were no significant differences in the rates of increase in thickness of the aperture lip in *P. porphyrostomus* when comparing snails from the Isle of Pines with those from dry forests in either juvenile (Mann-Whitney test $U=30.0$, $p>0.05$) or adult snails (Mann-Whitney test $U=2286.0$, $p>0.05$), or for increase in height for juveniles (Mann-Whitney test $U=20.0$, $p>0.05$) and adults (Mann-Whitney test $U=2143.0$, $p>0.05$).

Table 4.12: Mean growth ($\pm 95\%$ CI) in shell height and aperture lip (in mm per year) of juvenile and adult *P. fibratus* and *P. porphyrostomus* on the Isle of Pines and in dry forest recorded from 2005 to 2009 in the mark-recapture study.

	Isle of Pines				Dry forest			
	Juveniles		Adults		Juveniles		Adults	
	Lip	Height	Lip	Height	Lip	Height	Lip	Height
<i>P. fibratus</i>	1.97	8.44	0.53	0.41	-	-	-	-
	± 0.3	± 2.07	± 0.12	± 0.18				
	(204)	(203)	(755)	(707)				
<i>P. porphyrostomus</i>	0.87	6.45	0.50	2.42	1.15	8.49	0.38	0.29
	\pm	± 7.44	± 0.33	± 2.76	\pm	± 4.38	± 0.11	± 0.10
	0.77	(10)	(50)	(32)	1.20	(7)	(149)	(149)
	(10)				(7)			

One *P. fibratus* snail, D1, was found with an initial shell height of 38.04 mm and a weight of 5 g in January 2005 and was found again on each search session until 2009. It showed a linear rate of growth until the aperture lip started to become thicker when elongation started to slow (the aperture lip grew from 2.39 mm to 4.83 mm and

height from 91.32 mm to 92.34 mm between December 2006 and August 2007 (Figure 4.8)). During the linear growth phase, a significant regression of growth through time ($\text{Height} = 0.0698 \times \text{Days} + 43.832$, $R^2 = 0.79$) enabled date of birth to be estimated to be 7 May 2003. It therefore took four years to reach maturity (an aperture lip of 3.5 mm).

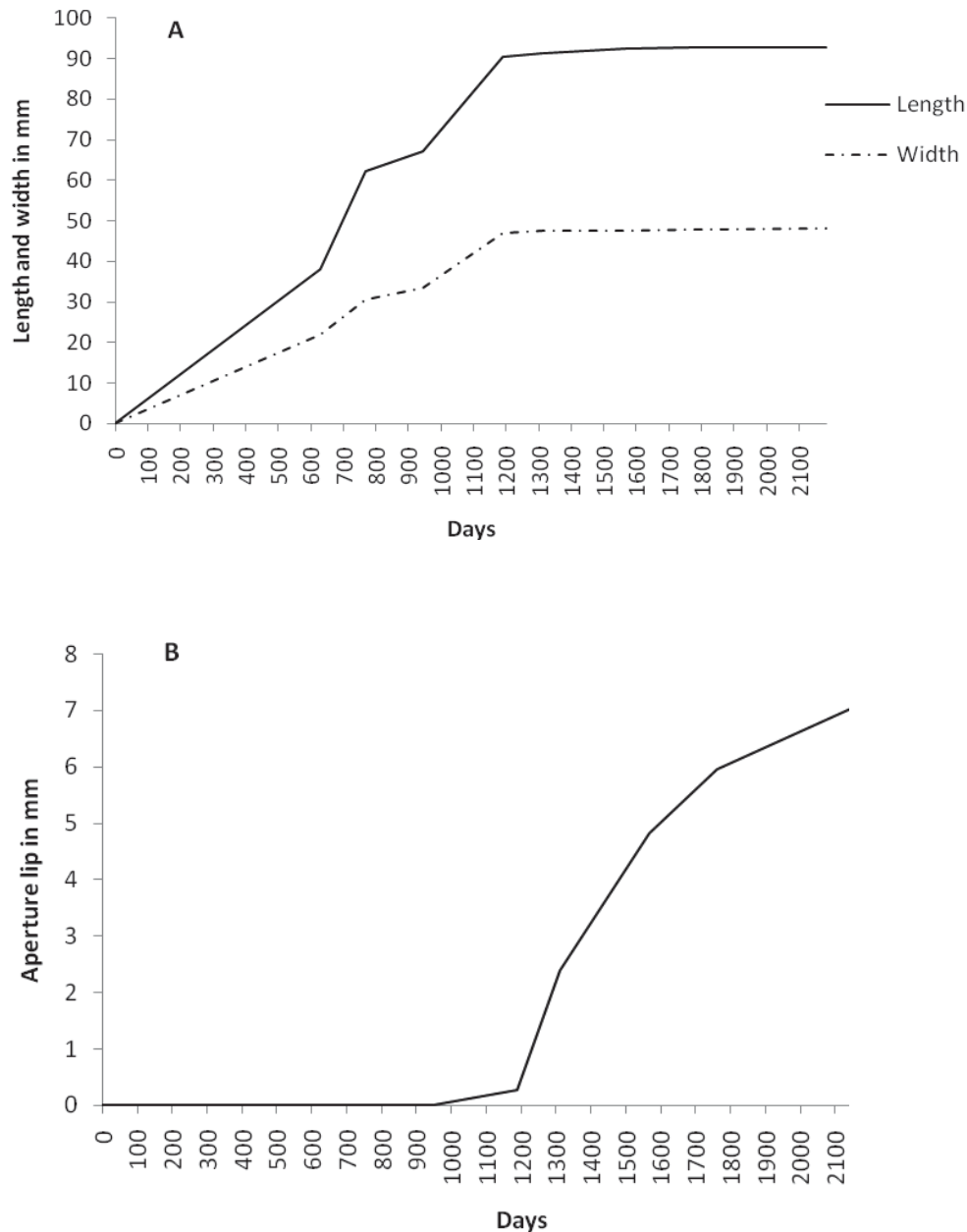


Figure 4.8: Growth of one *Placostylus fibratus* (D1) obtained from a linear interpolation of the observed growth in the first stages recorded in the mark-recapture study from its estimated date of birth in May 2003 to the last survey where it was found again in April 2009 on the Isle of Pines. A: growth in height and width; B: growth of the aperture lip.

4.4 Discussion

4.4.1 Snail density and population structure

Placostylus population densities, studied here between 2005 and 2009, differed across sites, with *P. fibratus* densities on the Isle of Pines in a well-preserved humid forest being greater (about 6 snail/100 m²) than the more scattered and isolated populations of *P. porphyrostomus* in dry forests (about 1 snail/100 m²).

All species of New Caledonian *Placostylus* were more abundant and widespread than they are today judging by historical records, and by the frequent presence of old shells in forests indicating former populations where no living snails exist today (Pisier 1985; Pöllabauer 1995; Brescia and Pöllabauer 2005; Philippe Bouchet, pers. comm. 1999). Empty shells are more common than live snails since empty shells can persist for many years on the forest floor. Indeed, the empty shell accumulation I recorded showed a long persistence of shells, up to 37 years for *P. fibratus*, 80 and 9 years for *P. porphyrostomus* respectively on Isle of Pines and in dry forest, and 1 to 2 years for the introduced African snail *Achatina fulica* in dry forest and Isle of Pines. Shell degradation appears dependant on environmental conditions and is accelerated when shells are exposed to direct sunlight, such as occurs in dry forests which are characterised by trees of medium height and an undercover that has been significantly damaged by introduced ungulates. Shell degradation is also dependant of the shell structure: *P. porphyrostomus* is thicker and more calcified than *P. fibratus*; while in contrast, *A. fulica* presents a much thinner shell. In these conditions, the presence of old *Placostylus* shells in forests is proof of past populations but does not provide reliable information about their past abundance and may give an illusion of once much high densities. Shells of *A. fulica* do not persist a long time in the field so high densities of empty shells on the ground would more accurately reflect high densities of live snails.

Adult-sized individuals predominate amongst both the live snails (62% for *P. fibratus* and 89% for *P. porphyrostomus*) and the empty shells (73% for *P. fibratus* and 91% for *P. porphyrostomus*) and possibly indicate aging *Placostylus* populations. For both species, recently-hatched or juvenile snails are rarely found in the field. Moreover, when they are found, a high proportion of the hatchlings and non-hatched eggs found are usually dead, suggesting that the eggs and hatchlings are very susceptible to desiccation or predation.

I found higher densities of juveniles in the Youaty district on the Isle of Pines compared to Gadgi and Keré. This may be related to the relatively lower rodent abundances at this site leading to reduced predation. In a previous study in July 2005 using snap-traps (Brescia 2005), I estimated the catch rates of ship rats *Rattus rattus* in Youaty as 8.8 rats per 100 corrected trap nights and the Polynesian rat *R. exulans* at 21.3 rats per 100 corrected trap nights. At the same time, rodent indices were five times higher for *R. rattus* and two times higher for *R. exulans* in Gadgi.

The population structure of New Caledonian *Placostylus* species appears to be similar to those of the New Zealand taxa reported by Choat & Schiel (1980), Penniket (1981), and Stringer *et al.* (2004) which have also been under sustained rat predation pressure for more than a century. The New Zealand *Placostylus* populations are now mostly small and widely isolated and persist by possessing a pool of large rodent-resistant and long-lived adults (Choat & Schiel 1980) with little recruitment (Penniket 1981).

In terms of density estimates, New Zealand and Lord Howe Island *Placostylus* are evidently much higher than seen in New Caledonian populations of *P. fibratus* and *P. porphyrostomus*. Mean densities of live adults and juveniles of *P. hongii* on the Poor Knights Islands were variously estimated at 0.78/m² (Stringer *et al.* 2004), 1.9/m² (Choat & Schiel 1980) and 8.1/m² (Penniket 1981). For *P. bollonsi*, Brook & Laurenson (1992) recorded densities of between 2-6/m² in local patches, but overall mean densities ranged from 0.15 to 0.35 /m². On Lord Howe Island, *P. bivaricosus* occurred at an average density of 0.24 live adults and 0.33 live juveniles per square metre, with localised densities of up to two live animals per square metre in patches of good microhabitat (Murphy & Nally 2004). These figures are several times higher than densities found for either *P. fibratus* or *P. porphyrostomus* in New Caledonia (0.06 and 0.02 / m², Table 4.2).

The giant African snail was introduced into New Caledonia in 1972 (Gargominy *et al.* 1996) and has spread rapidly all over the island from disturbed habitat to native vegetation and is at present locally surpassing the abundance of native malacofauna. Elsewhere where it has been introduced, *A. fulica* is considered a threat to the continued existence of the native flora (Mead 1979) and it may also compete with some local snail species (Craze *et al.* 2002). I found that the pestiferous giant African snail was between three and seven times more abundant than *P.*

porphyrostomus in dry forests, and it was the second most abundant species found in quadrats of the 2006-2008 survey on Isle of Pines after *P. fibratus* for both live and empty shells. But densities there were also probably higher: due to their arboreal behaviour and their ability to dig deep into the ground during dry periods, I have almost certainly underestimated their abundance.

4.4.2 Growth rate

My data showed that growth of *Placostylus* is slow and related to age. Shell height increments and aperture lip thickness were greater for juveniles than for adults. Shell growth in juveniles attained up to 10.51 mm per annum for *P. fibratus* on Isle of Pines, to 13.89 mm and 12.87 mm for *P. porphyrostomus* respectively on the Isle of Pines and in dry forests.

Placostylus appear to require almost four years to reach maturity. In a comparative study of growth under natural and artificial conditions, Brescia (2004) estimated mean increments of 18 mm in shell height per annum in 30 juveniles of *P. fibratus* monitored in forest habitat on the Isle of Pines between February and June 2004. In captivity over the same period, when snails were fed an artificial diet (see below), animals in the same age class had mean growth rates about 2.5 times higher (44 mm shell height per annum). In the dry year of 1994, Pöllabauer (1995) documented that growth rates (shell height increments) were in the order of 5 to 19 mm per annum. However, it appears that *P. fibratus* exhibits great plasticity in growth rates and is able to respond to favourable environmental conditions - one marked individual grew from a shell height of 2.4 cm to reach maturity at 9.6 cm over the course of a single year.

The rate of increase in shell height for the New Zealand *P. hongii* varied from 6 to 25 mm per year in juveniles with shells < 38 mm in height, but slowed when adults reached maturity. Subsequently, the lip thickness increased about 0.1 to 0.4 mm per year but this growth rate varied considerably between individuals. In a study of size-frequency of *Placostylus bollonsi caperatus* Powel, 1948 from West Bay on Great Island (Three Kings Islands), Brook and Laurenson (1992) indicated an increase in shell height of about 25-30 mm per year, and that snails attain adult size at about three years old.

4.4.3 Lifespan

Placostylus fibratus are large snails that reach 80–100 g when adult with a shell height of 9–15 cm while *P. porphyrostomus* are somewhat smaller (7–8 cm in shell height, 45 g). Pöllabauer (1995) estimated that *P. fibratus* reaches maturity at five years and, based on a prediction of shell growth rates, suggested that they may live 15 years and attain 11.7 cm shell height. Based on the annual growth rate in height for a juvenile, I estimate here that four years are needed for a newborn *P. fibratus* to become sexually mature. As the increase in shell height more or less stops when the snail reach maturity (3.5 mm for the aperture lip), I attempted to evaluate lifespan based on the growth of the lip on adults. The mean aperture lip observed in my surveys for both live and empty adult snails was 5.54 ± 0.09 mm (n=945) with a maximum observed of 10.57 mm. Considering the mean and range of annual increases in aperture lip thickness (Table 4.12), it may take somewhere between 19 to 30 years to reach the maximum observed lip thickness and between 8 to 12 years to attain the mean aperture lip size. Due to the lack of juveniles of *P. porphyrostomus*, my data did not enable us to estimate lifespan of this species. Nevertheless, observations reported in New Zealand on other species of *Placostylus* suggested a long lifespan for the whole genus. Thus, Parrish *et al.* (1995) re-captured alive in 1991 snails that had been first marked in 1979 and suggested that the New Zealand species *P. hongii* (Lesson, 1830) and *P. ambagiosus* (Suter, 1906) may live to 20 years or more. *P. hongii* have survived in captivity for more than five years (Penniket 1981), and in a growth study, Stringer *et al.* (2004) suggested that *P. hongii* may also live at least 10 years and possibly more than 30 years supporting the conclusions of Choat and Schiel (1980). In discussing New Zealand *Placostylus*, Penniket (1981) suggested that the long lifespan in these animals may be a strategy to compensate for living in environments where recruitment to the breeding population may be irregular and variable. Published literature would suggest that most temperate zone pulmonates would typically have a lifespan of only one or two years (Lazaridou-Dimitriadou 1995), although Okorie (2003) kept *Archachatina marginata* in captivity for 6.5 years.

4.4.4 Survival, fecundity and mortality

As has been observed in New Zealand (Choat & Schiel 1980), New Caledonian *Placostylus* populations appear to be maintained by a pool of large and long-lived adults which produce many juveniles each with a low expectancy of reaching adult size. I found that fecundity may be high in some populations of *P. fibratus* (e.g. in Youaty district with 1.7 new juveniles/adult per 6 month period), and variable in the dry forest populations of *P. porphyrostomus* (0.27 in Nékoro and 0.41 juvenile/adult/6 months in Mépouiri). On the Isle of Pines, I could not identify dead juvenile *P. porphyrostomus* due to the difficulty of distinguishing them from juvenile *P. fibratus*. Hence, juvenile natural mortality rates for *P. fibratus* were probably slightly over-estimated but the effect was likely to be minimal due to the much greater abundance of *P. fibratus* compared to *P. porphyrostomus* (996 snails versus 62 *P. porphyrostomus* on the Isle of Pines identified between 2005 and 2009 in the mark recapture study).

Annual adult survival was relatively high for *P. fibratus* (i.e. 70% calculated by MARK) and lower on *P. porphyrostomus* in dry forest (estimated from transpondered snails at 57%). Rodent predation appeared to be the major cause of mortality on juveniles, being responsible for 73.2% of the deaths of *P. fibratus* on Isle of Pines and 87.6% of deaths of *P. porphyrostomus* in dry forest. In this context, population viability remains uncertain for these populations and this is particularly true of the dry forest sites. The high level of rodent predation in these forests must seriously jeopardise recruitment. Rodent predation on *A. fulica* appears to be more common in dry forests than on the Isle of Pines (50.3% versus 2.7%). In the evergreen forests of the Isle of Pines, rodents may find food resources all through the year and therefore consume *Placostylus* at relatively moderate rates while in the mainland dry forest, and particularly during drought, *P. porphyrostomus* may represent a particularly attractive food source. Fewer empty shells of *A. fulica* were recorded as damaged by rodents; their arboreal behaviour may enable them to escape from rodent predation or the thin shells of this species may cause them to disappear quickly after being damaged by rats.

For *P. bollonsi* in New Zealand, at least 60% of hatchlings fail to attain adulthood (Brook & Laurenson 1992). This high juvenile mortality may be a natural feature of the population dynamics of *Placostylus* and one that is not conducive to rapid population recovery, but it is possible that it is the result of a novel additional source of mortality that may have driven the populations into decline. Brook and

Laurenson (1992) suggest that recruitment to the adult population, which is always uncertain, depends on favourable conditions of climate and habitat. The long life of adults may provide some buffering against this uncertainty. Penniket (1981) suggests that a low proportion of empty adult shells relative to live snails would be the first indication that a population is recovering.

Pöllabauer (1995) suggested that on the Isle of Pines, the presence of an indigenous carnivorous snail *Ouagapia inaequalis* (Pfeiffer, 1854) may further threaten *Placostylus* recruitment. She frequently observed up to three of these egg predators within *Placostylus* egg clutches, and noted that they have the potential to destroy all the eggs in a clutch. This is consistent with what I observed during this study, underling the fact that egg mortality rates may be very high in New Caledonian *Placostylus*, possibly exceeding 90%.

In the field, egg laying in New Caledonian species has been observed to occur primarily during the cool season, but the reproductive season of *P. fibratus* on the Isle of Pines can extend until October (Pöllabauer 1995). Clutches of 25 to 450 eggs are deposited in nests formed in depressions in the soil. *P. fibratus* kept in captivity under semi-natural conditions frequently produce eggs several times per year (observed range 1 to 4 clutches) at similar times of the year to snails in the wild (Brescia 2004, 2005). Clutches averaged 205 eggs (SD = 84; n=103, range 13 to 515). The hatching success in captivity is now in the order of 70%. However, newly-hatched or juvenile snails are rarely found in the field. Moreover, when they are found, a high proportion of hatchlings and non-hatched eggs are usually dead, suggesting that the eggs and hatchlings are very susceptible to desiccation and predation. Also, small juveniles show an arboreal behaviour and so empty shells of these fall to the ground.

4.4.5 Relevance to conservation management

The life history patterns of *Placostylus fibratus* and *Placostylus porphyrostomus* can be summarised as being species that exhibit slow growth and reach maturity late, laying high number of eggs per clutch but with high mortality of newborns, and have long life spans and reproductive life. New Caledonian *Placostylus* have evolved in the absence of vertebrate predators and their life history reflects this. Agents that selectively destroys the adults (such as human collection, predation by feral pigs) or the juveniles (rodent predation), or any modification of their habitat (destruction, impact of introduced ungulates) therefore threaten these populations.

Core goals for the preservation of the New Caledonian *Placostylus* should therefore include preservation of remaining habitats, translocations, reintroductions or supplementations with captive-bred snails, eradication or control of introduced predators (by rodent poisoning or fencing areas against feral pigs), control of the introduced African snail which may compete for food and shelter, and sustainable harvest for human consumption. From a conservation management perspective, Stringer *et al.* (2004) suggest that the recovery of *Placostylus* populations in New Zealand is likely to take many years if the number of adults is low to start with. Furthermore, Choat and Schiel (1980) argue that the persistence of populations is the result of a pool of long-lived large adults (10 to 30 years) which are better able to survive unfavourable conditions than small juveniles and thus the populations are best regarded as remnants with questionable long-term viability.

Further work is required to enhance knowledge of the life history of New Caledonian *Placostylus*, and particularly a more exact understanding of causes and rates of mortality of newborn stages is needed. Nevertheless, these first results on the demographic characteristics of New Caledonian *Placostylus*, are sufficient to serve as the basis for the construction of a demographic model that could be used to predict the effects of predation and harvests on snail dynamics and allow the development of a plan for the sustainable use of the resource and the long-term persistence of populations (Chapter 8).

4.5 Acknowledgements

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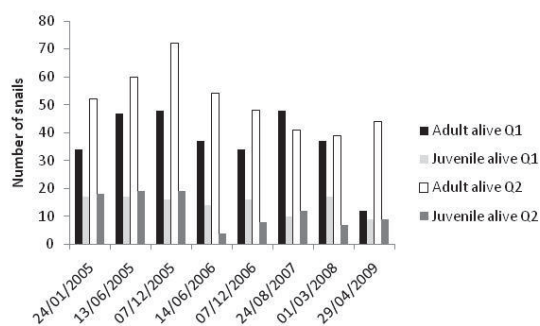
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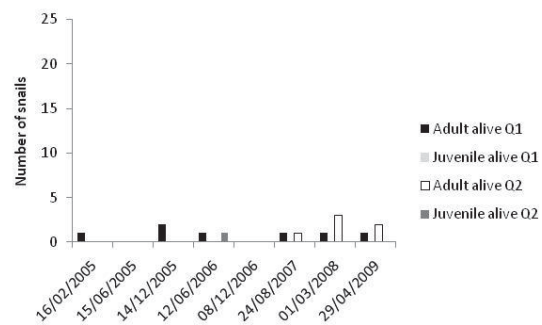
*4.7 APPENDIX 1: NUMBER OF LIVE ADULT AND JUVENILE PLACOSTYLUS AND ACHATINA
SNAILS FOUND IN EACH OF THE TWO QUADRATS FOR EACH SITE AND SPECIES IN THE MARK
RECAPTURE STUDY FROM 2005 TO 2009 IN DRY FOREST AND ON ISLE OF PINES*

GADGI

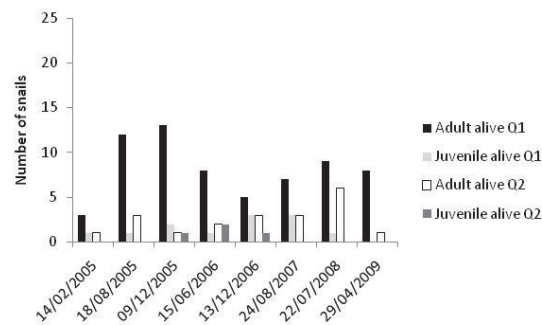
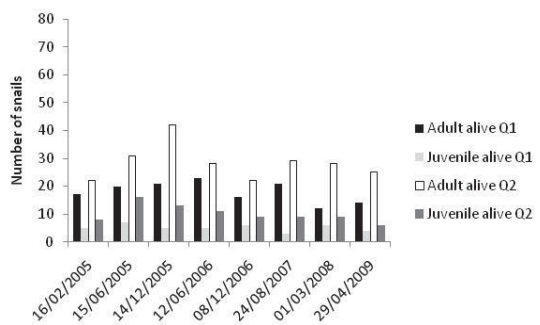
Placostylus fibratus



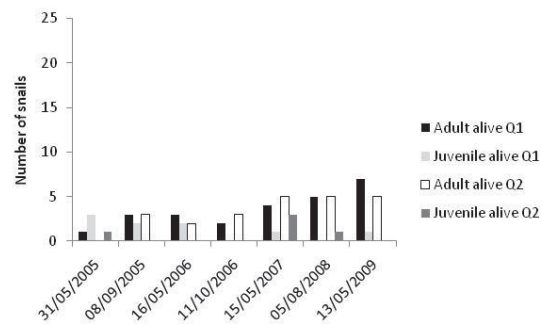
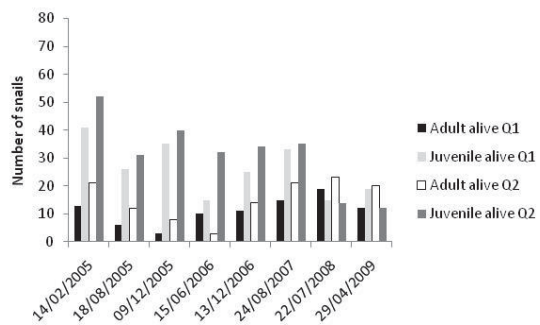
Placostylus porphyrostomus



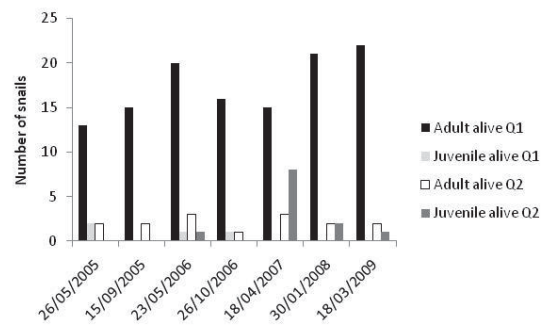
KERE



YOUATY



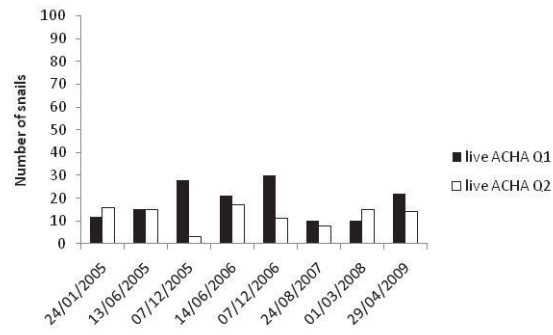
MEPOUIRI



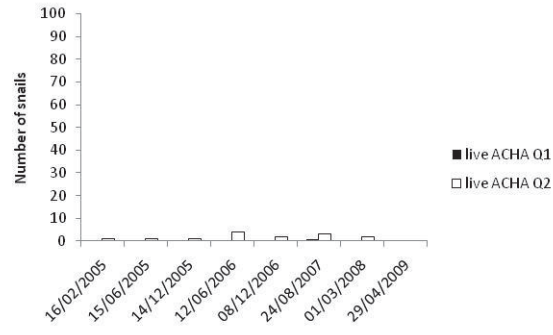
NEKORO

Achatina fulica

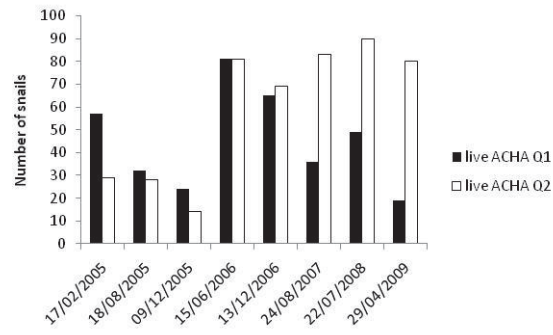
GADGI



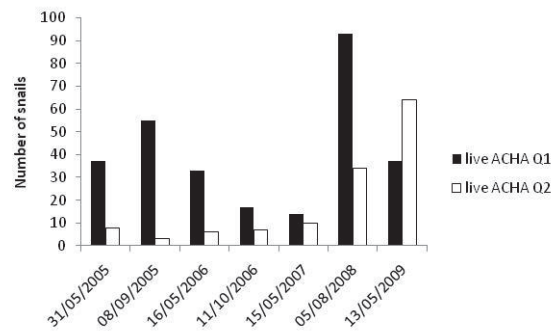
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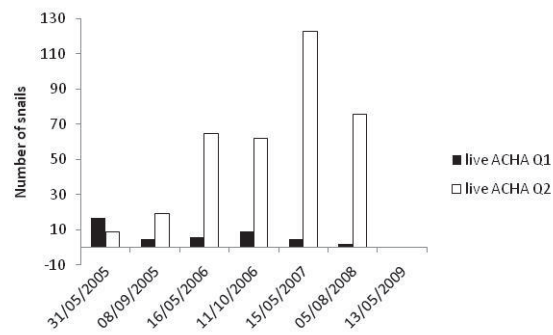
YOUATY



MEPOUIRI



NEKORO



CHAPTER 5

THE ABUNDANCE OF INTRODUCED RODENTS (*RATTUS* SPP. AND *MUS MUSCULUS*), AND THE EVALUATION OF TWO ABUNDANCE INDEX TECHNIQUES IN WET AND DRY FORESTS OF NEW CALEDONIA: APPLICATION TO THE CONSERVATION OF AN ENDEMIC LAND SNAIL OF THE GENUS *PLACOSTYLUS* (GASTROPODA: BULIMULIDAE)



Daily rodent catches with 50 rat traps (left), and rodent-damaged Placostylus shells easily identified by the broad spiral band removed from one or more whorls (right)

Abstract

Little information exists on rodent abundance in New Caledonia, and no information is available concerning the survey of relative and absolute abundances. We estimated ship rat (*Rattus rattus*), Polynesian rat (*Rattus exulans*) and mouse (*Mus musculus*) densities by snap trapping, tracking tunnels and wax blocks in a native rainforest on Isle of Pines in the south of New Caledonia, and in a remnant native dry forest on the west coast in the north of the New Caledonian mainland (Nékoro). In ten days of trapping (in an effective trapping area of 6.86 ha) 43 ship rats, 113 Polynesian rats and two mice were caught on the Isle of Pines, whereas in Nékoro 102 ship rats, 28 Polynesian rats and no mice were trapped. These data generated high density estimates of 25.4 rats ha⁻¹ in the rainforest (23.0 – 34.6 rats ha⁻¹, 95% confidence intervals) and 19.1 rats ha⁻¹ in the dry forest (18.9 – 23.6 rats ha⁻¹, 95% confidence intervals). Ship rats and Polynesian rats were found sympatrically. High dispersal from the untrapped surrounding forest into the trapping grids may have partially obscured the relationships between rat trapping rates, tracking rates and wax block bite marks. Rodent densities were high enough for tracking rates to saturate and reach 100% for much of the time in these forests whereas wax block chewing rates declined and apparently therefore more readily detected changes in these high-density rodent populations. We recommend the use of both techniques in future rodent control operations in New Caledonian forests to increase the confidence in population trends.

ABONDANCE DES RONGEURS INTRODITS (RATTUS SPP. ET MUS MUSCULUS), ET EVALUATION DE DEUX METHODES INDICIAIRES D'ABONDANCE EN FORETS HUMIDE ET SECHE DE NOUVELLE-CALEDONIE: INTERET POUR LA CONSERVATION DES ESCARGOTS TERRESTRES DU GENRE PLACOSTYLUS (GASTROPODES : BULIMULIDAE)

Résumé

Très peu de travaux ont été consacrés aux rongeurs introduits en Nouvelle-Calédonie, et les informations relatives au suivi des abondances relatives et absolues sont quasi-inexistantes. Les densités de rats noirs (*Rattus rattus*), de rats polynésiens (*Rattus exulans*) et de souris domestique (*Mus musculus*) ont été estimées par piégeage, par l'utilisation de tunnels à empreintes et d'appâts attractifs non empoisonnés (Waxtags) en forêt sèche à Nékoro (Poya) et en forêt humide sur l'Ile des Pins. Après 10 jours de piégeage consécutifs (dans une zone effective de piégeage de 6.86 ha), 43 rats noirs, 113 rats polynésiens et 2 souris ont été capturés à l'Ile des Pins, alors qu'à Nékoro, 102 rats noirs et 28 rats polynésiens ont été piégés (aucune souris). Les densités de rats apparaissent fortes et sont estimées à 25.4 rats ha⁻¹ en forêt humide (23.0 – 34.6 rats ha⁻¹, 95% IC) et 19.1 rats ha⁻¹ en forêt sèche (18.9 – 23.6 rats ha⁻¹, 95% IC). De manière singulière, les rats noirs et rats polynésiens peuvent vivre sympatriquement au sein du même habitat en Nouvelle-Calédonie. La relation entre la densité absolue obtenue à partir du piégeage, et la densité relative obtenue à partir des deux méthodes indiciaires (tunnels à empreintes et Waxtags) a été en partie masquée par des déplacements de rats en direction de la zone de piégeage. Les densités de rats ont été si élevées que les tunnels à empreintes sont arrivés à saturation (100%) dans les deux types de forêts alors que les appâts non empoisonnés (Waxtags) ont déclinés ; ceux-ci apparaissent alors plus aptes à détecter des variations au sein des populations de rongeurs dans ces zones à fortes densités. L'utilisation des deux méthodes indiciaires de manière conjuguée est recommandée lors des opérations futures de régulation des rongeurs dans les forêts calédoniennes afin d'augmenter la précision des observations relatives aux variations de populations de rongeurs.

5.1 Introduction

Introduced predators are thought to be the second most important cause of the extinction of species in island ecosystems next to habitat loss (Atkinson 1985; 1989; King 1985). In pre-human New Caledonia, the only native terrestrial mammals were bats (Revillod 1914). Polynesian rats (*Rattus exulans*) were introduced 3,000 years ago by the first human colonisers, and ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*) arrived in the 19th century (Gargominy *et al.* 1996; Pascal *et al.* 2006).

Rodents have the potential to impact on a great many species, and have been implicated in the decline of native species across a broad taxonomic spectrum (Varnham 2010). Together, these four rodents constitute a grave threat to native biota, particularly on islands (Atkinson, 1977, 1985). The land snail faunas of the islands of the tropical Pacific typically comprise species that are endemic to single islands or archipelagos (Cowie 1998), and have frequently suffered heavily from predation by rats (Hadfield 1986). In New Caledonia, snails from the genus *Placostylus*, which comprises six endemic species, are highly threatened by rodent predation, habitat loss and human harvesting for consumption (Brescia *et al.* 2008). In the evergreen forests of the Isle of Pines, *Placostylus fibratus* is favoured as food by humans, and as a result, has been over-collected from the wild, while in the sclerophyllous (dry) forests (currently the most endangered of the Caledonian biomes with only ca 1% remaining), *P. porphyrostomus* is threatened by habitat destruction and modification by feral introduced ungulates. An additional threat to both species is predation by rodents (Brescia *et al.* 2008). In New Caledonia, anecdotal studies have noted the species of rodents present in various locations (Nicholson & Warner 1953; Ekstrom *et al.* 2000), but little information exists on rodent abundance (Robinet & Salas 1996; Robinet *et al.* 1998; Rouys & Theuerkauf 2003) and therefore it is unclear what level of predation pressure rodents exert on vulnerable species.

As part of a larger study on the ecology of New Caledonian *Placostylus*, and more specifically to determine whether rodent control would assist in recovery of these snails, we conducted a survey of the relative and absolute abundance of rodents in evergreen and sclerophyllous forests using relative density indices and trapping with the scope to reach local extinction. The indices are less costly and time-consuming to measure than absolute abundance (Blackwell *et al.* 2002). Footprint tracking, snap

trapping and non-poison baits (Waxtags©) are the techniques commonly used to provide relative indices of rodent density in New Zealand (King & Edgar 1977; Innes 1990; Innes *et al.* 1995). However, comparisons of relative indices of population abundance to infer changes in absolute abundance assume that the index is directly related to real abundance (Brown *et al.* 1996).

The aims of the study were to (i) identify which species of rodents occur in evergreen and sclerophyllous forests of New Caledonia, (ii) estimate densities from trapping to local extinction, (iii) establish the relationship (calibration) between relative rodent abundance obtained by two index methods (footprint tracking and Waxtags©) and absolute density, and (iv) provide recommendations on the best way to survey New Caledonian rodent populations, an issue of major concern to managers undertaking rodent control programmes to determine when the target threshold density of rodent is attained and thus evaluate the success of operations.

5.2 Methods

5.2.1 Study areas

The work was conducted in New Caledonia which has three major seasons: a hot wet season (mid November-mid May; mid April-mid May is a transition period); a cool dry season (mid May-mid September); and a hot dry season (mid September-mid November) (ORSTOM 1981).

Two sites with contrasting vegetation were selected (Figure 5.1). The first site, Négoro, near Poya, is a privately-owned ranch located on the western coast of “Grande-Terre” (altitude 0-100 m asl). It is one of the last remaining moderately large remnant patches of native sclerophyllous forest (272 ha) with about 150 ha of forest recently fenced in 2007 to exclude rusa deer (*Cervus timorensis*) and cattle (*Bos taurus*). The forest contains a small remnant snail population (*P. porphyrostomus*) with a mean density of 2.3 snails / 100 m² (SD = 2.8) (Brescia & Pöllabauer 2004, 2005).

The second site is in Gadgi on the Isle of Pines (152 km²), an island 50 km south of the New Caledonian mainland. The vegetation here is a native evergreen humid forest on coral soil, 15-20 m high, composed of Kohu trees *Intsia bijuga*, Buni *Manilkara dissecta* and columnar pine trees *Araucaria columnaris*. This site has a

higher density of *Placostylus* snails (*P. fibratus*) (0.025 to 0.18 snails per m²) and they are regularly collected for sale to local restaurants (Brescia *et al.* 2008).

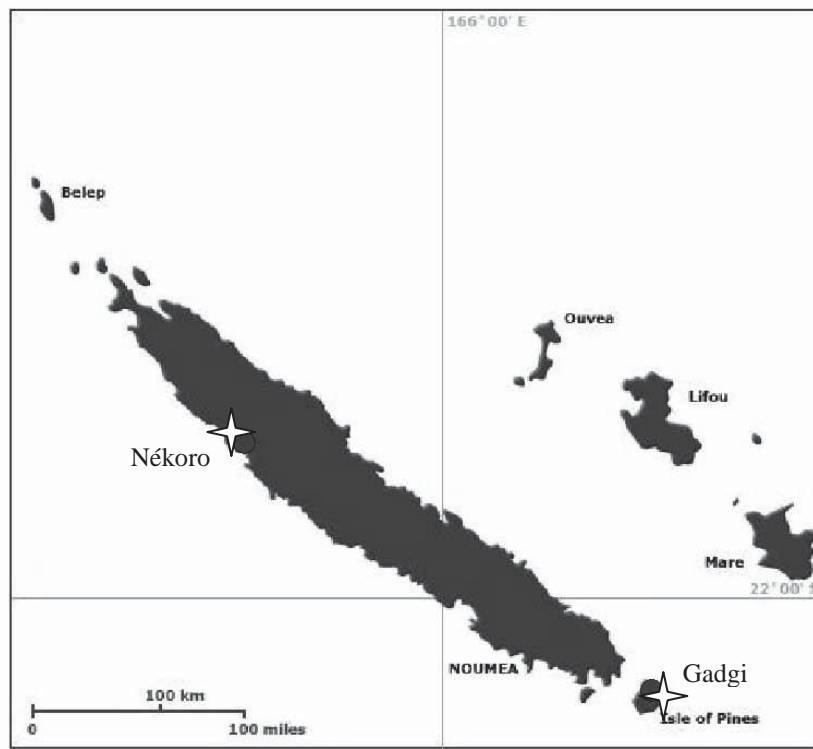


Figure 5.1: Map of New Caledonia and the two study sites: a rainforest on Isle of Pines (Gadgi) and a dry forest in Nékoro (Poya).

5.2.2 Grid trapping and tracking experiment

The absolute density of rodents was estimated by the “Zippin Removal” method (Zippin 1958). This method uses plots of nightly catch against cumulative catch to estimate by extrapolation the number of rodents left untrapped in the study area.

We followed a slightly modified version of the protocol of Brown *et al.* (1996). A 150 x 150 m grid was established at both sites. Ninety-eight “Trapper” snap-traps (Pest Management Services, NZ) - 49 Snap E rat trap and 49 “E” mouse traps - were placed in pairs on the grid at 25 m intervals. Traps were baited with cheese and peanut butter and were placed under plastic tunnels to reduce the risk to non-target species.

Traps were checked daily, and we noted at which traps rodents were caught, and whether bait was taken or the trap sprung. Trapping success was corrected for

sprung and bait-taken traps by subtracting half a trap night for each such occurrence (Nelson & Clark 1973).

An array of 16 rodent footprint-tracking tunnels (The Trakka, Connovation Ltd.) and 16 non toxic wax blocks (Waxtags©) (Thomas *et al.* 1999) were placed within one metre of the traps, at 50 m intervals on four lines. The wax blocks, which are bitten by rodents in search for food, measured approximately 25 x 15 x 5 mm and were moulded in plastic ice cube trays using microcrystalline wax containing 5% orange oil as an attractant. The tracking tunnels were baited with cheese and peanut butter each day and one-night tracking rates were recorded. The wax blocks were examined daily and the one-night frequency of rodent bite marks was determined. Used tracking cards and wax blocks were replaced daily.

At both sites, the tracking and bite-mark rates were started one day before the trapping started (6 June 2007 in Nékoro and 17 July 2007 on the Isle of Pines), and run over the subsequent 10 nights and for a further one night after the trapping session ended.

The effective trapping area was estimated by assuming a boundary strip of 56 m (Dice, 1938) beyond the 150 x 150 m area trapped. The boundary strip was determined by adding the radius ($r = 56$ m) of a circular average home range of 1 ha, based on radio telemetry of ship rats in North Island in New Zealand (Hooker & Innes 1995). This resulted in an effective trapping area of 6.86 ha at each study site. However, Rouys (2008), in a preliminary radio-tracking study, found smaller home ranges for New Caledonian rodent species: 0.86 ha for female ship rats and 0.35 ha for males, and 0.33 ha for female Polynesian rats and 0.95 ha for males. Considering the minimum and maximum home range values for New Caledonian rodents, the effective trapping area would vary from 4.33 to 5.87 ha.

The processing of the trapped rats followed the methods of Cunningham & Moors (1996) and included details of species based on measurements for head-body length (HBL) and tail length (TL), assignment to either adult or juvenile, and sex (Theurkauf *et al.* 2010). Any scavenged rats were identified to species and/or sex as best as possible, depending on the state of the remains.

5.3 Results

More rats were trapped on the Isle of Pines in evergreen forest (158) than in the dry forest in Nékoro (130) in the ten days of trapping ($\chi^2=7.47$, d.f.=1, $p<0.001$). On the Isle of Pines, 43 *Rattus rattus*, 113 *R. exulans* and 2 *Mus musculus* were caught whereas in Nékoro 102 *R. rattus*, 28 *R. exulans* and no mice were trapped. Thus, *R. rattus* were caught more often in the dry forest whereas *R. exulans* were more abundant in the evergreen forest of the Isle of Pines (Table 5.1 and Figure 5.2)

Table 5.1: Trapping results per night, number of traps in field (effort), and waxtag and tracking-tunnel interferences in Nékoro (5 to 16 June 2007) and Isle of Pines (16 to 27 July 2007).

	Nights	1	2	3	4	5	6	7	8	9	10	11
Nékoro	Snap traps	49	49	49	49	49	49	49	49	49	49	
	<i>Rattus rattus</i>	32	18	13	10	7	7	4	5	3	3	
	<i>Rattus exulans</i>	0	1	0	1	1	2	10	4	5	4	
	Total rodents caught	32	19	13	11	8	9	14	9	8	7	
	Tracking tunnels	16	16	16	16	16	16	16	16	16	16	16
	Waxtags	16	16	16	16	16	16	16	16	16	16	16
	Track+	9	8	7	6	3	5	1	4	4	4	2
	Wax+	5	1	0	0	1	0	0	0	0	0	0
Isle of Pines	Snap traps	49	49	49	49	49	49	49	49	49	49	
	<i>Rattus rattus</i>	8	5	3	6	7	5	5	3	0	1	
	<i>Rattus exulans</i>	8	22	21	14	13	13	8	5	2	7	
	<i>Mus musculus</i>	0	0	0	0	1	0	1	0	0	0	
	Total rodents caught	16	27	24	20	20	18	13	8	2	8	
	Tracking tunnels	16	16	16	16	16	16	16	16	16	16	16
	Waxtags	16	16	16	16	16	16	16	16	16	16	16
	Track+	5	8	12	12	12	11	9	7	9	8	8
	Wax+	5	4	6	1	1	1	0	0	1	0	0

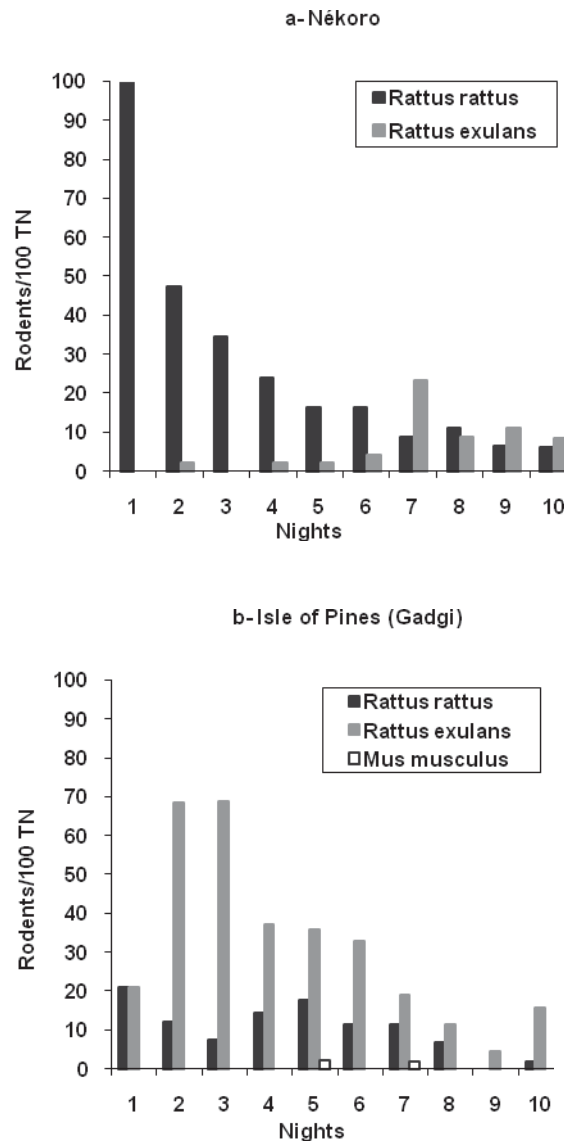


Figure 5.2: Nightly catches of rodents (per 100 corrected trap nights): a.- Nékoro and b.- Isle of Pines.

In the dry forest, the density of rats in the study area was estimated to be 19.1 ha^{-1} using the intercept value of the nightly catch regressed against the cumulative catch (131.3, Figure 5.3a.) and assuming an effective trapping area of 6.86 ha based on New Zealand rat home range sizes, but the true density may be as high as 30.3 ha^{-1} if the smallest home ranges estimated in New Caledonia by Rouys (2008) are used (Table 5.2).

On the Isle of Pines, the density of rats was estimated to be 25.4 ha^{-1} (an intercept value of 174.3 rats, Figure 5.3b) assuming New Zealand home range sizes or 40.2 ha^{-1} using the smallest New Caledonian home range estimate.

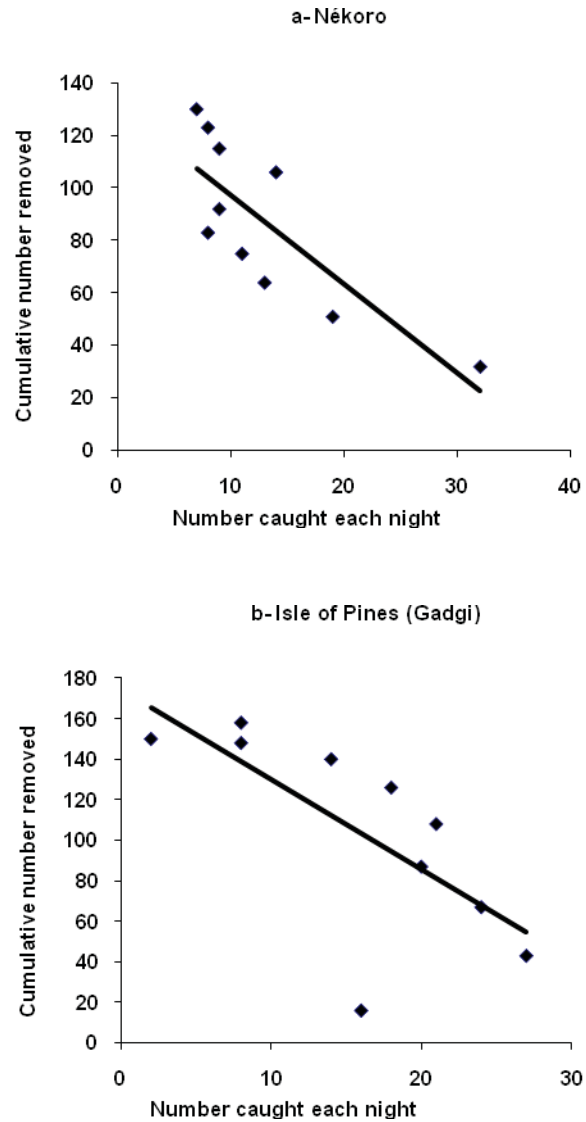


Figure 5.3: Nightly catch of rodents plotted against the cumulative number of rats killed

a- Nékoro in June 2007. The simple linear regression is given by the line.

$$y = -3.4x + 131.3 \quad (R^2 = 0.645).$$

b- Isle of Pines in July 2007. The simple linear regression is given by the line.

$$y = -4.4x + 174.3 \quad (R^2 = 0.500).$$

Table 5.2: Boundary effects on rodent density estimates based on home range size estimates for rodents in New Caledonian and in New Zealand.

	Nékoro			Isle of Pines	
Home range (Rouys, 2008)	Effective trapping area (ha)	Rat densities (rats ha ⁻¹)	95 % CI	Rat densities (rats ha ⁻¹)	95 % CI
Minimum = 0.35 ha	4.33	30.3	30.0-37.4	40.2	36.5-54.8
Maximum = 0.95 ha	5.87	22.3	22.1-27.6	29.7	26.9-40.4
New Zealand = 1 ha (Hooker & Innes, 1995)	6.86	19.1	18.9-23.6	25.4	23.0-34.6

At both sites, the percentage of tunnels tracked by rodents remained relatively high despite the presumed steady decrease in rat density due to trapping (Figure 5.4). High rates of tracking continued throughout this period presumably due to the attractive nature of tracking tunnels to the remaining rats and from dispersal. In contrast, the rodent use of wax blocks declined quickly in the trapped grid after the first three to four nights at both sites and then remained at zero until the end of the trapping session (Figure 5.4).

On the Isle of Pines, mouse footprint marks were recorded only on trapping nights 3, 5 and 6 (Figure 5.4b) and the percentage of tracking tunnels with mice did not increase with rat reduction.

To calibrate the two indirect indices of rat abundance against the estimated densities, we plotted each index against the absolute density of rats estimated to have been present on each successive night of the removal experiment at both sites in the 6.86 ha of effective trapping area based on average home range of ship rats in New Zealand. Simple linear regression analyses explained 69% ($p < 0.001$) and 73% ($p < 0.001$) of the variance in tracking rates respectively for Nékoro and Isle of Pines (Figure 5.5 a & b).

A linear regression forced through the origin explained 40% and 55% of the variance for the same sites. Similarly, a simple regression explained 55% ($p < 0.01$) and 74% ($p = 0.001$) of the variance in wax block chew-marks respectively for Nékoro and Isle of Pines, and a regression through the origin explained 44% and 68% of the variance for the same sites (Figure 5.5 c & d). The slopes of these regressions was less

for the wax blocks than for tracking tunnels as expected with the generally lower use of wax blocks, and in fact at both sites the correlations between the wax block index and the tracking index were not significant (Pearson Correlation, $R = 0.57$, $p > 0.05$ in Nékoro and $R = 0.08$, $p > 0.05$ on Isle of Pines).

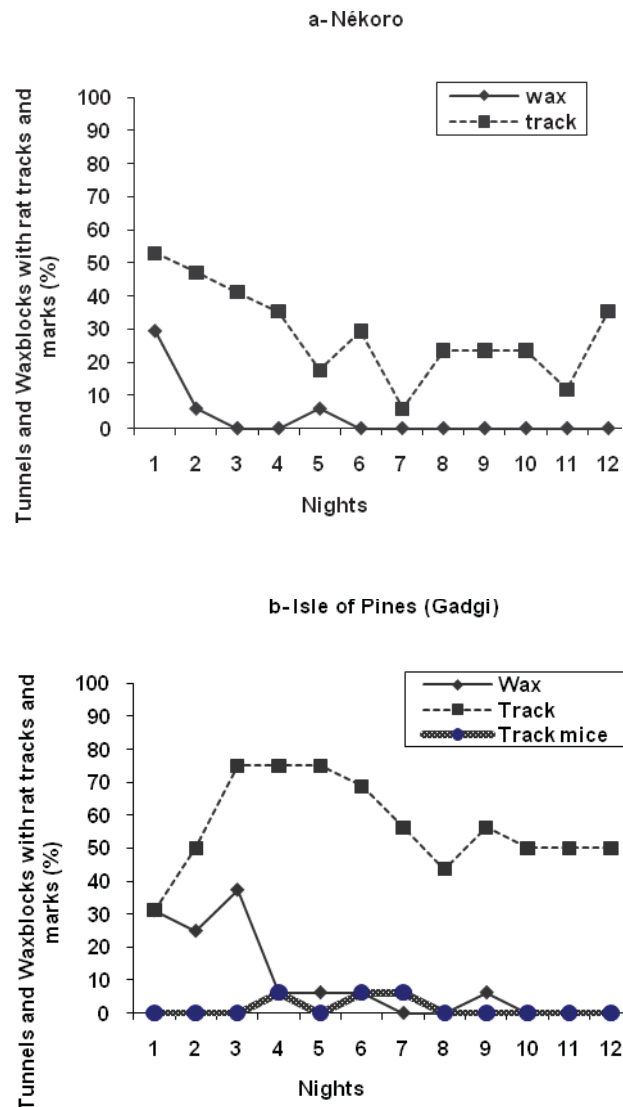


Figure 5.4: Percentage of tracking tunnels with rat footprint marks compared with the percentage of wax blocks bitten by rats:

a- Nékoro, 5 to 16 June 2007.

b- Isle of Pines, 16 to 27 July 2007.

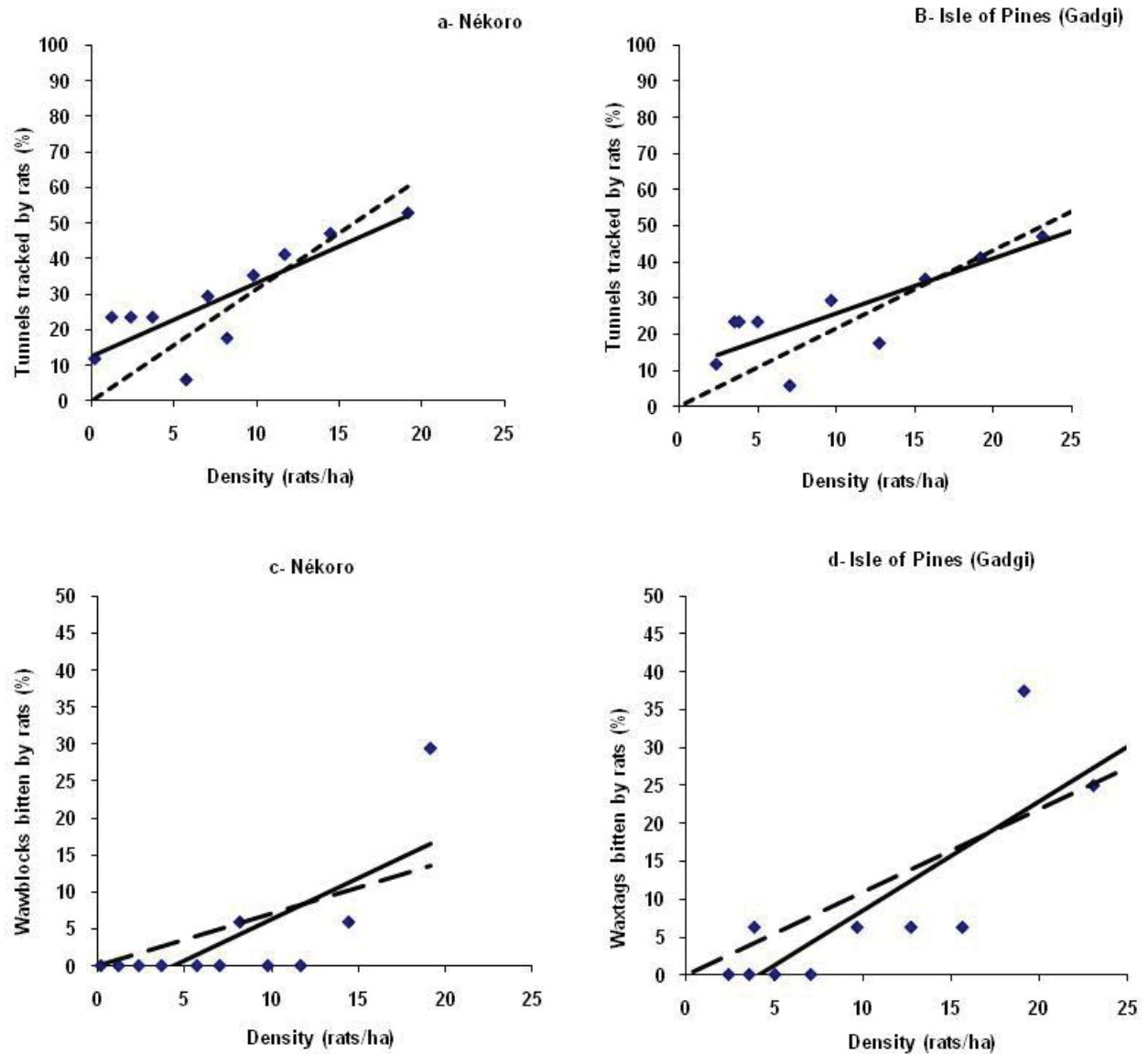


Figure 5.5: Calibration of nightly tracking and nightly wax block bite rates using the estimated number of rats still alive in successive nights in the Zippin removal experiment. The absolute density for each night was calculated as the average of the density at the end of trapping on the previous night, and the density at the end of the current night for which rate was measured.

- a- Tracking rates in Nékoro in June 2007. The simple linear regression is given by the line $y = 2.07x + 12.63$, $R^2 = 0.692$ and a regression forced through the origin is given by the dash line $y = 3.42x$, $R^2 = 0.402$.
- b- Tracking rates on Isle of Pines in July 2007. Simple linear regression $y = 1.52x + 10.68$ $R^2 = 0.349$ and forced through the origin $y = 2.16x$ $R^2 = 0.550$.
- c- Wax block bite rates in Nékoro. Simple linear regression $y = 1.11x - 4.71$ $R^2 = 0.549$ and forced through the origin $y = 0.71x$ $R^2 = 0.4386$.
- d- Wax block bite rates in Isle of Pines. Simple linear regression $y = 1.44x + 5.93$ $R^2 = 0.747$ and forced through the origin $y = 1.09x$ $R^2 = 0.683$.

5.4 Discussion

5.4.1 Species and abundance

This study provides one of the first quantitative rodent abundance estimates in New Caledonian forests and showed that ship rats *Rattus rattus* and Polynesian rats *Rattus exulans* are both very abundant in the sclerophyllous and evergreen forests of New Caledonia. The house mouse *Mus musculus* was found in evergreen forest only and then only in low numbers. We did not find any evidence of Norway rats *Rattus norvegicus*.

Similar removal studies in New Zealand have found much lower densities of rodents compared to our results for New Caledonian forests. We estimated 29.7 to 40.2 rats ha⁻¹ on the Isle of Pines and 22.3 to 30.3 rats ha⁻¹ in Nékoro compared to New Zealand estimates of 6.5 to 7.8 rats ha⁻¹ (Brown *et al.* 1996) and 7.1 to 8.2 ha⁻¹ (Blackwell *et al.* 2002). In native Hawaiian forests Sughara (1997) recorded densities more similar to ours; 13.0 rats ha⁻¹ in winter and 16.3 rats ha⁻¹ in summer for *R. rattus*. Varnham 2004, in a mark-recapture study on Rat Island, St Lucia indicated a density of 22.8 rats per hectare on a 1.4 ha island.

In the only other New Caledonian study that exists, carried out between April and August 2001 in six nature reserves in the South Provence, Rouys & Theuerkauf (2003) found densities of 8.6 rats ha⁻¹ for Polynesian rats and 8.9 rats ha⁻¹ for ship rats for a combined density of 17.5 rats ha⁻¹. They did not capture house mice or Norway rats. According to these authors, *R. rattus* and mice live in the coastal towns of Nouméa, while Norway rats may be found in mangroves and coconut plantations. However, in a recent eco-epidemiology leptospirosis study in New Caledonian, we also found Norway rats, associated with ship rats, Polynesian rats and mice, in an evergreen forest of the Central Chain, close to buildings and water in a tribe in Bourail (unpublished data). Mice were also captured in sclerophyllous forest in Mépouiri, in the vicinity of our study site at Nékoro (Brescia *et al.* 2005).

Capture rates appeared related to the dominance of rat species in each habitat (dry and evergreen forests): on Nékoro *R. exulans* were not captured until quite late in the trapping, while on Isle de Pines *R. exulans* were already captured very early. Weihong *et al.* 1999 captured Norway rats (*Rattus norvegicus*) and mice (*Mus musculus*) in Browns Island, New Zealand. Mice were caught in rocky areas covered

by dense vines, which probably provided sheltered sites inaccessible to Norway rats. According to Brown *et al.* 1996, a possible explanation for catching another species (mice) during a grid session is that a trapping grid, which is likely to remove a large proportion of the dominant species from the centre of the grid, is more effective than the traditional trap line for determining the presence of a subordinate rodent species, particularly when the subordinate species is present in much smaller numbers. However, Weihong *et al.* 1999 reported that mice began to appear in the traps before the rat trapping rate had decreased. Alternative explanations for catching mice on grids but not on lines are that trap grids are more likely to cover a higher proportion of microhabitat suitable to mice (with vines). Secondly, mouse abundance and/or trappability changed more between the two trapping periods than did that of rats.

Weihong *et al.* 1999 considered that trap grids would be better than trap lines for detecting the presence or absence of rodent species when two species coexist and one appears subordinate to the other.

The four introduced rodents have not been found to coexist in the same habitat anywhere in New Zealand except possibly on the Chatham Islands (King 2005), but in New Caledonia, like in Hawaii (Sugihara 1997), we found the four species to be sympatric. Innes 1990 mentioned that all four species of rodents are considered to interact to some extent (Innes 1990). This is evident from their distribution across New Zealand with no location where all four species occur sympatrically (Taylor 1978; Atkinson & Towns 2001). The distribution of any species is limited by environmental factors. Hutchinson (1957) developed the concept of the “ecological niche”. Multiple species can also persist on similar resources when differing levels of competitive success and dispersal are present (Tilman 1994).

Lomolino 2000 (in Russel and Clout 2004) proposed that the coexistence of these multiple species with similar niche requirements on some islands is possible though, because as well as interspecific interactions, differing dispersal abilities also facilitate coexistence.

Rodent densities in New Caledonia appear to be very high. No mice were caught during the experiment in the dry forest and only two were caught in the evergreen forest. Mouse footprint tracking rates did not increase during the extinction trapping session. Mice may have been present in these areas but at very low density,

but excluded from the tracking tunnels while rats were present. In New Zealand, Innes *et al.* (1995) observed after a poisoning operation of ship rats an increase in mouse numbers and/or distribution. Reduction of the antagonistic harassment from ship rats may be an explanation. Further studies on the interactions and competition between rat species and between rats and mice in New Caledonian forests as well as on seasonal variation in rodent abundance are needed.

5.4.2 Tunnels and snap-trap captures

The three assumptions of the Zippin (1958) removal method of population estimation are (1) the population must be essentially stationary during the period of trapping (births, deaths, immigration and emigration remain negligible), (2) the probability of capture is the same for each animal, and (3) the probability of capture remains constant from trapping to trapping (Zippin 1958). In our experiment, we have no reason to doubt the validity of assumptions 2 and 3. Concerning assumption 1, given the short time of trapping (10 days), it is unlikely that birth rates, death rates and emigration influenced the results. On the other hand, immigration is possible (Innes & Skipworth 1983) and quite likely judging by the number of rats still being caught on days 9 and 10, thus our overall density estimates may be somewhat inflated. In New Zealand, Brown *et al.* (1996) found immigration rates to be minimal but rodent densities were relatively low (7.1 to 8.2 rats.ha⁻¹). It is likely that in New Caledonia, where rodent densities are much higher, immigration rates are also higher.

5.4.3 Tracking tunnels and wax blocks

Footprint tracking rates and frequency of rodent bite marks both declined over the ten days of trapping. Nevertheless, with such high rat densities and also because some immigration likely occurred, the tracking index remained high throughout the period and appeared to be saturated most of the time. Footprint tracking tunnels thus appear unsuitable for detecting changes in rat populations in New Caledonia unless numbers drop dramatically. Wax blocks appeared to be more sensitive to small declines in rodent densities, as shown over the first three to four days of trapping, and therefore are more suitable for evaluating changes in rat populations at high density.

In New Zealand, Thomas *et al.* (1999) showed that the frequency of bite marks in wax blocks provided a feasible method for measuring changes in rat and brushtail possum (*Trichosurus vulpecula*) relative abundance. Given that the wax block method

is easier to deploy than trapping and tracking tunnel methods since they are small and lightweight and take less time to set and check than other monitoring techniques, more can be deployed in the field, increasing both accuracy and precision (Brown 2002).

5.4.4 Applicability of the rodent indices and recommendations for their use in New Caledonian forests

In general, managers prefer to use activity indices of murid rodent abundance rather than methods that give absolute population density estimates because index techniques are easier to use in the field. We have shown here that in places with high rodent densities footprint tracking tunnels and wax blocks should be used together as their sensitivity to changes in density differ and are complementary. Moreover, Kaukeinen (1979) recommends that a minimum of two independent census techniques should be used in each evaluation and Blackwell *et al.* (2002) also argue that the use of more than one index increases the confidence in population trends, and the quality and quantity of information gained.

We make the following recommendations for the deployment of these indices in New Caledonian forests.

- (i) Index techniques: tracking-tunnels should be run for a single night and Waxtags[®] for three consecutive nights.
- (ii) Environment conditions: as recommended by Blackwell *et al.* (2002) and Morgan *et al.* (2009), the index techniques should always be used to compare populations directly in the same habitat type only; the density index will then more accurately reflect differences in actual abundance than differences due to activity levels.
- (iii) Number and spacing: tracking tunnels are commonly spaced every 50 m in New Zealand, though Blackwell *et al.* (2002) considered that such close spacing may risk the effects of contagion through multiple tracking of tunnels by the same individual. A greater spacing (100 m) would mean a lower number of tunnels overall, but for larger home range sizes it may increase the reliability of the index. Taking into account current information pointing to smaller home range sizes for New Caledonian species, a 50-m spacing for tracking tunnels in New Caledonian forests is recommended. However, further investigations of rodent home ranges for each species are

needed. The wax block technique (Waxtags©) was developed in New Zealand by Thomas *et al.* (1999). They used a 10-m spacing on five separate lines. As seen previously, Waxtags© are easy to use and more can be deployed in the field, increasing both accuracy and precision (Brown 2002). We used a 50-m spacing here, but for the reasons given above and to increase the reliability, we recommend a 25-m spacing be used in future studies.

5.5 Acknowledgements

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CHAPTER 6

IMPACT OF THE INVASIVE LITTLE FIRE ANT (*WASMANNIA AUROPUNCTATA*) ON NEW CALEDONIAN *PLACOSTYLUS* (MOLLUSCA: GASTROPODA: BULIMULIDAE) IN SEMI- NATURAL CONDITIONS



*The introduced little fire ants *Wasmannia auropunctata* on an ant bait station baited with tinned tuna oil (left), and an ant-exclusion enclosure for snails (right)*

Abstract

We tested the vulnerability of the endemic New Caledonian *Placostylus fibratus* land snail to the effects of the introduced little fire ant *Wasmmania auropunctata* in an exclusion experiment run for one year under semi-natural conditions. The abundance of little fire ants varied across the year, but when ants were present at high density, the growth of the snails was impaired. After 12 months, the mean height of snails in the treatment chambers (little fire ants present) was 14 % smaller (i.e. 6.88 mm, SD=8.22; n=21) than that of snails in the control (fire ant-free). The presence of little fire ants did not affect snail survival. Little fire ants took advantage of their proximity to snails by using water in snail mucus, especially during dry conditions. Despite the retardation of snail growth, little fire ants may have a net positive effect on the demography of *Placostylus* snail populations by controlling natural predators such as Carabidae and influencing the distribution of rodents in infested areas.

Impact de la fourmi électrique (*Wasmannia auropunctata*) sur les escargots du genre *Placostylus* de la Nouvelle-Calédonie (Mollusques : Gastéropodes : Bulimulidae) en conditions semi-naturelles

Résumé

La vulnérabilité de l'escargot terrestre *Placostylus fibratus*, endémique à la Nouvelle-Calédonie, face à la fourmi électrique *Wasmannia auropunctata* a été testée dans un essai utilisant des enceintes d'exclusion en conditions semi-naturelles pendant une année. L'abondance des fourmis électriques a fluctué au cours du temps, mais leur présence a impacté la croissance des escargots. Après 12 mois, la longueur moyenne des coquilles des escargots placés en enceintes témoins (présence des fourmis) était plus courte de 14% (soit 6.88 mm, ET=8.22; n=21) que celle des escargots placés dans les enceintes traitées (fourmis absentes). Cependant, la présence des fourmis électriques n'a pas impacté la survie des escargots. Les fourmis électriques tirent profit de leur proximité avec les escargots en utilisant le mucus produit par ces derniers comme source d'eau, particulièrement durant les saisons les plus sèches. En conditions naturelles, *W. auropunctata* pourrait avoir un effet bénéfique sur les populations de *Placostylus* en contrôlant les prédateurs naturels comme les Carabidae et en influant sur la répartition spatiale des rongeurs introduits dans les zones infestées.

6.1 Introduction

New Caledonian land snails of the genus *Placostylus* comprise six endemic species, all of which are endangered. Habitat destruction or modification by people, human harvesting for consumption, the introduction of ungulates, and predation by introduced species are all contributing factors to their decline (Brescia *et al.*, 2008). *Placostylus fibratus* is found throughout New Caledonia, including the Loyalty Islands. This edible species is known as ‘the snail of the Isle of Pines’ (named after the coral island to the south of the mainland from which they are collected). Indeed, the Isle of Pines is the only island on which these snails are still being marketed commercially for consumption. Control measures on the harvesting of these snails have been imposed by the local authorities to try to protect the species from overexploitation (Délibérations 50-94/APS and 26-2000/APS of the Assembly of South Province).

The little fire ant, *Wasmannia auropunctata*, is a widespread and abundant invasive ant (Holway *et al.* 2002). Native to South and Central America, it is listed among “one hundred of the world’s worst invasive alien species” by the International Union for Conservation of Nature (IUCN) (Lowe *et al.* 2000). It is tiny, it stings, and it is known to cause severe environmental impacts: it has devastated local ant species on oceanic islands (Jourdan, 1997; Wetterer and Porter, 2003) through predation as well as competitive interactions like exploitation and interference (Lebreton *et al.* 2003). It is an important predator of other invertebrates and has caused population declines in a number of native species (Clark *et al.*, 1982, Romanski, 2001), and has harmed domestic stock and may possibly have a significant impact on wild vertebrates (Jourdan *et al.* 2001; Wetterer and Porter, 2003).

Wasmannia auropunctata was recorded for the first time in New Caledonia in 1972 (Fabres & Brown, 1978), and has spread rapidly and invaded a wide array of habitats including both rainforest and dry forest on the Mainland, Isle of Pines, Loyalty Islands and even small remote uninhabited islands (Jourdan *et al.* 2001). As part of a larger study on the demography and identification of the causes of mortality of the New Caledonian *Placostylus*, we aimed to enhance knowledge of interactions between little fire ants and these snails. Here, we test under semi-natural conditions the direct effect of little fire ants on the growth and survival of juvenile *Placostylus*, and discuss the implications of our findings for wild populations of *Placostylus* snails.

6.2 Methods

6.2.1 Study area

The work was conducted in New Caledonia which has three major seasons: a hot wet season (mid November-mid May; mid April-mid May is a transition period); a cool dry season (mid May-mid September); and a hot dry season (mid September-mid November) (ORSTOM 1981).

The study site is in Gadgi on the Isle of Pines (152 km²), an island 50 km south of the New Caledonian mainland. Vegetation is a native evergreen humid forest on elevated coral soil, with a 15-20 m high canopy.

6.2.2 Sampling and experimental design

Adult *P. fibratus* were gathered from forests within the Gadgi District on Isle of Pines and held for captive breeding in Paita, on the Mainland (see Appendix 2 for the rearing method). Three months after hatching, young snails born within this captive population in April 2005 were transported to the Isle on Pines for use in the following experiment.

Ninety juvenile snails were individually marked by engraving a number on each shell, paired with an individual of similar size, and randomly assigned to treatment and control groups. These were then divided into thirds, providing three replicates per treatment and control. The six groups, with 15 snails per group, were placed into six similar experimental plastic chambers (25 x 18 x 10 cm). The treatment (Ant +) chambers were placed under natural conditions within the Gadgi forest under a rudimentary open shelter consisting of a roof made with coconut palms in the pilot snail-husbandry site. They were easily accessible to little fire ants that were naturally present in the study area. The three control chambers (Ant -) were designed to exclude little fire ants. These were also placed in the forest, but in larger containers that were permanently supplied with water that created a moat that prevented little fire ants accessing the snails.

The chambers were lined with coco compost supplemented with calcium carbonate. Humidity was maintained by watering daily by hand and by a thick layer of leaves (e.g. papaya, banana) placed on top to keep humidity high and to limit the amount of light reaching the snails and to deter the arboreal behaviour of newborns. The snails were fed daily with an artificial diet of cereal flour (80% of dry weight)

supplemented with calcium carbonate (20%) (see Brescia 2000, 2001 for full husbandry details).

In order to maintain constant densities, snails that died during the experiment were replaced with similar snails from stock cultures held under similar conditions; however, only the snails that were present from the beginning of the experiment were used in the statistical analyses.

6.2.3 Abundance of ants

Non-toxic bait stations were used to assess the abundance of ants in the snail enclosures. Each month, three 4 cm x 2 cm plastic strips baited with tinned tuna in oil (Human & Gordon, 1999) were placed in each snail enclosure for three hours a day for three days. An index of fire ant abundance was then calculated by counting the number of workers foraging on the baits (i.e. the mean number of ants on each 8 cm² plastic strip).

6.2.4 Survival and growth of snails

Monthly, we recorded the following parameters: number of dead and live snails, individual growth of marked snails (increase in weight and height), and the presence or absence of live fire ants on the aperture of each snail's shell.

6.2.5 Analysis

For statistical analyses, we calculated monthly differences in height between each pair of treatment and control snails. We then performed paired sample t-tests on the differences after six and twelve months of the study. We used two sample t-tests to compare mean daily height (MDL) and mean daily weight (MDW) gain per snail between controls and treatments and a Mann-Whitney U test to compare ant abundance between controls and treatments.

Kaplan-Meier estimates of survival rates were made for both controls and treatments. Log-rank tests to compare the survival functions of the Kaplan-Meier estimations for controls and treatments were made using a chi-square test with 1 degree of freedom. All tests were performed using SPSS[®] 9.0 software.

6.3 Results

6.3.1 Abundance of little fire ants

The ant exclusion method was effective in reducing little fire ants in the control chambers relative to the treatments (Mann-Whitney U, $p < 0.001$), with the control enclosures remaining largely free of little fire ants (Figure 6.1). When little fire ants did succeed in accessing the control chambers, their densities were on average about 10-fold less than in the treatment chambers. Ant densities appeared to vary seasonally, being highest between February and June 2006.

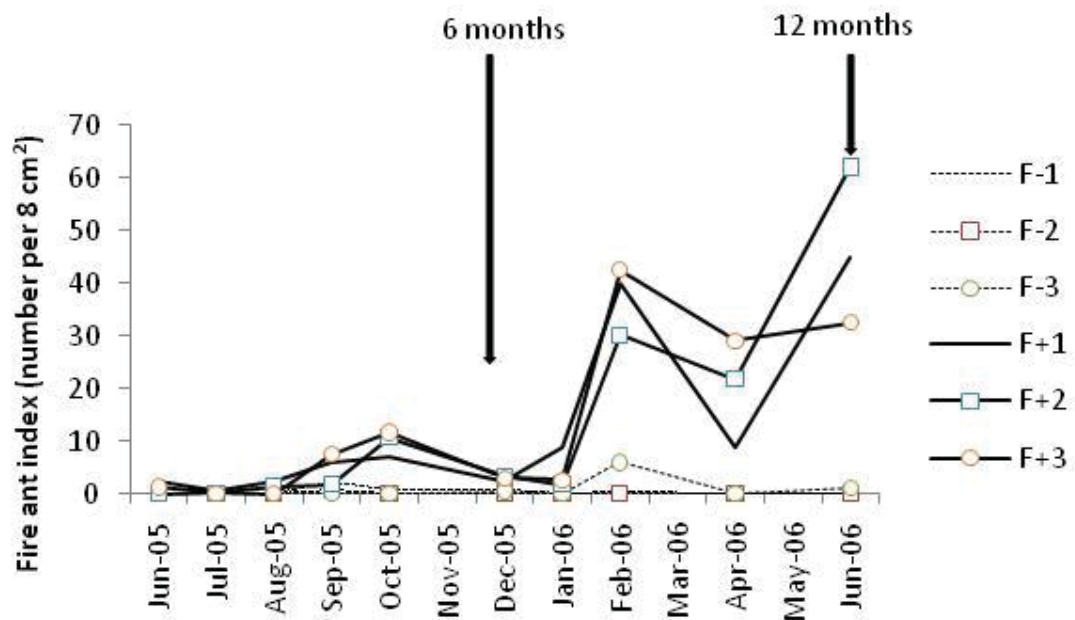


Figure 6.1: Little fire ant indices of abundance through time when little fire ants are excluded (three blocks in dot line) and when little fire ants are present (three blocks in solid line). The arrows at 6 and 12 months indicate the times that snails were re-measured, corresponding to low and high snail densities in the ant-present chambers.

6.3.2 Growth of snails

The initial and final (after a year of study) mean heights, widths and weights of snails in the control (fire ants excluded) and treatment (fire ants present) colonies are presented in Table 6.1. Twenty-one pairs of snails for the three replications were used in the Paired Sample T test analyses (Figure 6.2). With all blocks combined, differences were significant after both six months and 12 months (paired t tests, respectively $p < 0.05$ and $p = 0.001$). After six months, the mean height of Control snails

was 1.66 mm (SD=4.15, n=21) longer than that of the Treatment snails. After a year, the difference was 6.88 mm (SD=8.22, n=21).

Mean Daily Height (MDL) gain for ant-excluded controls was 0.048 mm per day (SD=0.020; n=37) and Mean Daily Weight (MDW) gain was 0.026 g per day (SD=0.015; n=37); which were both significantly higher than MDL and MDW in the ant-present treatment (Table 6.2) (respectively 0.032 mm per day (SD=0.019; n=29) and 0.019 g per day (SD=0.011; n=29)). There was evidence of a treatment x block interaction in height gain, indicating that the effect of the treatment differed somewhat among the three blocks.

Table 6.1: Morphometrics of snails: mean height (mm), width (mm) and weight (g), and (SD) between C = Control (Fire ants excluded) and T = Treatment (Fire ants present) from June 2005 to June 2006.

	C1	T1	C2	T2	C3	T3
Initial height	43.38 (6.49)	45.08 (5.98)	42.11 (5.37)	42.32 (4.63)	39.89 (3.03)	38.78 (4.53)
Final height	59.41 (10.64)	60.71 (8.02)	60.81 (8.86)	55.57 (5.83)	59.45 (7.18)	47.67 (7.76)
Initial width	25.28 (2.14)	25.25 (2.41)	24.27 (2.57)	24.49 (2.11)	23.18 (1.69)	23.51 (2.83)
Final width	32.85 (3.83)	31.90 (2.54)	32.09 (3.06)	30.19 (3.10)	31.97 (2.85)	27.55 (2.93)
Initial weight	9.20 (3.76)	10.13 (3.33)	9.47 (2.97)	11.33 (3.68)	8.93 (1.66)	8.53 (2.56)
Final weight	20.40 (6.85)	20.22 (7.03)	19.73 (6.40)	20.72 (6.15)	18.00 (5.66)	12.67 (4.79)

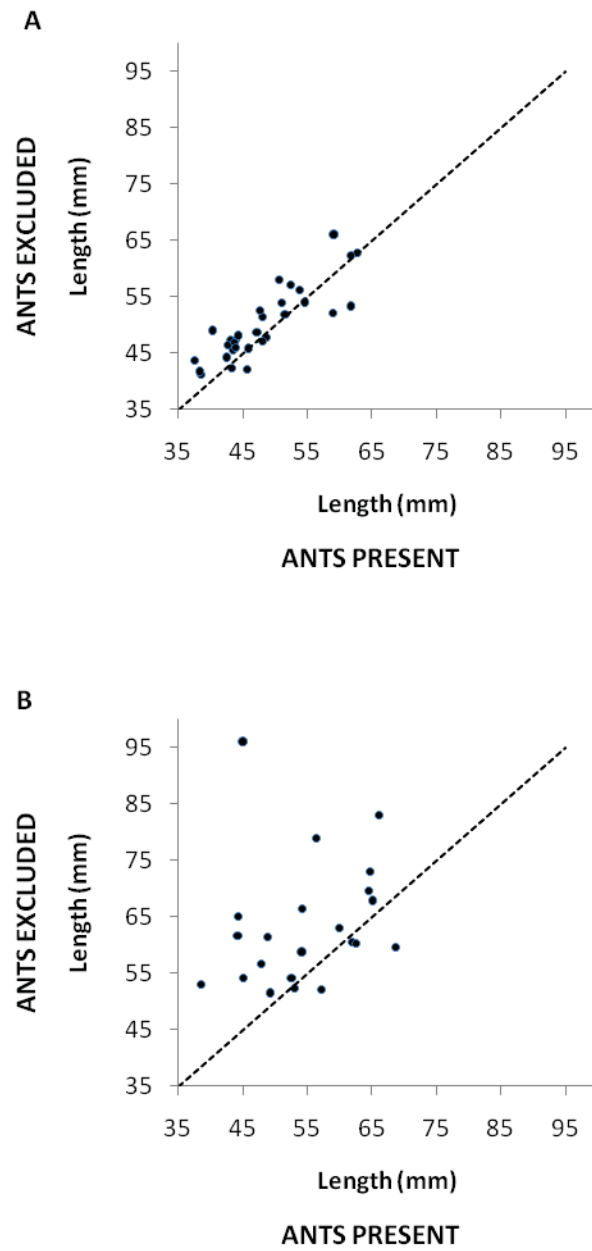


Figure 6.2: Differences in the relative height of paired snails after (A): 6 months and (B): 12 months isolation or exposure to little fire ants.

Table 6.2: ANOVA in mean daily height (MDL) and mean daily weight (MDW) gain per snail and the effects of the ant-exclusion treatment and the three blocks used in the experiment.

Sources of variations	MDW		MDL	
	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>
Treatment	1	4.983*	1	14.180***
Block	2	2.872	2	0.517
Treatment*Block	2	1.417	2	5.588**

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

6.3.3 Survival

Figure 6.3 shows the estimates of survival rates across time for controls and treatments. The mean survival rates were 0.94 (95% CI= 0.91-0.97) for controls and 0.90 (95% CI= 0.85-0.94) for treatments. The comparisons of the survival functions showed no significant difference on survival rate ($X^2 = 1.504$, $df = 1$, $p > 0.05$).

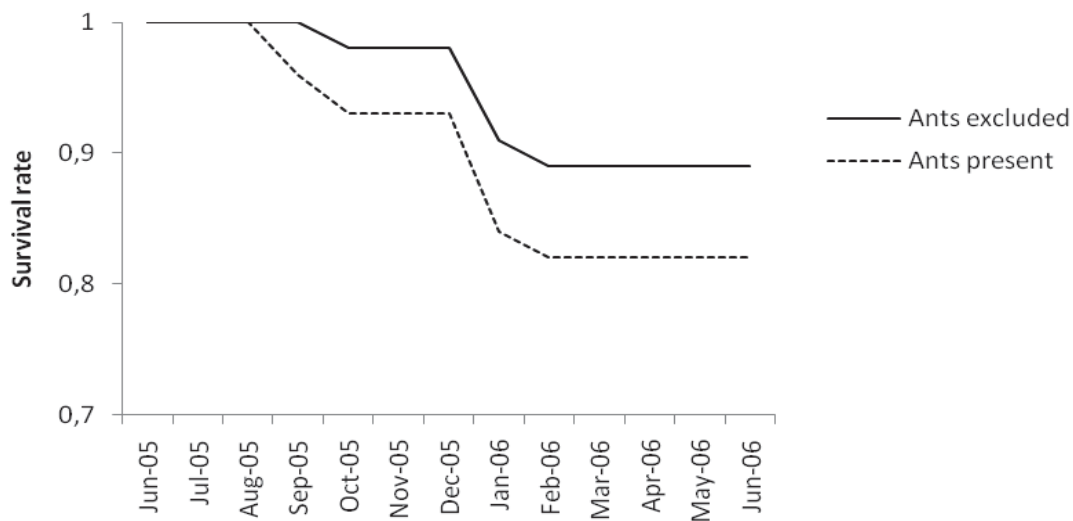


Figure 6.3: Kaplan-Meier estimates of the survival rate of *Placostylus* snails held under semi-natural conditions in the control (ants excluded) and treatment (ants not excluded) groups.

6.4 Discussion

This study found that under semi-natural conditions, the introduced little fire ant *Wasmannia auropunctata* had a negative impact on *Placostylus* growth but provided no direct evidence of ant predation on snails or any significant effects on survival. In contrast, in a laboratory experiment, Stevens *et al.* (1999) found that, in Florida, the fire ant *Solenopsis invicta* Buren attacked apple snails *Pomacea paludosa* Say, but questioned whether the ants kill snails under natural conditions. Yusa (2001) observed the fire ant *Solenopsis geminata* (Fabricius) consuming eggs of the apple snail *Pomacea canaliculata* (Lamarck, 1819) in the Philippines. *Solenopsis* workers are much larger (up to 6 mm in height) than the 1.5 mm little fire ants (Hedges, 1998; Wetterer & Porter, 2003).

A link between *W. auropunctata* establishment and a decline in other ground arthropod populations has been recorded elsewhere (Clark *et al.* 1982; Lubin 1984; Le Breton *et al.* 2003; Vonshak & Dayan 2010). In the Galapagos, Kastdalen (1982) reported that native ants have disappeared where the fire ant is present. Lubin (1984) found that areas with *W. auropunctata* present had not only lower diversity and density of other ants, but also lower densities of other insects, scorpions and spiders. Roque-Albelo & Causton (1999) noted a negative impact on young tortoises and birds. Also, a sharp decrease in the overall New Caledonian lizard abundance between *W. auropunctata* invaded and non-invaded areas has been reported (Jourdan *et al.* 2001).

In New Caledonia, our results in semi-natural conditions supported by observations in the field, has provided little compelling evidence that little fire ants are actively aggressive against healthy *Placostylus* snails. In cages, little fire ants are often observed inside the snail aperture in a feeding posture around the foot of the snail while it is retracted in the shell and this was also often observed in the wild in areas invaded by ants (FMB pers. obs.). However, infested *Placostylus* do not secrete their characteristic blue defence mucus against insects and seemed not to be disturbed by the presence of little fire ants that are probably searching for humidity and a water source in the mucus. *Wasmannia auropunctata* may exploit this during dry periods, especially in dry forests of New Caledonia. Nevertheless, even if snails are not attacked by the stinging little fire ants and tolerate their presence, the ants may cause an increase in the snails' metabolic requirements for water which may force them to continue active-foraging beyond their normal nocturnal activity period. This may explain their reduced

growth rates. Stevens *et al.* (1999) cited that similar disturbance of *Pomacea paludosa* by the fire ant *Solenopsis invicta* may result in depletion in energy reserves and may shorten the potential survival time of snails in dry conditions.

We showed that abundance of little fire ants varied across the year. Chazeau (2000) observed similar variation with little fire ants in New Caledonia being least abundance during the cool season, which is also generally the driest season, and most abundant between January and April. Our data are consistent with this, although we found that numbers remained high until June. In the wild, even if little fire ants have a negative impact on the growth of snails as we found under semi-natural conditions, the effect may be seasonal with reduction in growth rates during periods of high fire ant abundance being offset by increases in growth during periods of low ant abundance.

This kind of compensatory responses had been shown for the land snail *Balea perversa*. Initially kept at high population density, *B. perversa* responded with compensatory growth to the more favourable conditions of the later period and became equal in shell size to those kept at low population density (Baur & Baur 1992). Nevertheless, the authors mentioned that in contrast to the species that have indeterminate growth, shell growth in *B. perversa* is described as being determinate. Species with determinate growth cease increasing their height when a thickened aperture lip forms as they reach sexual maturity (which is the case for *Placostylus* snails). Barr & Barr (1992) considered that the fact that reproducing individuals of *B. perversa* showed compensatory shell growth most surprising. In our experiment, the determinate growth pattern restricted us to following the increase in shell height of juveniles. Nevertheless, it is known that environmental stress can cause a reduction in survival and/or growth rate as well as in reproductive output (Bradshaw and Hardwick 1989, Calow 1989, Grime 1989, Koehn and Bayne 1989). However, all stages of the life cycle are not equally susceptible; stress during some stage may have far greater consequences than at other times (Underwood 1989). Environmental conditions experienced during an individual's early life stages can affect its life history later on (Prout 1984, Prout and McChesney 1985, Semlitsch 1987).

Our observations from both dry forests and evergreen forests in New Caledonia led us to believe that when little fire ants are present, *Placostylus* densities tend to be higher, with “healthier” population structure, i.e. better representation of all life stages from newborns to adults, whereas in areas with low level of ants, snail populations comprise mostly adults. Thus, to a certain extent, little fire ants might have a net positive impact on *Placostylus* snail populations as they may control Carabidae and influence the spatial distribution of rodents, and possibly large introduced ungulates like feral pigs (*Sus scrofa*), a predator of snails, and rusa deer *Cervus timorensis russa* which seem to avoid infested areas. Vonskak & Dayan (2009) in Israel found that beetle abundances and species richness were negatively affected by *W. auropunctata*. Effects on mammals have also been recorded; Wetterer *et al.* (1999) found anecdotal evidence of an impact in Gabon on house cats developing corneal clouding and blindness. This is also commonly observed in pet dogs and cats in Melanesian tribes in New Caledonia (Chazeau *et al.*, 2002; FMB pers. obs). Lechner *et al.* (1996) observed some behavioural interactions between red imported fire ants *Solenopsis invicta* and three rodent species of South Texas (*Sigmodon hispidus*, *Peromyscus leucopus* and *Baiornys taylori*). Responses to the presence of ants differed across rodent species but all rodents tended to avoid areas with high numbers of fire ant mounds. Carabidae (Pöllabauer, 1993) and rodents of the genus *Rattus* (Brescia *et al.* 2008) are predators of New Caledonian *Placostylus*, consuming a large proportion of young snails, and contributing to decreases in snail populations.

6.5 Acknowledgments

This work was part of a study for the survey of snail stocks on Isle of Pines, and was funded by the Direction de l’Environnement de la Province Sud and the Institut Agronomique néo- Calédonien. We specially thank the Koteureu family on Isle of Pines for their daily care to captive snails and to ensure enclosures remained ant-proofed.

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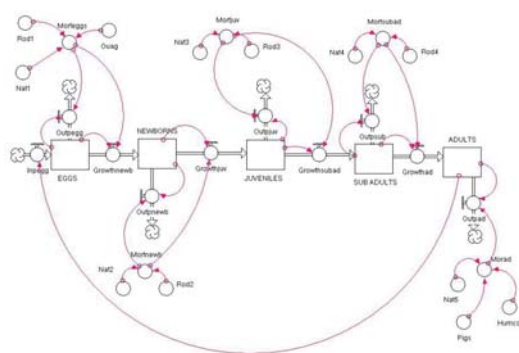
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CHAPTER 7

**EXPLORING PLAUSIBLE STRATEGIES FOR AVOIDING DISASTER: A POPULATION
DYNAMIC MODEL FOR THE EXPLOITED NEW CALEDONIAN ENDEMIC LAND SNAIL
PLACOSTYLUS FIBRATUS (MOLLUSCA: GASTROPODA: BULIMULIDAE)**



*A population dynamic model constructed under STELLA© for the exploited Placostylus
fibratus on Isle of Pines*

Abstract

A stage-structured population dynamics model was developed for an over-collected endemic land snail of New Caledonia, *Placostylus fibratus*, on Isle of Pines. The model was used to investigate the fate and persistence of the populations under various management options.

If the current harvest rate is maintained (ca. 120,000 adults snails per year, that is ca. 6% of the actual estimated adult stock), the model predicts that the population will decline at 0.52% per annum over the next 50 years. If the harvest rate is increased, the decline is accelerated. Sustainable exploitation is attained at a 3% harvest rate (ca. 70,000 snails per annum). This would allow collection for daily consumption by local people on Isle of Pines but would preclude commercial harvest. The model is sensitive to rodent predation and predicts that the *Placostylus* population would likely recover if rodent predation was decreased even slightly. Conversely, the model predicts that extinction will happen quickly if rodent predation rates increase. Active control of rodents by continuous poisoning thus appears to be a viable management option for increasing the sustainable harvest rate of snails by humans. Whether this option would be politically palatable is uncertain on this island where tourism is the primary income earner. The model helps identify priorities for further research and options for managing the snails and their mortality factors. Some options, such as reinforcing current restrictions on allowable harvest, despite considerable demand from local people to increase commercial harvest rates, require urgent action to maintain snail populations and assure their continued survival.

Stratégies envisageables pour éviter un désastre : un modèle dynamique de population pour l'escargot terrestre endémique et exploité de la Nouvelle-Calédonie, *Placostylus fibratus* (Mollusca: Gastropoda: Bulimulidae)

Résumé

Un modèle de dynamique de population basé sur les stades de croissance a été développé pour l'escargot endémique à la Nouvelle-Calédonie, *Placostylus fibratus*, exploité à des fins commerciales sur l'Ile des Pins. Le modèle a été utilisé afin d'envisager la destinée et la persistance des populations selon différents régimes de gestion.

Si le taux de collecte actuel est maintenu (120 000 escargots prélevés par an, soit 6% du stock adulte actuel estimé), les simulations prédisent que les populations présentent un risque significatif de déclin à un taux de 0.52% par an sur les 50 prochaines années. Si les quantités collectées augmentent, le déclin est accéléré. Une exploitation durable est atteinte pour un niveau de prélèvement de 3% du stock adulte actuel estimé (soit 70 000 individus par an). Ce niveau de prélèvement correspond uniquement aux volumes consommés par les foyers de l'Ile des Pins actuellement, et exclue ainsi la collecte à des fins commerciales. Le modèle apparaît très sensible à la prédation par les rongeurs, et prédit un rétablissement des populations si le niveau de prédation était abaissé même très légèrement. Inversement, une augmentation du niveau de prédation accentuerait le déclin. La régulation des populations de rongeurs par empoisonnement apparaît comme une opération de gestion qui pourrait être retenue afin d'envisager une augmentation de la collecte des escargots par l'Homme dans le cadre d'une exploitation durable. Cependant la mise en œuvre de ce genre d'opération sur une île aussi touristique reste incertaine compte tenu de réticences diverses qui pourraient être rencontrées. Le modèle contribue à établir des priorités pour des actions de recherche futures et la mise en œuvre de solutions de gestion. Des options telles que le renforcement de la réglementation actuelle afin de limiter les niveaux de prélèvements doivent être envisagées de manière urgente afin de maintenir les populations et assurer leur survie sur le long terme, en dépit de l'attente de certains habitants de l'Ile des Pins en vue d'augmenter la collecte à des fins commerciales.

7.1 Introduction

Wildlife and fisheries managers have to make decisions and this is where modelling enters the decision process. Lande *et al.* 1995 stressed the need to build models of optimal harvesting that include the risks of extinction from demographic and environmental stochasticity as well as harvesting. Models can be either deterministic or stochastic; a deterministic model is one in which variable states are determined by parameters in the model; conversely, in a stochastic model, randomness is present (Starfield 1997).

Wildlife has been exploited by people throughout history and is known to have caused the extinction of many species; exploitation pressures are greater today than ever before (Mace and Reynolds 2001). Overexploitation and extinction may be of real concern for populations that are not very large, species that have low growth rates, or are subject to highly variable environments (Lande *et al.* 1995). Overharvesting, which can proceed to a level of near extinction, has been a widespread issue for commercially exploited mammals and birds. For example, overharvesting combined with habitat destruction has caused local extinctions or severe depletion of numerous mammals including the African elephant, the jaguar, and the tiger (Cumming *et al.* 1990; Redford 1992; Linden 1994). Also, most of the world's fisheries are either fully exploited or overexploited (Botsford *et al.* 1997). Mortality due to fishing has had, and continues to have, major impacts on wild fish populations (Worm *et al.* 2009). The traditional key objective for fisheries management is that harvest should be as large as possible but nevertheless sustainable in the long term (Punt and Smith 2001).

Since the early 1970s, various ecological modelling approaches have been developed (Jorgensen *et al.* 2008), both for conservation purposes (e.g. for the endangered Large Blue Butterfly, *Maculinea arion* (Griebeler and Seitz 2002); for a rare carnivorous land snail in Australia (Regan *et al.* 2001); and for the kiwi (McLennan *et al.* 1996) and the kakapo parrot (Elliott 2006) in New Zealand), or for the sustainable exploitation of biological resources (Dew 2001; Aubone 2003; Tyutyunov *et al.* 2002; Arreguin-Sanchez *et al.* 2004).

Placostylus land snails (Family Bulimulidae, subfamily Placostylinae), found only on few islands of the Western Pacific, are large, slow moving, slow developing and long-lived. The six species found in New Caledonia (*Placostylus fibratus*, *P.*

porphyrostomus, *P. caledonicus*, *P. eddystonenis*, *P. bondeensis* and *P. scarabus* (Neubert *et al.* 2009)) are all endemic and are either threatened or endangered (Brescia *et al.*, 2008). They are relatively specific in their habitat requirements, being primarily associated with calcium-rich soil, and inhabiting exclusively native dry or evergreen forests (Brescia *et al.* 2008). Factors contributing to their decline include habitat destruction and modification by introduced ungulates, harvesting for human consumption and predation by introduced species (Brescia *et al.* 2008).

Placostylus fibratus is the largest (60-100 g when adult) and most polymorphic species and is found throughout New Caledonia, including the Loyalty Islands, but is known as “the snail of the Isle of Pines”, referring to the coral island to the south of the mainland from which they are collected. The only snails to be marketed commercially for consumption come from this island. Adult snails are widely harvested but the harvest is regulated by control measures imposed by the local authorities charged with environmental protection. Nevertheless, in chapter 3 we found that the population had undergone a significant decline in both adult and juvenile snail abundance from 1993 to 2008, apparently due to overharvesting.

Additionally, the populations are threatened by rodent predation, which is a major cause of juvenile mortality. In a mark-recapture study (Chapter 4) we recorded a 67.1% mean annual rodent predation rate on juvenile *P. fibratus* on the Isle of Pines. This seriously diminishes recruitment and threatens the viability of these populations. Strategies for the sustainable harvest of snails on the Isle of Pines are needed both to ensure the continued survival of the snails and to secure and potentially increase an important source of income for the local people.

Placostylus fibratus is collected and consumed by Kuniés (the local inhabitants of Isle of Pines) and is an important part of the Melanesian culture and tradition on the Isle of Pines. They have always been an important food item (Pöllabauer 1994; Lepoutre 1999; Brescia 2004, 2005). Thus, *P. fibratus* progressed from a gastronomic speciality to a delicacy in Nouméa (the New Caledonian capital) when it started to be marketed. From 1950, snail-harvesting for consumption from the natural populations on the Isle of Pines increased progressively, reaching 48 tonnes (about 700,000 adult snails) in 1993 (Pöllabauer 1995), and the export of the snails became an important economic activity for the island inhabitants, assessed at US \$180,000 annually. Since

then, various control measures have been adopted to reduce the harvest including restricting allowable collection periods and, in 2001, prohibiting the export of snails from the Isle of Pines. These strategies appear to have been effective at reducing the number of snails collected annually (Chapter 3).

Over the last decade, at the request of Kuniés worried about the growing scarcity of the resource, a number of studies have been undertaken to improve knowledge of New Caledonian *Placostylus* biology, ecology and population dynamics with the aim of developing a sustainable management regime (Pöllabauer 1995, 2002; Brescia 1997, 1999, 2000, 2001, 2004, 2005; Brescia *et al.*, 1998).

In this paper, we present a deterministic model of the combined impacts of various stage-related mortality factors in the population dynamics of New Caledonian *Placostylus* snails. The model is based on current knowledge of the biology and ecology of these snails, their predators, and human harvest practices. Sensitivity analyses are conducted to determine the relative importance of the various mortality factors. The construction of the model serves two main needs: as a tool to assess the likely efficacy of various management options for conservation of the snails; and to allow an assessment of management options that might secure and potentially increase their sustainable harvest.

7.2 Methods

7.2.1 Study area and species

This paper focuses on the Isle of Pines (152 km²), an island located 50 km south of the New Caledonian mainland which includes about 6,000 ha of humid forest on elevated coral soil.

7.2.2 Model description

We choose a stage-structured deterministic model to project the future population structure based on important stages in the development of the snails (egg, newborn, juvenile, sub-adult and adult) and on possible management actions. We constructed the model based on stages rather than on ages and included a survival estimate for each stage, the probabilities of transition from one stage to the next, and the fecundity of adult snails. Thus, we built a “simple-biology”, population-structured

dynamic model (Jorgensen, 2008). “Simple biology” means that development time is assumed to be constant, and that mortality risk remains a constant for each stage.

The five-stage model was implemented in STELLA, Version 9.1.3 (High Performance Systems, Inc.). STELLA uses an icon-based graphic interface specifically designed for dynamic systems modelling (Costanza and Voinov, 2001). The model was calibrated with field data on *Placostylus* of Isle of Pines and different scenarios were tested to model the effects of changes in survivorship or of progression probabilities.

7.2.3 Historic data on *Placostylus fibratus* harvest rates and population trends

The population stock and annual harvest of snails collected on Isle of Pines were surveyed from 1993 to 2008 (Pöllabauer 1995, 2002; Brescia 2002; Chapter 3). The annual harvest peaked in 1993 at around 700,000 leading in 1994 to a new law being passed by the South Province Assembly of New Caledonia (Délibération 50–94/APS) to regulate the collection and the transportation of *P. fibratus* on the island. As a result of these legislative changes, the number of snails collected annually dropped to around 300,000 from 1994 to 2001. The law was reinforced in 2001 with further restrictions and as a result the number of snails collected dropped further to about 120,000 per annum where it now remains. This represents approximately 6% of the 2,160,000 adult snails estimated to have been present on the Isle of Pines in 2008.

7.2.4 *Placostylus fibratus* life history

In Brescia *et al.* 2008 (Chapter 2) and in chapter 4, we reported detailed aspects about the life history of New Caledonian *Placostylus*, allowing the development of a dynamic model. *Placostylus* are large, slow-moving, slow-developing and long-lived land snails. They reach maturity at approximately four years and may live 19-30 years. Maturity is defined as the age at which they first lay eggs, and occurs in snails once they have developed a shell with a thickened aperture lip of ≥ 3.5 mm. Thus, we classified *Placostylus* as adults when the aperture lip was ≥ 3.5 mm, as juveniles when the lip thickness was < 3.5 mm but the shell height was > 10 mm, and as infants (newborns) when the aperture lip thickness was equal to 0 and the snail was ≤ 10 mm long. In chapter 4, we found that large juveniles (shell height > 50 mm with a lip of

between 0 and 3.5 mm) represented 91% of the snails found in forest, so here we recognise these snails in a separate stage class as sub-adults rather than juveniles.

Placostylus, like all pulmonates, are hermaphroditic; all individuals are potentially capable of producing eggs once a year though snails require a mate to reproduce. *P. fibratus* is capable of a high fecundity rate and snails kept in captivity under semi-natural conditions produce several egg clutches per year (observed range 1 to 4 and 72% of adults laying at least one clutch per year), with each clutch on average containing 205 eggs (SD = 84; n=103, range 13 to 515) (Brescia 2000). In the field, egg-laying occurs primarily during the cool season, but the reproductive season of *P. fibratus* on the Isle of Pines can extend from April until October (Pöllabauer 1995). The egg clutches are deposited in nests formed in depressions in friable humus-rich soil often near coral blocks or close to tree roots. Hatching success in captivity is in the order of 70%, but is very low in natural conditions due to predation of eggs by a native carnivorous snail *Ouagapia inaequalis* which has the potential to destroy the majority of clutches. We recorded a predation rate on clutches of 68% for *P. fibratus* with 1.56 ± 0.66 *O. inaequalis* per clutch (Chapter 4).

In a mark-recapture study (Chapter 4) we found that the annual survival rate was approximately 59.0% for juveniles and 70.0% for adults and the mean fecundity was 0.53 young recruited per adult per year. The identified causes of snail deaths based on examination of empty shells found were natural mortality, rodent predation, pig predation and trampling by feral cattle on the Isle of Pines. Rodent predation was recorded only on juvenile stages. The mean overall annual rodent predation rate on juvenile *P. fibratus* was 67.1%.

The high juvenile mortality may be a natural feature of the population dynamics of the genus *Placostylus*. For *P. bollonsi* in New Zealand, Brook and Laurenson (1992) show that at least 60% of hatchlings fail to attain adulthood but this is from multiple natural causes rather than the result of a single group of introduced predators.

Only adult snails were found to be eaten by escaped domestic pigs. This kind of predation was recorded only in a very small number of localized areas on the Isle of Pines, where it reached 48.6% of empty adult shells in some permanent quadrats (Chapter 4) but it was considered as insignificant here for the Isle of Pines as a whole.

7.2.5 Parameters and model construction

Using our knowledge of the life-history of New Caledonian *Placostylus*, we built a model with a relatively simple structure: new individuals input newborns into the system by eggs laid by adults, these pass to a juvenile stage and later to sub-adults. Individuals exit the system at each stage through mortality (natural causes and predation) and by human collection for *P. fibratus* (Figure 7.1). In the model, we made the assumptions that a year is required to pass through each age-class from newborns to adults. Also, we assumed a theoretical eternal lifespan for adults. As discussed previously, parameters for the model were gained from available literature on New Caledonian *Placostylus* and from data collected as part of this thesis. The list of variable names and acronyms, and their units is given in Appendix A.

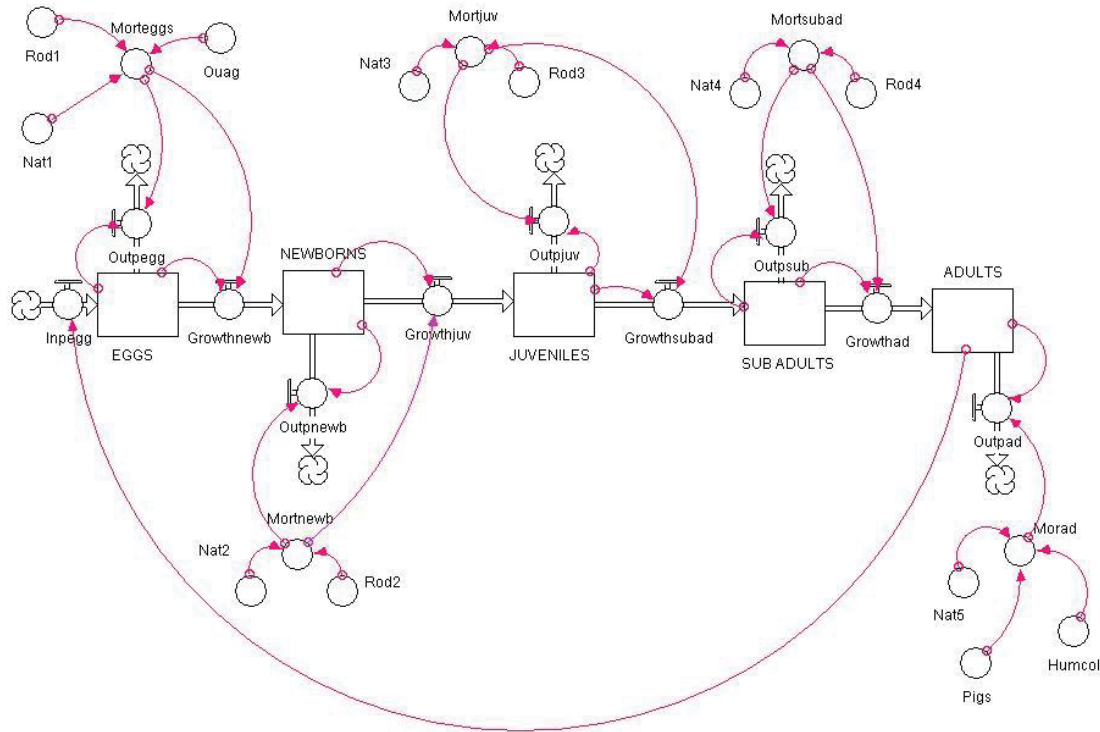


Figure 7.1: STELLA diagram of *Placostylus* model.

7.2.6 Equations

Upper case letters represent the stock of animals in each stage class; italics represent fluxes between these stages.

Adult population

Number of adults present in the model after each iteration was given by:

$$ADULTS_t = ADULTS_{t-dt} + (GrowthAd - OutpAd) * d_t$$

where $ADULTS_t$ is the number of adult snails, $GrowthAd$ is the rate at which a number of snails enter the adult stage and is given by:

$$GrowthAd = SUB_ADULTS * (1 - MortSubad)$$

where SUB_ADULTS is the number of sub-adults and $MortSubad$ is the mortality on sub-adult stages.

Adults output ($OutpAd$) is given by:

$$OutpAd = ADULTS * MortAd$$

Where $MortAd$ is the sum of each source of mortality (“ $Nat5$ ” is the natural mortality of the 5th lifestage [adults], human collection “ $Humcol$ ” and pig predation “ $Pigs$ ”) exerted on adult stage:

$$MortAd = Pigs + Nat5 + Humcol$$

Egg stock

The number of eggs entering the system after each iteration was given by:

$$EGGS_t = EGGS_{t-dt} + (Inpegg - Growthnewb - Outpegg) * d_t$$

Where $EGGS$ is the number of eggs, $Inpegg$ is the number of eggs initially present, $Growthnewb$ is the number of eggs that attained the newborn stage and is given by:

$$Growthnewb = EGGS*(1-Morteggs)$$

where *Morteggs* is the mortality on egg stages, comprising natural decaying “*Nat1*”, predation by the carnivorous snail *Ouagapia inaequalis* “*Ouag*” and rodent predation “*Rod1*”

$$Morteggs = Nat1 + Ouag + Rod1$$

Outpegg is the egg output after mortality affected the eggs stock.

$$Outpegg = EGGS * Morteggs$$

Newborn population

The number of newborns entering the system after each iteration was given by:

$$NEWBORNS_t = NEWBORNS_{t-dt} + (Growthnewb - Growthjuv - Outpnewb) * dt$$

Where *NEWBORNS* is the number of newborns, *Growthnewb* is the number of eggs that attained the newborn stage (as presented previously), *Growthjuv* is the number of newborns that attained the juvenile stage and is given by:

$$Growthjuv = NEWBORNS*(1-Mortnewb)$$

where *Mortnewb* is the mortality on newborn stages, comprising natural mortality “*Nat2*” and predation by rodents “*Rod2*”

$$Mortnewb = Rod2 + Nat2$$

Outpnewb is the newborn output after mortality affected the newborn stock.

$$Outpnewb = NEWBORNS * Mortnewb$$

Juvenile Population

The number of juveniles entering the system after each iteration was given by:

$$JUVENILES_t = JUVENILES_{t-dt} + (Growthjuv - Growthsubad - Outpjuv) * dt$$

Where JUVENILES is the number of juveniles, *Growthjuv* is the number of newborns that attained the juvenile stage and was presented below, *Growthsubad* is the number of juveniles that attained the sub-adult stage and is given by:

$$Growthsubad = JUVENILES * (1 - Mortjuv)$$

where *Mortjuv* is the mortality on juvenile stages, comprising natural mortality “*Nat3*” and predation by rodents “*Rod3*”

$$Mortjuv = Rod3 + Nat3$$

Outpjuv is the juvenile output after mortality affected the juvenile stock

$$Outpjuv = JUVENILES * Mortjuv$$

Sub-adult population

The number of sub-adults entering the system after each iteration was given by:

$$SUB_ADULTS_t = SUB_ADULTS_{t-dt} + (Growthsubad - Growthad - Outpsub) * dt$$

where SUB-ADULTS is the number of sub-adults, *Growthsubad* is the number of juveniles that attained the sub-adult stage and was presented below, *Growthad* is the number of sub-adults that attained the adult stage and is given by:

$$Growthad = SUB_ADULTS * (1 - Mortsubad)$$

where *Mortsubad* is the mortality on sub-adult stages, comprising natural mortality “*Nat4*” and predation by rodents “*Rod4*”

$$Mortsubad = Rod4 + Nat4$$

Outpsub is the sub-adult output after mortality affected the sub-adult stock.

$$Outpsub = SUB_ADULTS * Mortsubad$$

7.3 Results

7.3.1 Calibration of the model

Data on the survey of snail stock from 1996 to 2008 on Isle of Pines forests (Chapter 3) were used to calibrate the model. The population trends for adults and sub-adults predicted by the model were compared to population trends from the field data sets for each stage (Figure 7.2). Rodent predation on juvenile stages evaluated at 67.1% in Chapter 4 resulted in a rapid population crash within five years. We set it at 65% and found that at that level, the model correctly predicted the population trends. For adults, predicted values were slightly higher than observed data. For sub-adults, the fluctuations in the field population were around a long-term trend of a slow decline in keeping with the models predictions.

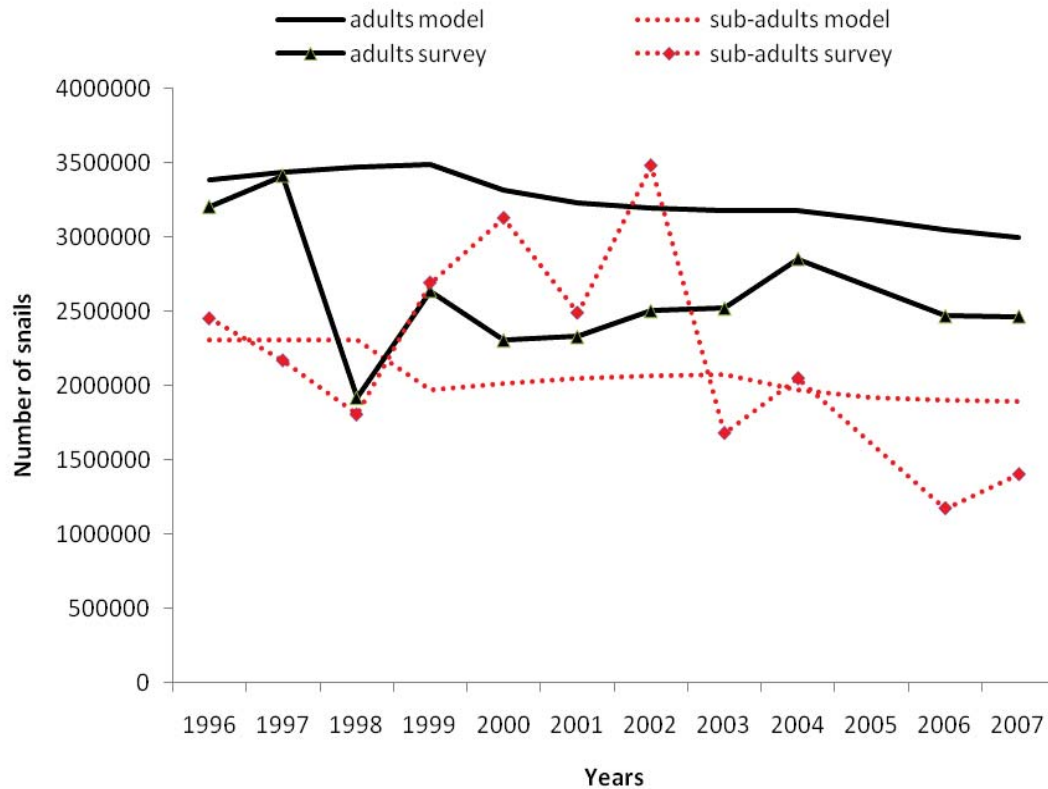


Figure 7.2: Calibration of model output with field data for adults and sub-adults *P. fibratus* on Isle of Pines from 1996 to 2008. Data are from Chapter 3.

7.3.2 Population trends

When the model was run for 50 years, starting with the reported 1996 population estimate and subjected to the current level of human collection of 120,000 adult snails per year and the other sources of mortality, the population declined at an overall rate of 0.52% per annum for adults and 0.50% per annum for juveniles (Figure 7.3). This is consistent with the available annual survey data. After 50 years this would represent an adult decline of 42% and sub-adults of 41%.

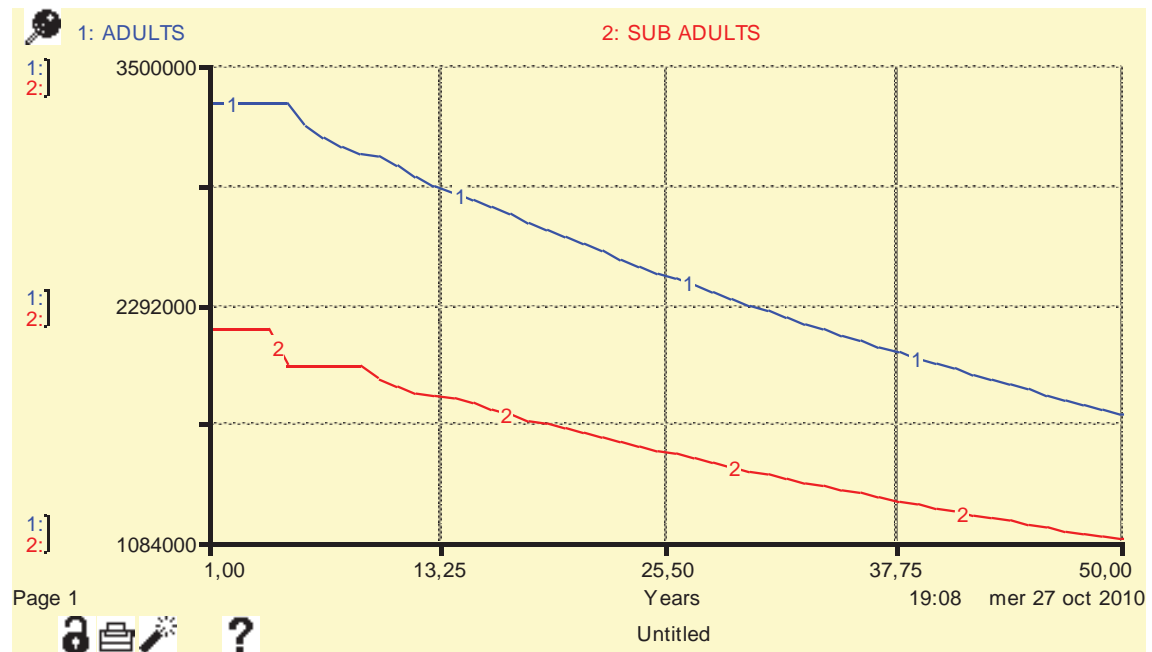


Figure 7.3: Population trends of adult and sub-adult *P. fibratus* on Isle of Pines for 50 years from 1996 given a constant human harvest of 120,000 adult snails per year (6% of the estimated adult stock for the period 2007-2008).

7.3.3 Sensitivity analysis

Several tests of parameter sensitivity were conducted. Key parameters such as the level of human collection (*HumCol*) and rodent predation (*Rod*) were selected to consider the effectiveness of potential control that might realistically be achieved in field management options.

7.3.3.1 The effect of human collection

The effects of human collection was investigated by scaling the number of adult snails collected in forest from 0%, corresponding to a cessation of collection, to 20% exploitation rate per year starting at the 2008 estimated adult stock of 2,160,000 (that would correspond to the collection of 430,000 snails per year). Assuming a

constant collection level for each rate tested during the period, Figure 7.4 shows the effects of these changes on the adult population over a year period of 50 starting in 1996.

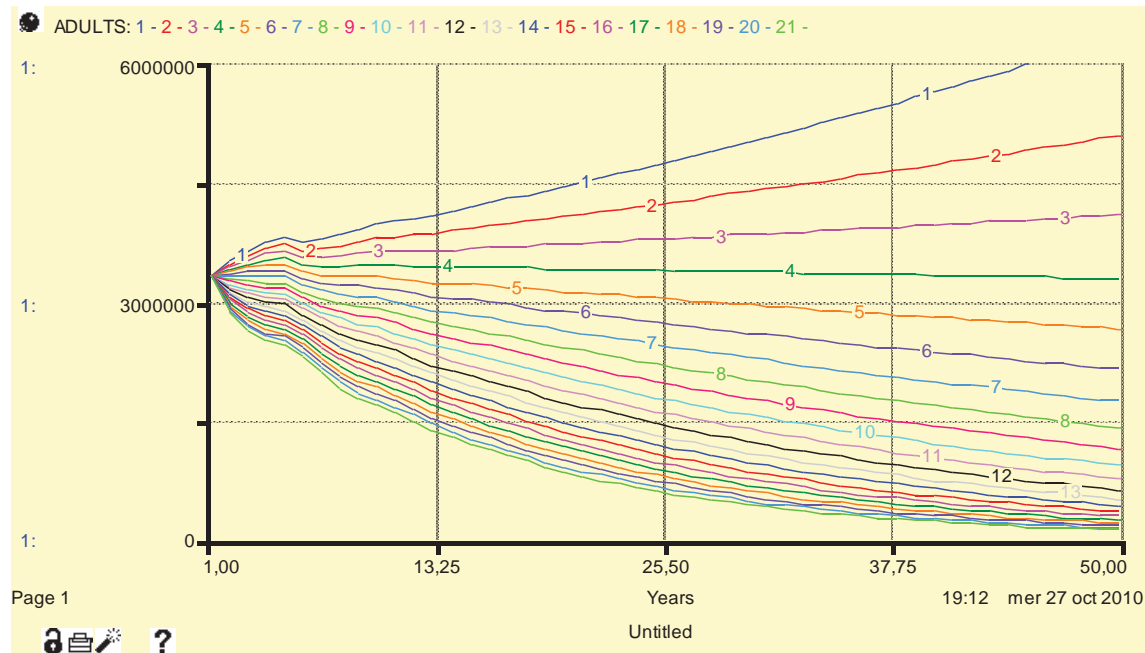


Figure 7.4: Simulation of the change in the adult snail population on Isle of Pines from 1996 to 2008 in a sensitivity analysis conducted on the human collection parameter (1% increments in collection are shown from 1: human collection is stopped (0%) to 21: a collection rate of 20% of the 2008 estimated adult stock (c.a. 2,160,000 snails); 7 is the actual exploitation rate of 6% of the estimated adult population in 2008).

If harvesting was stopped, the response of the adult snail population would be a steady increase (Figure 7.4 line 1), with the adult population doubling within 50 years. If the current level of harvest is maintained (Figure 7.4 line 7 = 6% of the estimated adult population in 2008), the adult population would continue its decline as described in Figure 7.3. Any increase in annual harvest would accelerate the decline. Population stability occurred at a harvest rate of 3% per annum (c.a. 70,000 adult snails per year from the 2008 estimated adult stock) (Figure 7.4 line 4).

7.3.3.2 Significance of rodent predation

The model showed the snail population to be very sensitive to changes in the rate of rodent predation. A sensitivity analysis conducted on rodent predation on juveniles (*Rod3*), the most vulnerable stage of the cycle of snails, showed that a reduction of just 1% of the rodent predation of juveniles led to a significant recovery of the snail population (Figure 7.5). A reduction of only 1% of rodent predation on all vulnerable snail stages is predicted to lead to a rapid increase in both adult (estimated as 373% in 50 years) and sub-adult snails (estimated as 392% in 50 years) (Figure 7.6 a). Conversely, a 1% increase in rodent predation would lead to the eventual extinction of adults (only 6% of the original stock will remain after 50 years) and sub-adults (only 5% of the original stock will remain after 50 years) (Figure 7.6b).

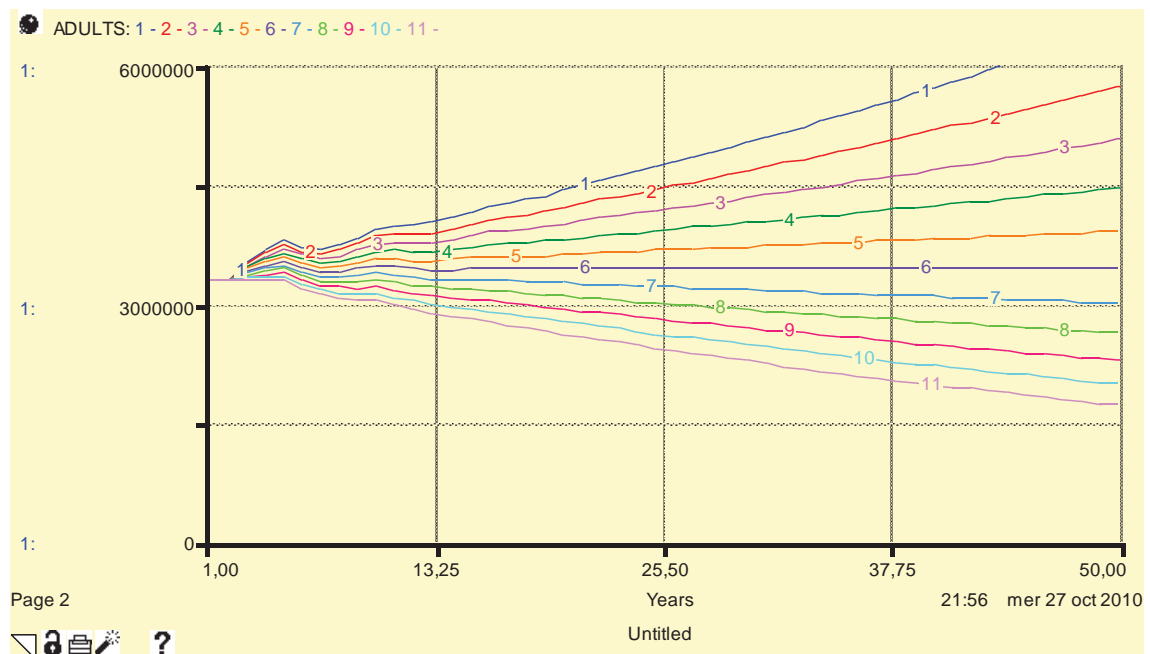


Figure 7.5: Simulation of the change in the adult snail population on Isle of Pines from 1996 to 2008 in a sensitivity analysis conducted by reducing by 1% the rodent predation (*Rod3* parameter) exerted on juveniles (0.01% increments in predation are shown from line 1: rodent predation rate is 0.64 to line 11: actual rodent predation of 0.65).

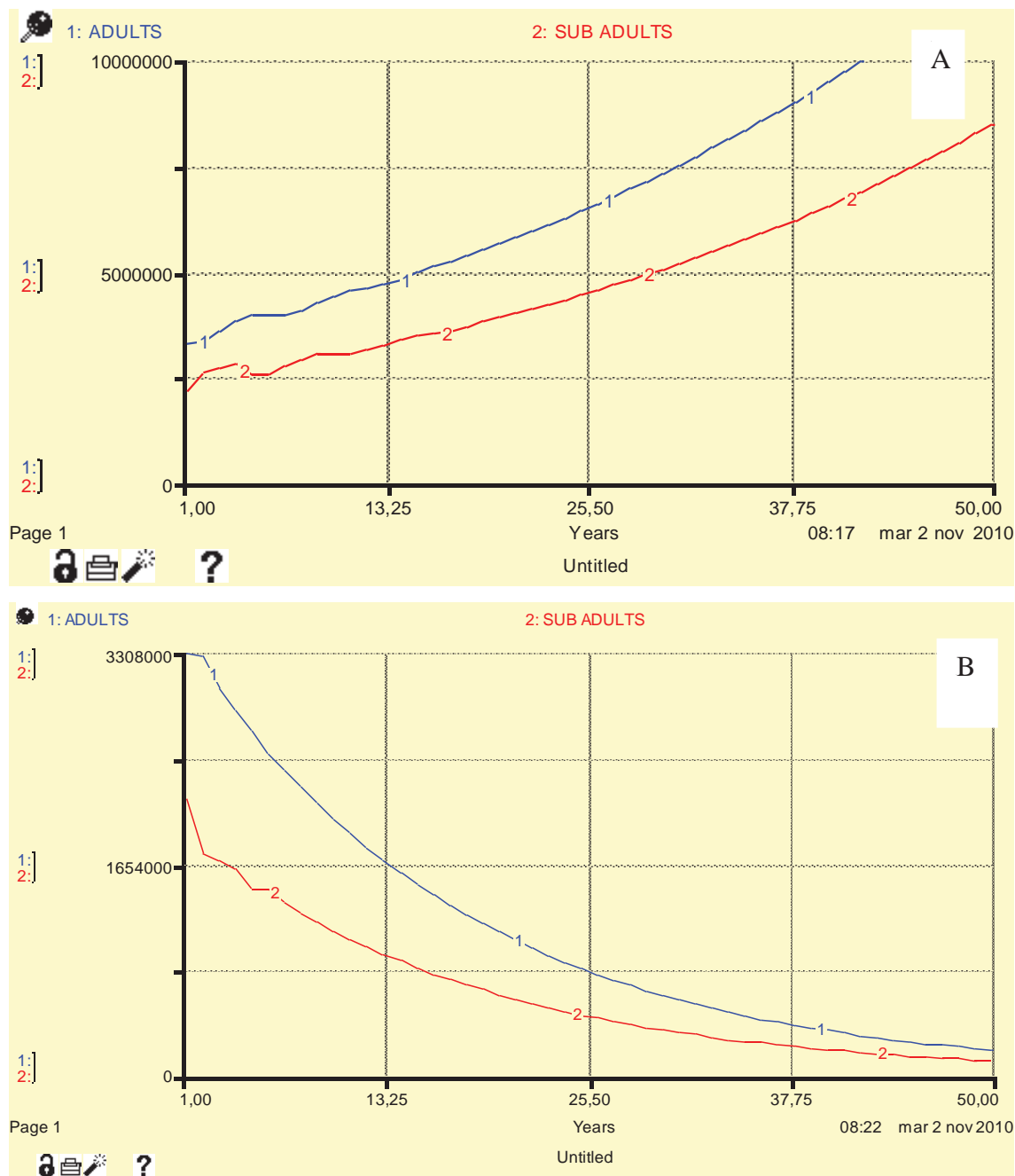


Figure 7.6: Population trends of adult and sub-adult *P. fibratus* on Isle of Pines for 50 years from 1996 with A) a rodent predation rate decrease of 1% and B) a rodent predation rate increase of 1%.

7.4 Discussion

7.4.1 A first simple simulation model for *P. fibratus*

A computer stage-structured dynamic model for the exploited endemic land snail *P. fibratus* in New Caledonia was constructed. Due to our initial management and conservation objectives and the data available, we did not expect the model to produce precise predictions of the future numbers of snails at this stage; instead, we were more interested in using the model to generate predictions of future population trajectories and to explore management strategies that could limit the decline observed in the field.

7.4.2 Assumptions and validity of the model

In contrast to the survey data, the model contained no year-to-year fluctuations, so the fit was not perfect. This was expected because we did not build any stochasticity into our model. Also, some of the parameter estimates used here, such as natural mortality rates for early stages (eggs and newborns) and, to a lesser extent, rodent predation rates on juveniles, were “best-guess” estimates based on observations in captivity and also on limited data on what happens in the field.

The assumption of one year duration of each life stage was likely to have only a negligible effect because we set mortality rates for the one year period to equal mortality rates determined for each stage (e.g. entire duration of egg or juvenile stage). The duration will affect the per annum rate of change but not the shape or direction of change. Also, we did not impose any maximum age for adults because the mortality factors impinging on the adults effectively ensured that they did not live forever.

7.4.3 Fate and persistence of populations

The model highlights the importance of two key parameters that realistically could be manipulated in the field as feasible management options to ensure the persistence of *P. fibratus* snails on the Isle of Pines: the level of human harvest and the intensity of predation by rodents. If no new management is undertaken and if the harvest level remains at a rate of around 120,000 adult snails per year (in other words if nothing is done), our analysis makes a pessimistic forecast that mirrors the pattern shown by the longitudinal field-based survey data (Chapter 3); i.e. the population will continue to decline with a loss of about 0.52% per annum for adults and will reach seriously low levels within the next 50 years. If the harvest stopped completely, the snail population should recover over the next 50 years, whereas any increase in collect

rate will accelerate the rate of decline. The model also predicts that the current sustainable harvest rate (i.e. where the total population would remain essentially stable through time) is 3% of the actual estimated stock, which equates to about 70,000 adult snails per year. This is half the current annual harvest. However, if rodent control operations were initiated and succeeded in reducing predation by rats by even a very small amount (in a range of 1%), and the annual harvest of snails was unaltered, it might be possible to achieve an increase in the *Placostylus* population.

Nevertheless, the high sensitivity of the model to rodent predation rates needs careful evaluation. Rodent densities and hence predation rates are likely to fluctuate by far more than 1% across years under natural conditions, and thus the effects of rodent predation on the actual population of snails might be buffered or dampened by other factors. One likely scenario is that snails do not represent the primary food of rodents but are eaten opportunistically. This would make this system very different from typical predator-prey systems (such as the Lotka-Volterra predator prey model (Begon *et al.* 2002)), in which the predator species is dependent on a single prey species and prey numbers drive predator numbers with feedback loops. The effects of rodent predation on *Placostylus* populations might also be different in areas where snail densities are higher (different spatial distribution of food density) and/or consumption rate might vary seasonally.

7.4.4 Suggestions for management

7.4.4.1 Limit the harvest by reinforcement of control measure

Sustainable population growth was predicted with increased protection (i.e. a reduction in the number of snails collected to 70,000 per year). Without a reduction in harvest, the population either remains stable or decreases steadily. The first conservative measure that we recommend is to reinforce measures to limit the harvest. In chapter 3, we found that the actual estimated total number of snails collected from forests on the Isle of Pines was 120,000 per annum. This represented 6% of the mean estimated adult wild stock of 2,160,000 snails for the year 2008. Included within this are snails collected for daily consumption by Kunié households, estimated at $42,624 \pm 26,208$ snails per year. Our simulation showed that snails may be harvested sustainably by removing up to 3% of the 2008 adult stock (c.a. 70,000 snails). Therefore, collection for commercial use would need to stop because the actual stock can only support the Kuniés' own consumption. Yet a recurrent demand by the local people to

the regulatory authority is for an increase in the permissible harvest and reinstatement of the right to sell to restaurants and supermarkets on the mainland. Our simulation clearly indicates that increasing the harvest would hasten population decrease and seriously threatened the persistence of *Placostylus* populations on Isle of Pines.

7.4.4.2 Continue monitoring population trends

The monitoring of snail abundance on Isle of Pines started in 1993 and has continued almost annually till 2008. We recommend that annual surveys continue to enable ongoing assessment of population trends and the impact of any future changes in management, and also to re-evaluate periodically harvest strategies and acquire accurate data on the numbers of snails being collected as a proportion of the total population.

7.4.4.3 Involvement of locals

Involvement of local people in management would facilitate the development of more responsible approaches to resource use. Kuniés could also be involved in the monitoring programme that eventually could be devolved to them by local authorities.

7.4.4.4 Rodent control

The sensitivity analyses performed in this study suggest that population trends are very sensitive to rodent predation because they have a large effect on recruitment from juveniles to adults. Management strategies aimed at rodent control or eradication would likely have profound benefits for the conservation of the snails. Toxic baits have been shown to successfully eradicate rodents from Pacific islands (Howald et al 2007, Parkes 2009) when applied using extensive bait stations and/or broadcast either by hand or, more usually, from a helicopter to cover the whole island (Parkes 2009). Aerial baiting is now the usual method for tackling rats on large, densely vegetated or topographically complex islands (Howald *et al.* 2007). The Isle of Pines is a relatively large island (152 km²) covered by about 6,000 ha of native evergreen forest on coral soil and is thus best suited to aerial baiting, but the island is inhabited by about 1,500 Kuniés. The local economy on this island, which is often nicknamed “l’île la plus proche du paradis” (“the closest island to Paradise”), is based mainly on tourism. The locals value the forest and its natural resources and recognise the importance of the island for tourism, but they are averse to the widespread use of poison baits. Indeed, large-scale rodent control operations using poison baits are novel in New Caledonia

and the only project of this type, conducted on an uninhabited islet near Nouméa, has been highly controversial and is set to be cancelled due to public pressure. Thus, there is currently little chance that such operations on Isle of Pines would be accepted by either the local people or the relevant authorities. Nevertheless, localised rodent control operations based on trapping might be possible in small areas where snail numbers decrease rapidly or to provide refugia for snails where they could be maintained at high densities.

7.4.4.5 Recommended research

The model we constructed in this study generated population trends similar to those observed in the field, but this is very much a first attempt to develop a tool for managers and local people to investigate management options for the conservation and sustainable harvest of *P. fibratus* snails. The model is useful as-is, but its development highlights the need for better estimates for some parameters such as natural mortality rates of eggs and newborns. The values used here for these were “best-guess” estimates based on observations in captivity and need to be investigated further. It would also be worthwhile investigating spatial variation in mortality factors across the eight districts on the Isle of Pines. Also, understanding the efficacy of localised pulsed rodent control on reversing population decline and possibly facilitating localised increases in harvest would be invaluable. Finally, more information is required on the potential effects of different harvesting strategies such as annual, periodic or delayed harvests (strategies that would certainly require a complex management system, these might not be compatible with the financial spin-off expected by Kuniés and illustrates the need to work closely with locals to develop management strategies that will meet the complex and often divergent goals of conservation and economic development.

7.5 Acknowledgements

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7.6 Appendix A- Parameters used for the calibration of the *Placostylus* model

Symbol	Name	Units
STOCKS		
ADULTS	Number of adults present in the model after each year	Snails
SUB_ADULTS	Number of sub-adults present in the model after each year	Snails
EGGS	Number of eggs present in the model after each year	Eggs
JUVENILES	Number of juveniles present in the model after each year	Snails
NEWBORNS	Number of Newborns present in the model after each year	Snails
MORTALITY		
<i>Humcol</i>	Number of adult snails collected	Proportion/year
<i>Nat1</i>	Natural mortality rate for eggs	Proportion/year
<i>Nat2</i>	Natural mortality rate for newborns	Proportion/year
<i>Nat3</i>	Natural mortality rate for juveniles	Proportion/year
<i>Nat4</i>	Natural mortality rate for sub-adults	Proportion/year
<i>Nat5</i>	Natural mortality rate for adults	Proportion/year
<i>Ouag</i>	Predation by <i>Ouagapia inaequalis</i> on eggs	Proportion/year
<i>Pigs</i>	Pig predation rate on adults	Proportion/year
<i>Rod1</i>	Rodent predation rate on eggs	Proportion/year
<i>Rod2</i>	Rodent predation rate on newborns	Proportion/year
<i>Rod3</i>	Rodent predation rate on juveniles	Proportion/year
<i>Rod4</i>	Rodent predation rate on sub-adults	Proportion/year

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CHAPTER 8

A LAND-SNAIL RESTORATION ATTEMPT: RODENT POISONING IN A REMNANT DRY FOREST PATCH IN NEW CALEDONIA



Characteristic rat-damaged shell of Placostylus and rodent bait station used in the rodent poisoning operation

Abstract

Only small, isolated, remnant populations of the New Caledonia endemic land snail *Placostylus porphyrostomus* remain in dry forests of the Mainland. These forests are the most threatened biome of the archipelago, and their remnant snail populations are threatened by habitat loss and predation by introduced rodents. In an attempt to restore a remnant *P. porphyrostomus* population in a dry forest patch, we controlled rodents for 22 months by continuous poisoning (with diphacinone). At the end of the trial, rodent abundance, as indicated by tracking tunnels, had been reduced by 84% in poisoned areas, but the poison apparently also affected adjacent non-treatment areas where tunnel tracking rates reduced by 34%. After six months of poisoning there was evidence of an initial increase in juvenile *P. porphyrostomus* densities in the poisoned sites relative to the non-poison sites, but after 15 months, the differences in snail recruitment rates were no longer significant. Similarly, there was no significant effect of the rodent control on the introduced pestiferous African snail *Achatina fulica*. However, after 15 months of poisoning, the proportion of empty rodent-damaged shells of *P. porphyrostomus* decreased to become less abundant than empty, whole shells suggesting a change in the main causes of mortality. New Caledonian *Placostylus* are quite specific in their habitat requirements, are large long-lived snails with slow growth rates and have natural high mortality rates during the young stages. Consequently, they are quite slow to recover from predation pressure. Controlling rodents appears to be beneficial to the recovery of *Placostylus* in dry forest ecosystems but sustained recovery will require long-term poisoning coupled with habitat restoration and perhaps population supplementation with captive-bred snails to speed the recovery progress.

Une tentative de restauration d'une population d'escargots terrestres: empoisonnement des rongeurs introduits dans un lambeau de forêt sèche de la Nouvelle-Calédonie

Résumé

De petites populations isolées de l'escargot terrestre endémique *Placostylus porphyrostomus* se rencontrent encore dans certains lambeaux de forêts sèches de la Grande-Terre de la Nouvelle-Calédonie. La forêt sèche est l'écosystème le plus menacé de l'archipel, et les populations résiduelles d'escargots sont mises en péril par la perte de leur habitat préférentiel et la prédation par les rongeurs introduits.

Afin de tenter de rétablir les effectifs d'une petite population de *P. porphyrostomus* dans un lambeau de forêt sèche à Poya, nous avons régulé localement la population de rongeurs par empoisonnement continu (diphacinone) pendant 22 mois. A la fin de l'essai, l'abondance des rongeurs, évaluée grâce à la méthode indiciaire des tunnels à empreintes, a été réduite de 84% dans les zones empoisonnées tandis que l'empoisonnement a aussi affecté les zones témoins non empoisonnées qui ont vues les indices d'abondance diminués de 34%. Après six mois d'empoisonnement, il a été observé plus d'escargots juvéniles de *P. porphyrostomus* par rapport à la situation initiale, dans les zones régulées. Mais après 15 mois, les différences de recrutement au sein des populations n'apparaissaient plus significatives entre zones empoisonnées et zones non empoisonnées. De façon similaire, il n'y a pas eu d'effet significatif sur les populations d'escargots géants Africains *Achatina fulica*. Cependant, après 15 mois de régulation, la proportion de coquilles vides de *P. porphyrostomus* endommagées par les rongeurs a diminué et celles-ci sont devenues moins abondantes que les coquilles vides intactes suggérant un changement dans la cause principale de mortalité. Les escargots du genre *Placostylus* présentent des exigences en termes d'habitat très particulières, ont une durée de vie très longue et des taux de croissance relativement faibles, ainsi qu'une mortalité chez les stades jeunes naturellement élevée. En conséquence, le rétablissement des effectifs lorsque la pression de prédation a été réduite apparaît être un processus long.

La régulation des rongeurs apparaît bénéfique à la restauration des populations de *Placostylus* des forêts sèches mais un rétablissement durable et rapide nécessiterait de coupler l'empoisonnement sur le long terme avec des opérations de restauration de

l'habitat, et peut être aussi d'inclure des opérations de renforcement des populations à partir d'individus nés en captivité afin d'accélérer le processus.

8.1 Introduction

The six endemic species of New Caledonian *Placostylus* (Pulmonata: Bulimulidae) inhabit exclusively native dry or evergreen forests where they are generally found under leaf litter (Brescia *et al.* 2008). These are large, slow-moving, slow-developing and long-lived land snails that appear to be relatively specific in their habitat requirements and so they are now concentrated in remnant pockets of suitable habitat. *Placostylus porphyrostomus* Pfeiffer, 1851 is the most common species in sclerophyllous forests (Chérel-Mora 1983), which is the dominant vegetation type in dry areas of the west coast of the mainland (less than 1100 mm annual rainfall, mostly falling in three months of the year). This forest type is characterized by a high diversity of plant species but is currently the most threatened of the Caledonian biomes (just 1% remains) due to deforestation and habitat modification by feral ungulates (Programme Forêt Sèche 2007). A conservation programme with ten international, national and local partners (“Programme Forêt Sèche”) has been initiated recently in an attempt to try to save this highly endangered biome and its associated specialised fauna and flora. In 1996, *P. porphyrostomus* was registered as Vulnerable on the Red List of IUCN (Bouchet 1996). The reasons for the decline of New Caledonian *Placostylus* snails are now fairly clear; habitat destruction or modification, human harvesting for consumption, and predation by introduced species (Brescia *et al.* 2008).

Introduced mammals such as feral pigs and rodents appear to contribute seriously to the decline of New Caledonian *Placostylus* populations. As well as destroying native vegetation and disturbing the leaf litter, feral pigs are predators of *Placostylus* (Pöllabauer 1995; Brescia *et al.* 2008; chapter 4). Moreover, in sclerophyllous forests, rodents (Polynesian rats *Rattus exulans* (Peale, 1848), ship rats *R. rattus* (Linnaeus, 1758), and house mice *Mus musculus* Linnaeus, 1758) eat juvenile *Placostylus* up to 5 cm shell height (Brescia & Pöllabauer 2005). Rodent-damaged *Placostylus* shells are easily identified because rodents typically remove a broad spiral band of shell from one or more whorls starting from the aperture lip (Sherley *et al.* 1998). Ship rats and Polynesian rats are found sympatrically in these forests, an unusual situation in New Zealand where the two species rarely coexist. Also, compared to New Zealand, rodent densities appeared very high in these forests (Chapter 5). In Chapter 4 we found that in permanent quadrats used in a mark-recapture study in sclerophyllous forests to measure survival rates, up to 86.6% (95%

CI= 76.4-96.8%) of juvenile shells on the ground showed signs of rodent predation. Mice have been recorded eating entire *Placostylus* egg clutches under semi-natural captive conditions on the Isle of Pines (Brescia 2004). Thus rodents appear to be potentially very harmful to *Placostylus* populations as they systematically eat eggs, hatchlings and juveniles, exacerbating the already high natural mortality rates of hatchling and juvenile size classes. The combined effect may greatly reduce recruitment to adult size and progressively contribute to ageing populations. In New Zealand, predation by introduced pigs, rodents, and birds has also been implicated in the decline of *Placostylus* along with habitat destruction and modification by farming and burning (Penniket 1981; Parish *et al.* 1995; Sherley *et al.* 1998).

In pre-human New Caledonia, the only native terrestrial mammals were bats (Revillod 1914). Polynesian rats were introduced 3,000 years ago by the first human colonisers, and ship rats, Norway rats (*Rattus norvegicus*) and house mice arrived in the 19th century (Gargominy *et al.* 1996; Pascal *et al.* 2006). The islands of the tropical Pacific typically are characterized by land snail faunas comprising species that are endemic to single islands or archipelagos (Cowie 1998) and as a group, these species have frequently suffered heavily from predation by rats (Hadfield 1986).

In New Zealand, major successes in eradicating rodents have been achieved on islands; but mainland ecological restoration is relatively recent. Eradication of introduced mammals is usually not practicable on the mainland for financial, technical or social reasons (Sherley *et al.* 1998). Nevertheless, intensive control of mammal pests in selected areas where there are chances of increasing the numbers of a threatened species has been successful (Atkinson, 2001; Innes *et al.* 1999). The New Zealand Department of Conservation developed the concept of “Mainland Island” in 1995 (Saunders *et al.* 2001) in which pest control regimes are more intensive and run for longer than on islands, and sustained either by pest-proof fences preventing re-invasion, or by ongoing trapping or poisoning. Mainland Island projects have shown that intensive control of multiple pests is achievable at mainland sites, and there are also some indications that as a result of management regimes in place populations of native species have been enhanced and ecological processes re-vitalised. Most importantly, Saunders *et al.* 2001 considered also that these projects have demonstrated that further declines in biodiversity are not necessarily inevitable on the mainland.

In this study, we undertook the first long term rodent control operation in New Caledonia. The objectives of this study were to (i) determine the feasibility by poisoning operation of reducing rodent abundance on the mainland of New Caledonia and (ii) to determine whether rodent control would assist in recovery of the endemic *P. porphyrostomus* in a patch of New Caledonian dry forest.

8.2 Methods

8.2.1 Study area

This study was conducted in a native sclerophyllous forest in Nékoro, near Poya, on a privately-owned ranch located on the western coast of “Grande-Terre” (altitude 0-100 m asl). Nékoro is one of the last remaining moderately large remnant patches of dry forest (272 ha) and in 2007, about 150 ha of forest was fenced to exclude rusa deer (*Cervus timorensis*) and cattle (*Bos taurus*) (Programme Forêt Sèche 2010). The forest contains a small remnant *Placostylus* snail population (*P. porphyrostomus mariei* (Crosse & Fisher in Crosse, 1867)) with an estimated mean density of 2.3 snails / 100 m² (SD = 2.8) (Brescia & Pöllabauer 2004, 2005) and the introduced African snail (*Achatina fulica*) is also present. In Chapter 5 we estimated rat densities in this patch by snap-trapping to local extinction. Ship rats and Polynesian rats were both present but no mice were captured. Rodent densities were estimated in June 2007 at 19.1 rats ha⁻¹ in Nékoro (18.9 – 23.6 rats ha⁻¹, 95% confidence intervals).

Baits were distributed within rodent bait stations to minimise non-target poisoning of avifauna (see below). The avifauna of New Caledonian dry forests comprises 41 terrestrial species (183 species have been described for the archipelago), none of which are specific to the dry forest biome and all are not considered as rare or endangered at the New Caledonian scale (Desmoulins and Barré 2005). We thus considered that any low-level collateral poisoning of birds in the study area was acceptable given the underlying conservation goal of attempting to save the threatened snails.

8.2.2 The rodent poisoning design

In December 2007, ten 20 x 20 m permanent quadrats separated by about 200 m were established in areas found to host snails in a pilot survey. Five quadrats were

assigned to receive rodent poison and the remaining five quadrats were set aside to be left untreated.

A 100 x 100 m rodent plot was centred over each of the ten 20 x 20 m permanent snail monitoring quadrats. Within each of the rodent plots, an array of nine rodent footprint-tracking tunnels (The Trakka, Connovation Ltd.) spaced at 50 m intervals in a 3 x 3 grid, and 25 bait stations (Rodent Baiter 19RBS03, Pest Management Services, NZ) in a 5 x 5 grid at 25 m spacings were established. In the non-poison quadrats only the footprint-tracking tunnels at the same spacing described for controls were established. In the treated zone, the poisoning area was thus 1 ha per quadrat, i.e. 5 ha for the five quadrats. The effective poisoning area was estimated by assuming a boundary strip of as much as 56 m (Dice, 1938) beyond the 100 x 100 m area poisoned, estimated as the radius of a circular home range of 1 ha, which is a typical size based on radio telemetry of ship rats in the North Island of New Zealand (Hooker & Innes 1995). This would suggest an effective poisoning area of 22.5 ha for the combined control quadrats but Rouys (2008), in a preliminary radio-tracking study, found smaller home ranges for New Caledonian rodent species: 0.86 ha for female ship rats and 0.35 ha for males, and 0.33 ha for female Polynesian rats and 0.95 ha for males. Considering the minimum and maximum home range values for New Caledonian rodents, the effective poisoning area may have varied from 13.4 to 18.4 ha. The poisoned and non-poisoned plots were not able to be interspersed since the area was not large enough to ensure that the poisoned plots would not deplete rats in the non-poisoned plots.

Distribution of anticoagulant poison baits started in August 2008 and consisted initially of 12 mm diameter pellets of “Pestoff Rodent Bait 20 R, Animal Control Products, NZ” (brodifacoum 0.02 g/kg) replaced once a week until the rate of poison removal became relatively low and stable, and then once a month until November 2008 when an invasion of feral pigs (*Sus scrofa*) in the fenced forest forced us to change the poison to “Pestoff Rodent Bait 50D, Animal Control Products, NZ” (diphacinone 0.005 g/kg) to limit the risk of human brodifacoum contamination since pigs are hunted regularly in this area. Diphacinone is less persistent in body tissues than brodifacoum (e.g. rat liver, Fisher *et al.* 2003) and has lower toxicity to mammals and birds than brodifacoum (EPA, 1998).

Changes in the rodent population were assessed using tracking tunnels baited with cheese and peanut butter that were run for one night once a month from June to August 2008 prior to poisoning and then from September 2008 to June 2010. Two hundred and fifty non-toxic wax blocks (Waxtags®), placed every 25 m on the 100 x 100 m grid, were also employed before poisoning in August 2008 and again after poisoning in September 2008 to provide a second index of rodent abundance. These were run for three consecutive nights as recommended in Chapter 5.

8.2.3 Information collected on snails

To facilitate the snail search, each 20 x 20 m quadrat was divided into four 10 x 10 m quadrats. The number of live snails found per quadrat was noted and three size measures were recorded for each snail: weight, height and thickness of the lip aperture of the shell. The lip thickness is an indicator of adulthood: Pöllabauer (1995) considered that adult *P. fibratus*, a New Caledonian congeneric of *P. porphyrostomus*, are those characterized by a shell with a thickened aperture lip (more than 4 mm) while our observations in captivity indicated that snails with an aperture lip of 3.5 mm were sexually mature (laying eggs). Breeding in captive-born *P. porphyrostomus* was also often observed for this species once snails had attained a lip size of more than 3 mm (F. M. Brescia Pers. Obs.) Thus, snails were classified as adults when the aperture lip was ≥ 3.5 mm, as juveniles when the lip thickness was < 3.5 mm but the snail was > 10 mm long, and infants (newborns) when the aperture lip was un-thickened and the snail was ≤ 10 mm. In addition, each shell was classified as being live, an undamaged but empty shell, or as a predator-damaged shell. Similar data were recorded for *A. fulica* but in the absence of reliable criteria to characterize sexual maturity (we often observed snails of different sizes laying eggs, and the lip does not thicken in this species), we did not distinguish between adult and juvenile African snails.

The empty shells of both species were discarded outside the quadrats so they were not included in subsequent samples, but live snails were returned to the quadrat. Individual identifying numbers were engraved on the shells of live snails > 15 mm long by carefully grinding the periostracum using a portable engraver (“Arlec”, Dick Smith Electronics). Harmonic radar transponders were attached to live snails to help locate them again (Stringer *et al.* 2004, see 4.2.2.). Transponders were fixed in the middle of the shell when snails were sub-adults or adults, and a slightly lighter transponder was

attached to the apex of the shell of juveniles where it would not interfere with growth as the shell enlarged.

In each 10 x 10 m sub-quadrat, snails were searched for within the leaf litter by at least three people for about one hour, until no empty shells and no new unmarked live snails were found. The area was then rechecked with the radar to ensure that all transpondered snails had been found. The quadrats were first searched in January 2008 before the poisoning started. These surveys provided baseline data (T). The sites were searched again in January 2009 six months after the start of poisoning (T₊₆) and finally in November 2009 after fifteen months of poisoning (T₊₁₅).

8.3 Results

8.3.1 Impact of poisoning on rodent abundance

The first three monthly assessments of rodent abundance before poisoning gave a mean tracking rate of 75.5% in the designated poisoned quadrats and 57.7% in the designated controls (Figure 8.1). One month after poisoning started in August 2008, the indices of rodent abundance declined in both the control and poisoned areas although the decline was more pronounced in the poisoned areas. Between February and March 2009, bait stations were not restocked because access to the forest was prevented by adverse weather conditions during the wet season. Following this, the tracking rates increased for a short time, but for most of the 22 months of control, rodent abundances were kept at very low levels compared to the initial situation in the poisoned areas and appeared to be somewhat depressed in the non-poisoned areas (mean tracking rates were 49.9% versus 9.9% respectively for non-poisoned and poisoned areas from the period extending from May 2009 to June 2010). This suggests a flow-over effect of rodent poisoning from the treatment areas to the adjacent non-poisoned due presumably to the foraging range of rodents, the small size of the Nékoro patch of dry forest, and the spacing of adjacent quadrats.

Waxtags, the second index technique used in the study, showed rat bite mark rates of 23.9% (95% CI= 18.1-29.7%) in the designated non-poisoned quadrats and 18.1% (95% CI= 8.8-27.3%) in the poisoned quadrats in August 2008 prior to poisoning. In September 2008 following poisoning, rates were reduced to 0% and 3.8% (95% CI= 0-8.0%) respectively in poisoned and non-poisoned areas.

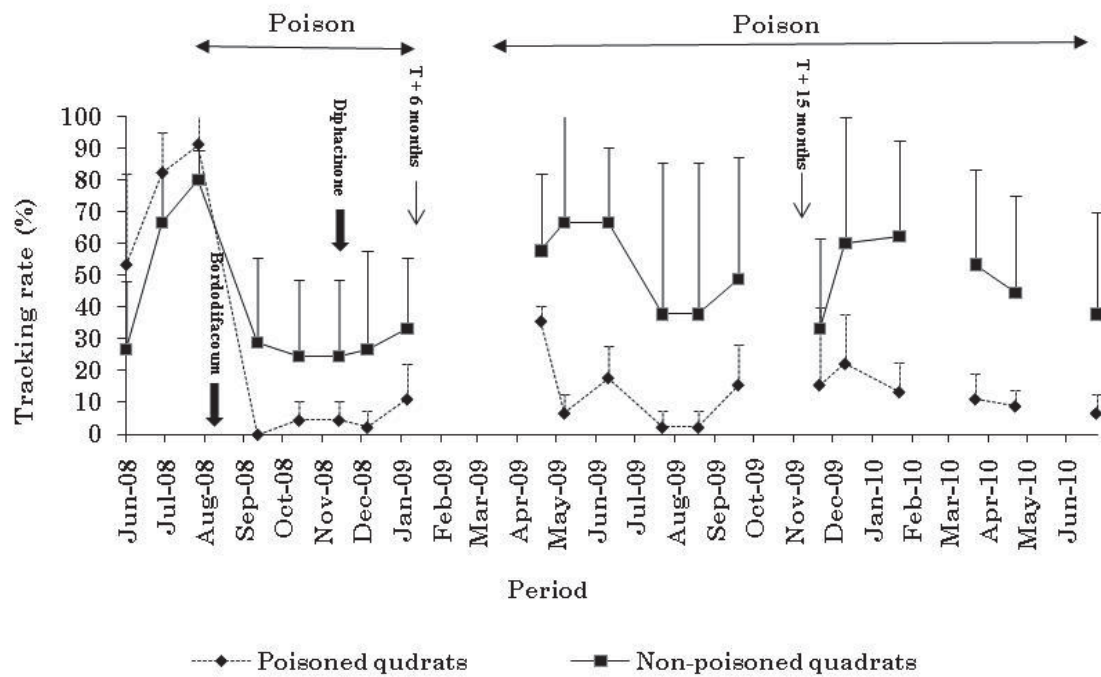


Figure 8.1: Monthly one-night tracking rates average and standard deviations in poisoned and non-poisoned areas in Nékoro from June 2008 to June 2010.

8.3.2 Snail mortality

The two main causes of juvenile *Placostylus* mortality were natural death (i.e. undamaged empty shells) and rodent predation. In the pre-poison survey, empty rodent-damaged shells predominated among empty shells found on all plots (Figure 8.2). After 15 months of poisoning, the proportion of rodent-damaged shells had decreased and become less common than empty whole shells in both the poisoned and non-poisoned areas. At T_{+6} (six months after the poison was applied) the number of empty shells actually increased but this period included seven months of no poisoning after the quadrats were first searched before poisoning began. Importantly, the number of empty shells remained high in the non-poisoned areas ($n=38$) whereas it decreased ($n=16$) in the poisoned areas.

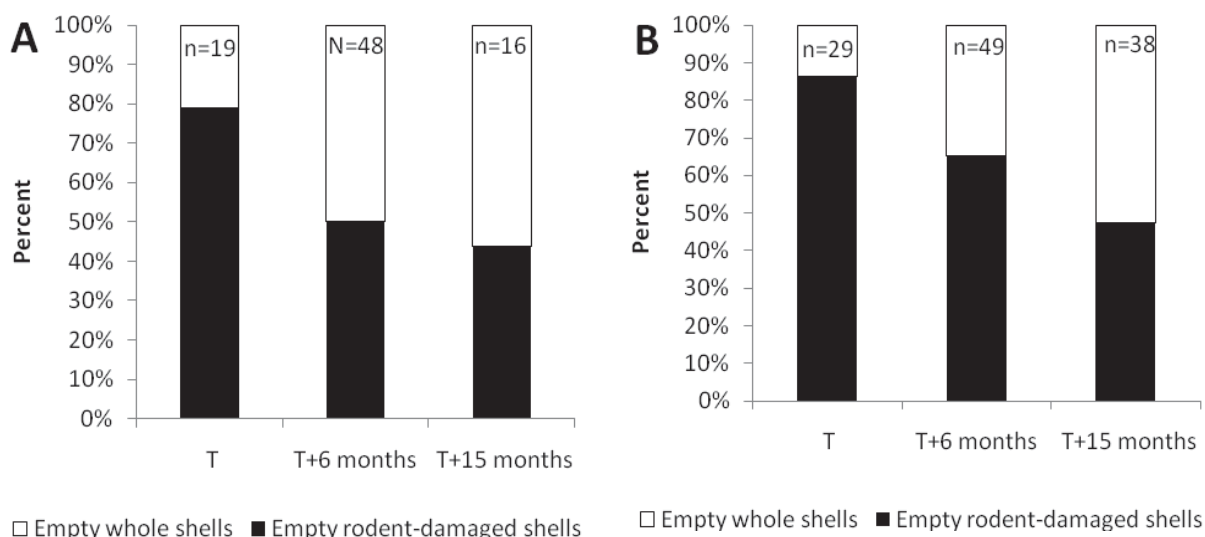


Figure 8.2: The proportion of empty rodent-damaged and empty whole shells of juveniles *P. porphyrostomus* in (A) poisoned quadrats, (B) non-poisoned quadrats before the poisoning started in August 2008 (t), after six months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months).

There was a significant change through time in the proportion of dead shells that showed rat sign (Binomial ANOVA $F_{2,24}=8.27$, $P<0.0001$). But the poisoning did not change the proportion of deaths through time across all the quadrats in the treatment plots nor in the non-poisoned plots: no overall treatment effect (Binomial ANOVA $F_{1,23}=2.38$, $P>0.05$), nor any interaction between time and treatment exists (Binomial ANOVA $F_{2,21}=0.22$, $P>0.05$).

The only cause of adult-sized *Placostylus* mortality recorded was natural (i.e. the shells were not damaged). In these snails, the proportion of live adults remained much higher than empty shells in all plots (Figure 8.3) except at T_{+15} in the non-poisoned areas when for unknown reasons there was a major loss of adult snails (only two snails alive whereas 36 were present previously). It is possible that flooding, that by chance was most prevalent in non-poisoned areas (due to their proximity to a temporary creek), may have drowned these snails. A less likely possibility would be that perhaps a local disease was responsible for these losses, but why this should have affected only non-poisoned areas is unknown.

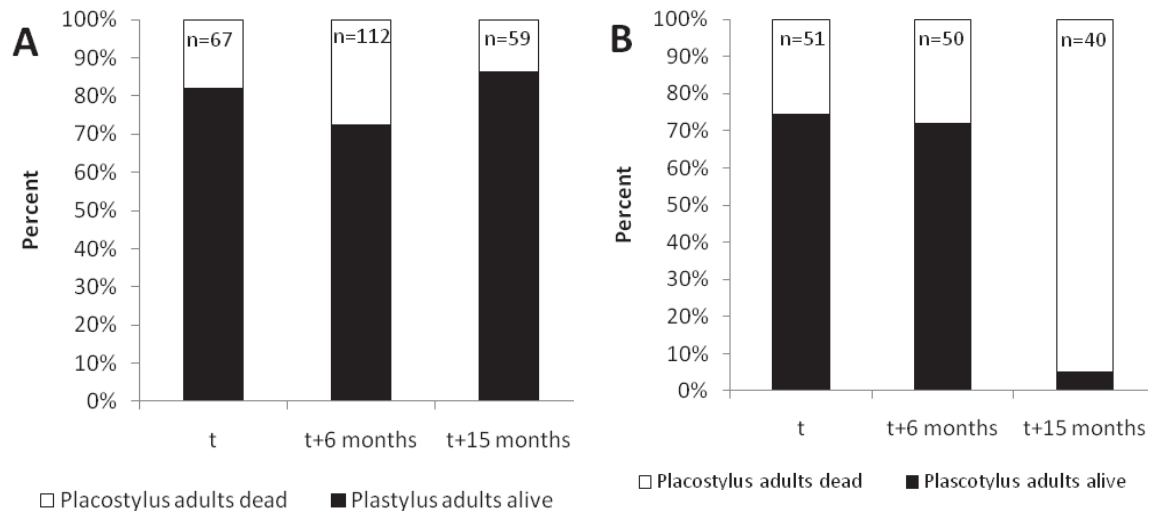


Figure 8.3: The proportions of live and dead adult *Placostylus porphyrostomus* in quadrats in (A) poisoned and (B) non-poisoned quadrats before the poisoning started in August 2008 (t), after six months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months).

Identification of the causes of mortality was sometimes difficult in *A. fulica*; the shells of this species are less calcified than in *Placostylus* and deterioration is faster and when pieces of shells were found it was not easy to discriminate between mortality caused by rodents and natural mortality. However, throughout the study, the proportion of identifiably rodent-damaged shells remained constant at roughly half of the proportion of empty whole shells in the non-poisoned areas (Figure 8.4). After six months of rodent poisoning, rodent-damaged shells predominated in the poisoned area but after 15 months, empty whole shells became much more common. The general tendency over the 15 months in both the poisoned and non-poisoned areas was for a reduction in the number of shells found, especially in the poisoned areas (n=44).

In both poisoned and non-poisoned sites, the proportion of dead *A. fulica* found was always far higher than live ones (Figure 8.5). Live snails were more abundant initially in non-poisoned quadrats but subsequently decreased more sharply than in the poisoned quadrats.

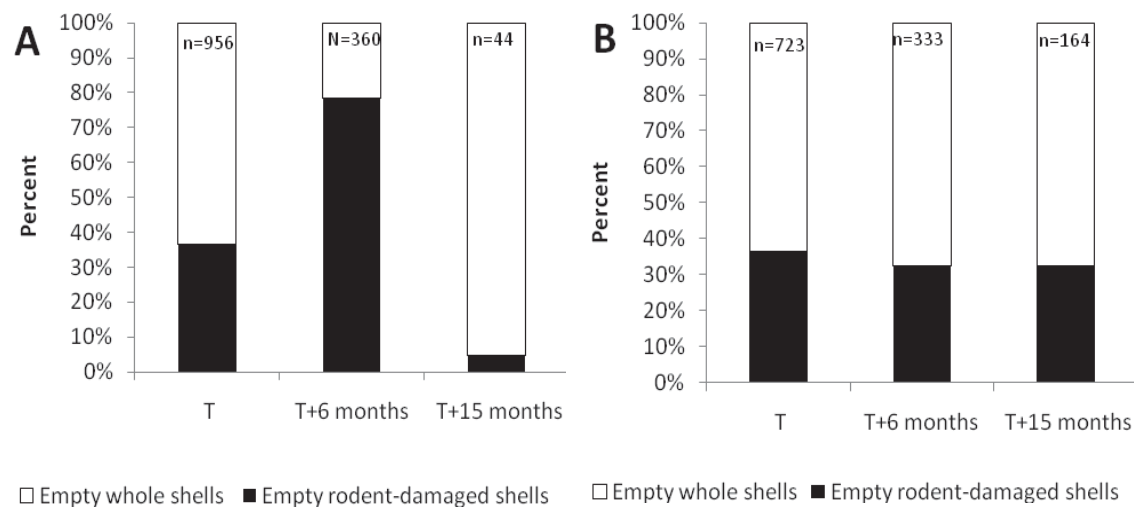


Figure 8.4: The proportions of empty rodent-damaged and empty whole shells of *A. fulica* before the poisoning started in August 2008 (t), after six months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months) in Nékoro in (A) the poisoned quadrats and (B) non poisoned quadrats.

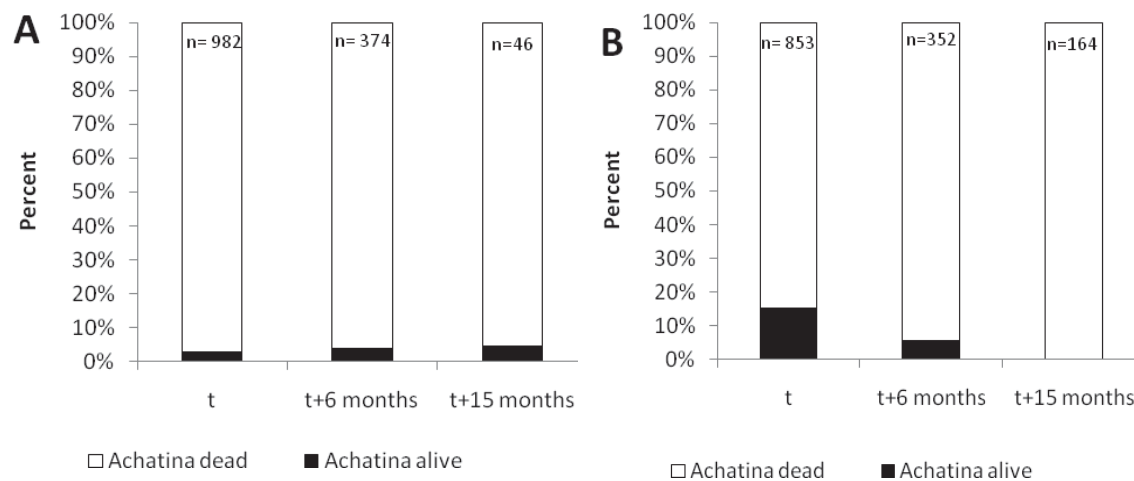


Figure 8.5: The proportions of alive and dead *Achatina fulica* in quadrats with and without poison before the poisoning started in August 2008 (t), after 6 months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months) in Nékoro in (A) the poisoned quadrats and (B) non poisoned quadrats.

8.3.3 Changes in the population of live *P. porphyrostomus* and *A. fulica*

The proportions of live juvenile, sub-adult and adult *P. porphyrostomus* did not change markedly during the poisoning period (Figure 8.6).

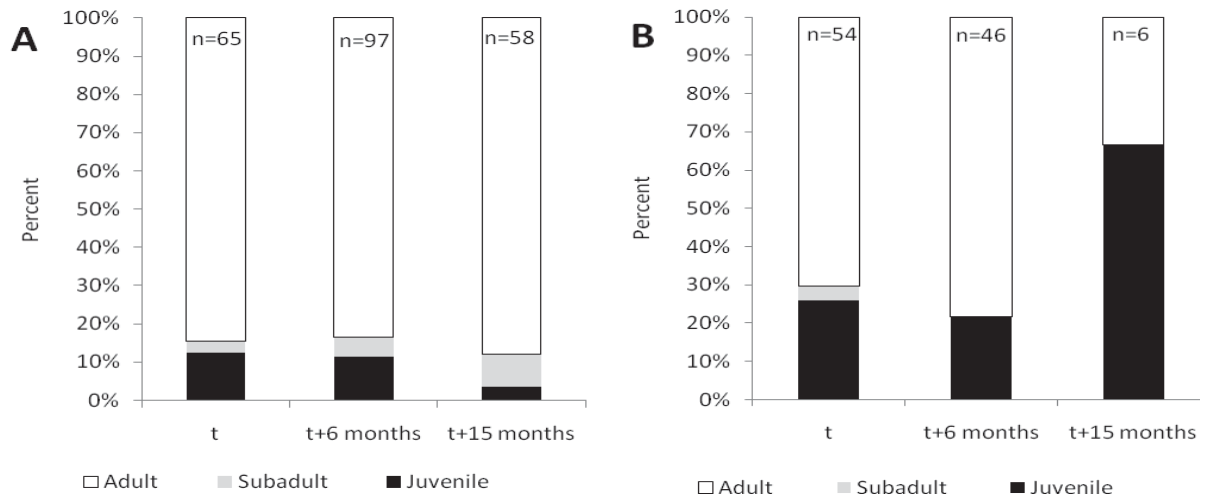


Figure 8.6: The proportions of live juvenile, sub-adult and adult of *P. porphyrostomus* in (A) the poisoned quadrats and (B) non-poisoned quadrats before the poisoning started in August 2008 (t), after six months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months).

The number of juveniles with shell heights less than 60 mm was significantly higher in the poisoned quadrats than in the non-poisoned quadrats six months after the poisoning started (Exact T Test, $p < 0.01$), but this trend was not evident at T_{+15} (Exact T Test, $p > 0.05$) (Figure 8.7).

There was an increase in density of juveniles and sub-adults density six months after poisoning in the poisoned areas which contained significantly more snails of these size classes than in the non-poisoned quadrats (Fisher Exact Test, $n=45$, $p=0.0065$) but no significant differences at the other times. Before the poisoning started, mean juvenile densities were 0.005 ± 0.008 ($n=5$) per m^2 and 0.007 ± 0.009 ($n=5$) per m^2 respectively in poison and non-poison plots. After 6 months of poisoning densities were 0.008 ± 0.004 per m^2 ($n=5$) and 0.002 ± 0.004 per m^2 ($n=5$) respectively in poison and non-poison plots and after 15 months of poisoning juvenile densities were 0.004 ± 0.002 per m^2 ($n=5$) and 0.003 ± 0.002 per m^2 ($n=5$) respectively in poison and non-poison plots.

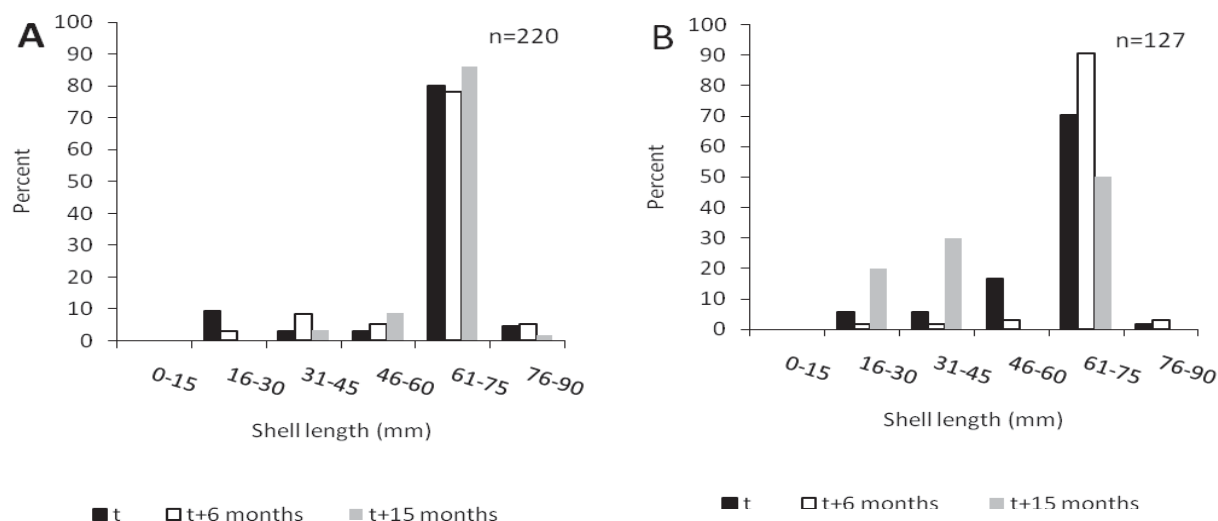


Figure 8.7: Proportional changes in the heights of live *P. porphyrostomus* observed in (A) the poisoned quadrats and (B) the non-poisoned quadrats before the poisoning started in August 2008 (t), after six months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months) in Nékoro.

Proportional changes in the heights of live *A. fulica* in the poisoned and non-poisoned sites through time are shown in Figure 8.8. For both poisoned and non-poisoned areas, similar profiles for snail categories were observed between T_0 and T_{+6} . At T_{+15} , 100% of the *Achatina* found belonged to the 61-75mm size class in the poisoned areas whereas no snails were found in the non-poisoned areas. There was a significant difference between the number of snails at T_0 and T_{+6} ($X^2=16.3$, $p<0.001$) and T_0 and T_{+15} ($X^2=22.3$, $p<0.001$) between controls and treatments where more snails appeared in the non-poisoned areas, but no significant differences between T_{+6} and T_{+15} ($X^2=3.33$, $p>0.05$).

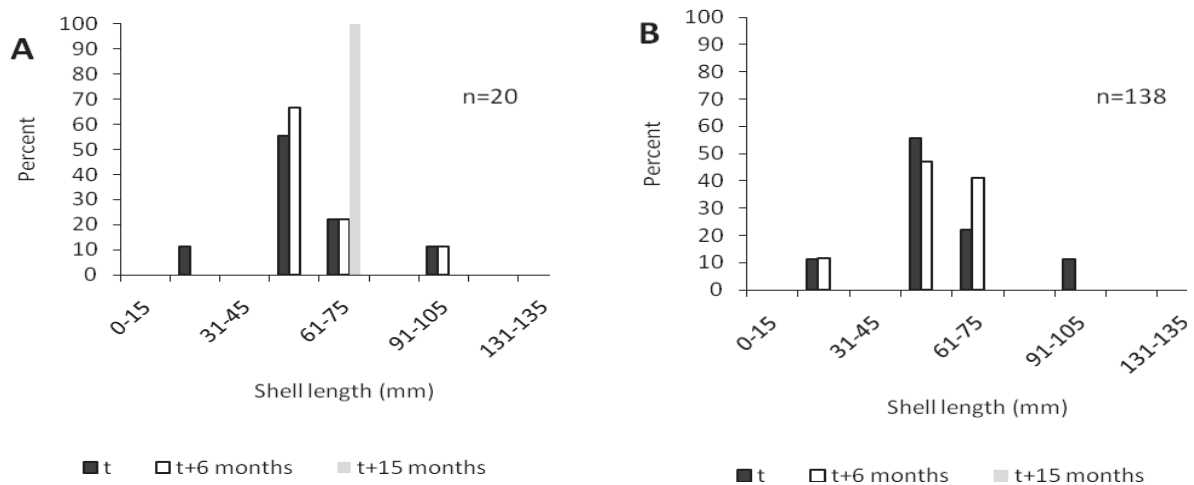


Figure 8.8: Proportional changes in the heights of live *A. fulica* observed in (A) the poisoned quadrats and (B) the non-poisoned quadrats before the poisoning started in August 2008 (t), after 6 months of poisoning in January 2009 (t+6 months) and after 15 months of poisoning in November 2009 (t+15 months).

8.4 Discussion

8.4.1 Effectiveness of rodent control

This is the first study to experimentally test the efficacy of poison baits to control rodents for conservation management of a threatened species on the mainland of New Caledonia. Our rat poisoning experiment reduced the tracking indices of rat abundance by 84% in the poisoned quadrats and maintained low levels of tracking for several months. However, due to the proximity of our poisoned and non-poisoned grids (separated by 200 m) the poison appeared to extend its effect into the non-poisoned sites where tracking rates were also reduced by 34%. A larger separation between poison and non-poison sites was not possible because of the small size of the Nékoro dry forest remnant. After a month of poisoning, indices obtained with Waxtags© declined by 21% in the non-poisoned areas but reduced to zero in the poisoned areas. We do not know precisely how these reductions in tracking indices translate into reductions in rodent densities, but data from Chapter 5 suggest a likely reduction from 19.1 rodents/ha to nearly 0 rodent/ha in the poison sites, and 19.1 rodents/ha to 15.1 rodents /ha in the non-poison sites.

For practical reasons aimed at reducing costs and in order to develop a standardized method that managers could implement in the future, we chose to monitor the impact of rodent poisoning with relative indices of abundance (footprint tracking tunnels and Waxtags©) rather than using absolute population estimates. We recently tested the reliability of these indices in wet and dry forest types in New Caledonia (Chapter 5) and found that tracking tunnels provided a more reliable estimate of true density than Waxtags©.

Following the period when bait stations had not been replenished for two months, the indices of rodent abundance increased rapidly. This recovery in rat abundance is more likely the result of immigration from adjacent areas rather than from poison resistance or reproduction of residual rodents. This demonstrates that a rodent control programme in New Caledonian dry forest needs to be sustained or carried out over large areas to be effective. In New Zealand, Smith *et al.* 2009 tested the effectiveness of poison bait stations at reducing ship rat during an irruption in a *Nothofagus* forest and observed that despite ongoing poisoning, rat abundance increased over the four months of the study. The three possible suggestions to explain their observation were immigration from adjacent populations, low rat acceptance of the rodenticide and/or or effectiveness of the rodenticide used, and interspecific competition from mice in high densities in the area contributed to emptying the bait stations and limiting bait availability for rats.

Moors *et al.* (1992) explored the possibility that rodents could acquire resistance to anticoagulants during poisoning. Sherley *et al.* (1998) suggested that this might be minimised by rotating through a variety of different poisons, stopping poisoning for one or more years before resuming again, or changing the periods between laying poisons. Our study was planned to be long-term and we may provide answers to this challenge in the future.

8.4.2 Costs

The resources required for the study which used a 1-ha 25 m poisoning grid (not including the time taken to mark out the grid and transects) were 9.4 kg of poison per year and 10 hours of labour per month. This represents USD \$70 a year per hectare for the poison and \$10.95 monthly per hectare for labour. Costs for equipment and supplies were incurred mostly during the first year and diminished in subsequent years.

In comparison, Nelson *et al.* 2002 found that a combination of rodenticide baiting and snap-trapping effectively controlled rodents in a 48-ha montane forest in Hawaii. They calculated that in the first year, the cost for baiting was 2.5 times higher than for snap-trapping, and in subsequent years the cost of baiting was eight times higher than for snap-trapping because of the need to purchase new bait each year. They recommended increasing the distance between stations to 100 m to reduce costs. In New Caledonia, snap-trapping may therefore be more cost-effective and would certainly be more acceptable to locals in inhabit areas; thus it would certainly constitute a solution to explore when poison control is not possible for social reasons.

8.4.3 Impact of poisoning on snail populations

After 15 months of poisoning we did not find significant changes in the proportion of juveniles of *P. porphyrostomus* in poisoned sites compared to non-poisoned sites. Nevertheless, we showed some evidence of a beneficial effect on juveniles in the six first months of poisoning even though this was not maintained to the next survey. We suggest three possible explanations:

- (i) the poisoning also affected the designated non-poison sites so that all quadrats had reduced rodent density.
- (ii) the recovery of *Placostylus* populations is too slow to respond over this time period (15 months).
- (iii) the potential for natural recovery may already be affected by the low density of the residual snail population.

Placostylus are long-lived snails (25 years or more) and live in a specific habitat; they show a very slow growth rate and mortality rate is naturally high on young stages which are prone to desiccation and predation by natural enemies (Brescia *et al.* 2008). Thus modification of the habitat, periods of drought, and other factors that increase mortality risk can cause spikes in mortality and introduce demographic troughs that obscure underlying longer-term trends. In the present study 94.5% of adult snails apparently died in the treatment sites after nine months through misadventure, possibly drowning or disease which affected the subsequent recruitment.

Typically, the majority of mainland New Caledonian remnant *Placostylus* populations are dominated by adults (Brescia *et al.* 2008; chapter 4). However, the

high level of mortality at T_{+15} in the non-poisoned areas meant that juveniles were twice as common as adults at that time. Juveniles less than 60 mm are vulnerable to rodent predation, and importantly, the number of these snails was significantly higher in the poisoned quadrats than in the non-poisoned quadrats six months after the poisoning started (this trend was not maintained at T_{+15}). In Chapter 4 we found that the mean height of shells showing rodent damage was 29.6 ± 1.4 mm ($n=110$; min=15 mm; max=50 mm) in the same area of study, and that 87.6 % of the empty juvenile shells found in the mark-recapture study during four years of survey appeared to have died from rodent predation.

Sherley *et al.* (1998) showed an increase in the proportion of large juveniles of the *P. ambagiosus paraspirtus* after six years of rodent poisoning in the far north of New Zealand (vs. 15 months of monitoring in the present ongoing study). They suggested that the recovery may take many years if the number of adults is low to start with. Choat and Schiel (1980) suggested that a population of *Placostylus* maintained by a pool of long-lived large adults is better able to survive unfavourable conditions than a population composed mostly of small juveniles. We suggest here that stochastic events that cause unexpected and unexplained mortality seriously affect the reproductive pool. Stringer *et al.* (2004) thought that as long as pigs are absent (pigs can eat adult snails but they can be excluded by fencing or hunting), pulsed rodent control could be effective in protecting a snail population. However, in the case of macro-invertebrates like *Placostylus* where the juvenile stages have a very low growth rate and remain vulnerable to rodents for a long period (almost a year), the period of control for pulse poisoning may need to be relatively long and planned for almost 1 to 2 years and then could be followed by several years of no control.

Brescia *et al.* (2008) suggested that active management of *Placostylus* colonies from the dry forests was urgently needed to prevent the extinction of the most distinctive races or morphs. In addition to predator control, supplementation of threatened New Caledonian *Placostylus* populations with captive-reared individuals is now feasible (see Chapter 9) and may provide some security against extinction (Brescia *et al.* 2008)

The introduced and pestiferous African snail *A. fulica*, particularly in a dry environment like sclerophyllous forest, acts mostly as a competitor with *Placostylus*

for habitat because they are found in high moisture areas, and to a lesser extent for calcium and food. Therefore controlling rodent populations by poisoning to enhance recovery of *Placostylus* could cause collateral and unexpected damage by facilitating *Achatina* populations to increase. However, we found no evidence of an increase of *A. fulica* in non-poisoned areas after either 6 months or 15 months of rodent poisoning but it should be noted that we primarily focused our study on *Placostylus* and our sampling method might be less effective at sampling African snails. It is highly possible that their abundance was initially under-estimated, perhaps due to the very dry conditions when quadrats were first searched; indeed *A. fulica* shows arboreal behaviour and is also able to dig itself down into the soil to avoid desiccation (Stiévenart and Hardouin 1990; Craze and Mauremootoo 2002) making it difficult to find in dry conditions. The general tendency over the 15 months in both the poisoned and non-poisoned areas was for a reduction in the number of *Achatina* shells found, especially in the poisoned areas. Nevertheless, anticoagulants are generally considered unlikely to affect invertebrates, which have different blood-clotting systems from vertebrates (Shirer 1992) so we do not think this is a direct poisoning effect.

During an operation to control rodent populations by poisoning in order to protect New Zealand *Placostylus*, Sherley *et al.* (1998) also noted a rise in the population of the garden snail *Cantareus aspersus* (Müller) which was sufficient to cause significant *Placostylus* habitat modification but they considered that the observed improvement in recruitment into older age groups of *Placostylus* more than offset any disadvantages due to increased numbers of *H. aspersa*.

Preserving and restoring habitat through re-vegetation and restoration of dry forests, combined with rodent control programmes, would certainly contribute to maintaining *Placostylus* populations. Also, protection of the habitat of existing colonies in the wild may require fencing to exclude pigs and Rusa deer (*Cervus timorensis russa*) (Brescia *et al.* 2008).

8.4.4 Conclusion and prospects

Our study is the first investigation into the efficacy of rodent control in a mainland New Caledonian forest ecosystem on the recovery of a target native species. The application of rodenticide baits was sufficient to reduce and maintain rodent activity at reduced levels but we were unable to conclusively demonstrate a significant

recovery of *P. porphyrostomus* after 15 months of rodent control. This suggests that the control may need to be continued for several years to yield benefits or that the more intensive baiting over a larger area might be required. Supplementation of these populations by adding captive-bred snails may speed recovery in rodent-poisoning areas.

Future research into reducing costs for controlling rodents by combining rodenticide baiting and snap-trapping should be examined. Also, effective methods for monitoring the introduced African snails need to be developed. Finally, it would be useful to try to enhance our knowledge of how the composition of rodent species and other aspects of rodent biology (e.g. home ranges competitive interactions with other rodents, and the foraging strategies of each species) change after poisoning. A better understanding of rodent ecology should help develop efficient rodent control techniques adapted to the New Caledonian context of very high rodent densities.

8.5 Acknowledgements

All the work in dry forest reported here was funded by the Programme de Conservation des Forêts Sèches. We thank Jean-Claude Hurlin, Pierre-Louis Nédia, Stanley Poarairoua, Samuel Daye and Olivier Bokoe-Gowe for helping with fieldwork.

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CHAPTER 9

**TRIAL RELEASE OF THE ENDEMIC LAND SNAIL *PLACOSTYLUS PORPHYROSTOMUS*
(MOLLUSCA: GASTROPODA: BULIMULIDAE) IN A REMNANT PATCH OF DRY FOREST
OF NEW CALEDONIA**



*A *Placostylus porphyrostomus mariei* equipped with a transponder and released in the 8 ha isolated patch of dry forest in Mépouiri (Poya) fenced in 1994 against introduced ungulates.*

Abstract

A trial release of twenty one captive-bred *Placostylus porphyrostomus* was conducted in an isolated patch of dry forest in New Caledonia in July 2007. Two release procedures were tested: seven snails were released following a partial acclimatation and fourteen following no previous acclimatation. After two years of survey the trial was deemed a success. The mean survival rate was 100% for snails with no previous acclimatation and was surprisingly significantly higher than snails released after partial acclimatation (70%) after twenty five months. No differences in growth rate (weight and aperture lip thickness) were recorded in the two release procedures. Snails partially acclimated travelled shorter distances from the release point than snails released with no previous acclimatation and showed significantly higher site fidelity. Supplementation of wild populations with captive-bred snails appeared to be a viable option for the conservation management of New Caledonian *Placostylus* in dry forests provided that the causes of the original decline, such as habitat loss or degradation and predation by introduced rodents, have been removed.

Un essai de renforcement d'une population de l'escargot endémique *Placostylus fibratus* (Mollusca: Gastropoda: Bulimulidae) dans un lambeau de forêt sèche de la Nouvelle-Calédonie

Résumé

De manière expérimentale, 21 *Placostylus porphyrostomus* nés en captivité ont été relâchés dans un lambeau de forêt sèche de la Nouvelle-Calédonie en juillet 2007. Deux techniques de lâcher ont été testées : 7 escargots ont subi une pré-adaptation au lâcher (soft release) alors que les 14 autres ont été lâchés tels quels sans pré-adaptation préalable (hard release). Après deux années de suivi, les résultats apparaissent encourageants. Au bout de 25 mois, le taux moyen de survie a été de 100 % pour le groupe des « hard release » et a été significativement plus faible pour le groupe ayant subi une pré-adaptation (70%). Aucune différence sur la croissance des escargots (en poids et en épaisseur de la lèvre coquillière) n'a été enregistrée selon la technique de lâcher employée. La distance parcourue au point de lâcher a été significativement plus courte pour le groupe ayant subi une pré-adaptation au lâcher qui présente ainsi une fidélité au site plus importante. Le renforcement des populations d'escargots du genre *Placostylus* de la Nouvelle-Calédonie apparaît comme tout à fait envisageable au sein des lambeaux de forêts sèches à condition que les facteurs ayant conduit au déclin soient levés au préalable (perte et dégradation de l'habitat, prédation par les rongeurs introduits).

9.1 Introduction

Land snails of the genus *Placostylus* Beck, 1837 (Pulmonata: Bulimulidae) are found only in the Western Pacific, from the Melanesian Plateau to New Zealand. The six endemic species found in New Caledonian are all endangered (Brescia *et al.* 2008). These large, slow-moving, slow-developing and long-lived land snails appear to be relatively specific in their habitat requirements and are found only in native dry or evergreen forests where they are generally found under leaf litter (Brescia *et al.* 2008). *Placostylus porphyrostomus* Pfeiffer, 1851 is the most common species in sclerophyllous forests (Chérel-Mora 1983), which is the dominant vegetation type in dry areas of the west coast of the mainland (less than 1100 mm annual rainfall). This forest type is characterized by a high diversity of plant species. The sclerophyllous forest is currently the most threatened of the New Caledonian biomes due to deforestation and habitat modification by feral ungulates. A conservation programme with ten international, national and local partners (“Programme Forêt Sèche”) has been recently initiated in an attempt to try to save this highly endangered biome and its associated specialised fauna and flora. Since 1996, *P. porphyrostomus* have been registered as Vulnerable on the Red List of IUCN (Bouchet 1996). Reasons for the serious decline of *P. porphyrostomus* in dry forests include habitat destruction (only 1% of this biome remains), modification by human activities and introduced deer *Cervus rusa timorensis*, predation by introduced species (especially rodents *Rattus* spp. but also feral pigs *Sus scrofa*) and, to a lesser extent, human harvesting for consumption (Brescia *et al.* 2008). Some previously known populations have already vanished (pers.obs., Neubert *et al.* 2009).

The genus *Placostylus* is at risk in other parts of its range too. In New Zealand, according to the criteria of Molloy *et al.* 2002, the endemic *P. hongii* is classified as ‘Range Restricted’, and *P. ambagiosus* is classified as either ‘Nationally Critical’ or ‘Nationally Endangered’, depending on the subspecies (Hitchmough *et al.* 2007). Parrish *et al.* 1995 suggested that captive-bred snails could be used to supplement a colony of *Placostylus* if it was severely reduced. Salas *et al.* 1997 also suggested for New Caledonian *Placostylus* that farming might enable restocking of small populations where they have almost disappeared. Brescia *et al.* 2008 considered that active management of *Placostylus* in sclerophyllous forests of New Caledonia is

urgently needed to prevent further extinction of the most distinctive races or morphs. Captive breeding of the most threatened races and development of techniques for their translocation to supplement wild populations were identified as priorities.

A successful rearing method has now been developed for New Caledonian *Placostylus* following many years of trials (Brescia, 1997, 1998, 1999, 2000, 2001; Brescia *et al.* 1998, 2008), and it is now possible to produce each species *en masse* in captivity (Brescia and Pöllabauer 2004, 2005). Thus, the supplementation of threatened New Caledonian *Placostylus* populations using captive rearing is now feasible and this may provide some security against extinction. Accordingly, snails from some of the most threatened populations of the sclerophyllous forests are now being maintained in captivity to complement the on-going management of wild populations, and the first trials on the release of these captive-reared snails into the wild are now possible.

Here, we report on the first trial supplementation of a wild population of *P. porphyrostomus mariei* in a remnant patch of dry forest with captive-bred snails. We considered that this operation, associated with intensive post-release monitoring, would not further endanger the existing very isolated and threatened host population; indeed, only one live snail was found in the selected release site despite repeated searches from 1993 to 2003. We tested two release procedures: a ‘soft’ release involving an acclimation period of confinement of individuals (Scott and Carpenter, 1987) and a ‘hard’ release involving the immediate release of the snails into the wild. The experiment was designed to establish strategies for future larger-scale programmes for the supplementation of wild *Placostylus* populations with captive-reared snails and to assess the viability of population supplementation. The specific aims of this study were to investigate (i) how well the captive-reared snails survived in their natural habitat post-release, and (ii) to refine procedures for release by comparing soft and hard release strategies.

9.2 Methods

9.2.1 Study area and release site

The study was conducted in New Caledonia which has three major seasons: a hot wet season (mid November-mid May; mid April-mid May is a transition period); a cool dry season (mid May-mid September); and a hot dry season (mid September-mid

November) (ORSTOM 1981). The study area was a native sclerophyllous forest in Mèpouri, in Poya, in a privately-owned ranch located on the western coast of “Grande-Terre” (altitude 0-100 m asl). The vast majority of the land here is farmed, but there is a small patch of remnant dry forest (99 ha) in which 8 ha was fenced in 1994 with an additional patch of 6 ha fenced in 2000. The fences were intended to exclude rusa deer and cattle, but they also successfully exclude feral pigs. According to the landowners the forest has been known to shelter *Placostylus* since at least the 1970s and in the past they even collected snails for consumption; the former presence of the snails is confirmed by old weathered shells that can often be found nowadays both in the remnant patch of dry forest and also on pasture outside the fence where forest extended in the past. Intensive searches from 1993 to 2003 resulted in only one live adult snail being found in 2003 within the 8 ha remnant that was fenced in 1994 (Brescia & Pöllabauer 2004, 2005). In 2005 more snails were found, but overall Brescia & Pöllabauer (2005) estimated that *P. porphyrostomus mariei* is now very rare at the site with a mean density of 0.9 snails / 100 m² (SD= 0.6) while no *Placostylus* appear to remain in the more recently fenced 6 ha remnant.

The release site chosen was the 8 ha patch of dry forest because the vegetation here was comparatively well-preserved and it appeared to contain suitable habitat for snails.

9.2.2 Captive breeding and individual selection

The only adult snail found in 2003 was placed in a reproduction enclosure in the experimental farm of the Institut Agronomique néo-Calédonien (IAC) in Païta, 200 km southward from Poya. This snail was held under the husbandry protocol developed by IAC as presented in Brescia *et al.* 2008 (Chapter 2) and Appendix 2. This included the snail being fed an artificial diet based on cereal flour supplemented by calcium carbonate to neutralize acidity and drinking water *ad libitum*, with humidity controlled by daily watering and by a thick layer of leaves (papaya, banana) on a neutral coco compost substrate. Between 2003 and 2005 this snail laid three successive clutches that presumably had been fertilized by sperm stored from matings that must have taken place in the wild before its removal into captivity, and this resulted in a small captive population of 100 snails. After 1.5 years in captivity, these snails attained adulthood at which the shell aperture started to thicken (aperture lip ≥ 3.5 mm, Pöllabauer 1993).

Released individuals needed to be large enough to withstand predation pressure from introduced rodents. In M  pouiri, it has been shown that rodents (Polynesian rats *Rattus exulans* (Peale, 1848), ship rats *R. rattus* (Linnaeus, 1758), and house mice *Mus musculus* Linnaeus, 1758) eat juvenile *Placostylus* with a shell height of up to 5 cm (Brescia & P  llabauer 2005). Compared to New Zealand, rodent densities are very high in these forests (Chapter 5). In Chapter 4 we found that in a mark-recapture study in sclerophyllous forests, up to 86.6% (95% CI= 76.4-96.8%) of juveniles shells on the ground inside permanent quadrats had been depredated by rodents. Given the lack of any rodent control in this patch of dry forest, we choose to select young adult captive-bred snails for our experimental release to avoid losing individuals to rats. Moreover, we assumed that young adults would be better at resisting environmental stressors (such as climate and fluctuations in food availability).

In an attempt to remove potentially confounding variation in body weight, height and behaviour once released, individuals of similar height and aperture lip size were chosen. None of them had laid eggs in captivity. Twenty one snails were thus selected and separated into two groups. One group comprised 14 snails with a mean aperture lip of 6.02 ± 0.44 mm and mean height of 79.4 ± 0.44 mm. The second group comprised 7 snails with a mean aperture lip of 5.82 ± 0.68 mm and mean height of 79.0 ± 1.8 mm. No significant differences existed between the two groups either for mean aperture lip ($t = -0.25$, $P > 0.05$) or for mean height ($t = -0.50$, $P > 0.05$).

9.2.3 Preparation before release

Individual identifying numbers were engraved on the shells of snails by carefully grinding the periostracum with a portable engraver (“Arlec”, Dick Smith Electronics). Harmonic radar transponders were attached to the middle of the shell of the snails to help locate them again. The transponders followed the design of Stringer *et al.* (2004) and consisted of an aerial of thin copper strap (about 7 mm wide and 0.25 mm thick) folded into the shape of an open triangle with a 5082-2800 Schottky diode (Farnell InOne, UK) soldered across the ends. The transponders were fixed to the shells with Neoprene Glue Sader (Bostik S.A.) after the shells had been cleaned and dried with tissue paper and lightly buffed with fine carborundum paper.

The two groups of snails received different treatments before release. The group of 14 snails was allocated to the hard release treatment. These snails were

maintained under the captive conditions from hatching until the day of release. In order to reduce the risk of spreading disease and parasites, the neutral coco compost substrate of the cages was changed weekly beginning 45 days before the release. The second group comprising 7 snails was allocated to the soft release. These were also maintained on coco compost as described previously for 15 days, but one month before the release they were gradually acclimated to the wild by slowly introducing soil and leaf litter that had been collected in M  pouri forest into their enclosures in place of coco compost and papaya and banana leaves, and they were fed with leaves of wild plants collected from the dry forest as a replacement of their usual artificial food and exotic leaves. The daily watering of the enclosures was reduced progressively until it stopped completely one month before the release.

9.2.4 Release procedure and monitoring

To maximize the likely success of the translocation, snails were released in July 2007 at a period when conditions generally became more favourable with frequent rainfall and relatively low temperatures. The snails were released in the dry forest in seven clusters placed 30 m apart along a transect line in the 8 ha of dry forest that had been fenced in 1994. Each cluster consisted of three individuals: two selected from the hard release group and one from the soft release group. Snails were placed with the front of their shells slightly embedded in the soil in suitable micro-habitat, and then covered with leaf litter. For each cluster, the release point was identified with a peg. Over the following two years until August 2009, snails were searched for monthly both by direct searching and with the aid of a hand-held harmonic radar unit (Type R5P1, Recco AB, Sweden). The detection range was about 3 to 5 m.

The following data were recorded each time a captive-reared snail was recaptured: (i) whether the snail was found or not found, (ii) whether it was found alive or dead (if found alive, we noted its position (angle and distance from the release point but also angle and distance from its previous position that was identified with a coloured plastic band), and (iii) weight, and (iv) the thickness of the aperture lip.

9.2.5 Analyses

9.2.5.1 Survival

Kaplan-Meier estimates of survival rates were made for both the soft and hard released snails separately and combined. Log-rank tests to compare the survival

functions of the Kaplan-Meier estimations for soft and hard released snails were made using a chi-square test with 1 degree of freedom (Kaplan and Meier 1958).

9.2.5.2 Growth

In each released cluster, snails intended for a soft release were randomly paired to one of the snails chosen for hard release. We calculated monthly differences in aperture lip growth and weight gain in each pair of hard- and soft-released snails and performed paired-sample t-tests on the differences after 25 months of the study.

9.2.5.3 Movement distances and direction between surveys

We used analysis of variance to compare the daily distances travelled between recaptures [$\ln(\text{distance}+1)$] in the two groups of snails after tests suggested that the assumption of ANOVA (homogeneity of group of variances (Sokal and Rohlf 1981) was met. Time elapsed was used as a covariate and the interaction between release procedure and the covariate was evaluated. All tests were performed using SPSS[®] 9.0 software. For the two release procedures, vectors (directions and distances travelled between the last known position of a snail and its actual position on the following survey) were examined for significant directional preferences with the Rayleigh-test of uniformity (Batschelet 1981; ORIANA 3.13, Kovach Computing Services, Anglesey, UK), using season as a grouping variable. Vectors were then tested for differences in distribution between release procedures with the Watson's U_2 test (Batschelet 1981; ORIANA 2.02).

9.3 Results

9.3.1 Fate of released snails

One of the seven clusters of released snails disappeared completely only one month after they were introduced into the wild. None of these three snails were found again in the subsequent surveys, so we excluded this cluster from the analyses. We suspected that the New Caledonian Crow *Corvus moneduloides* or the introduced rodent *Rattus rattus* may have removed snails out of the study area. Only two captive-bred snails out of the remaining 18 died during the study. One died in October 2007, two months after release, and the other one died in December 2007 four months after the release. These two snails both came from the soft-release procedure. The proportions of *P. porphyrostomus* snails recorded alive, dead or not found during each survey are presented in Figure 9.1).

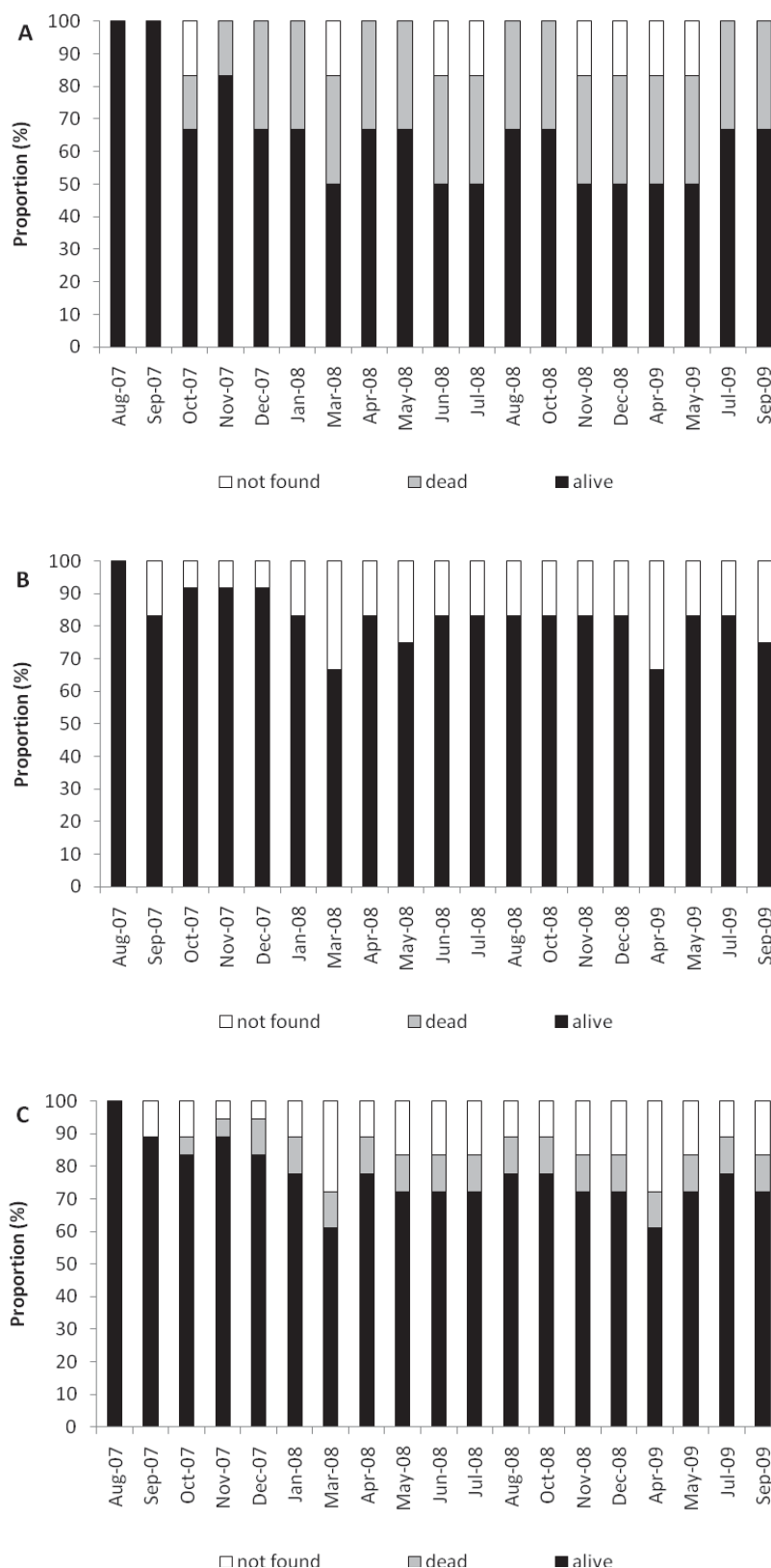


Figure 9.1: Proportions of *Placostylus* snails recorded alive, dead or not found from August 2007 to September 2009 after (A) the soft release ($n=6$), (B) hard release ($n=12$), and (C) the two groups combined ($n=18$).

9.3.2 Survival

Figure 9.2 shows the estimates of survival rates across time for the released snails. The mean survival rates were 1 for hard release, 0.70 (95% CI= 0.60-0.80) for soft release and 0.86 (95% CI= 0.81-0.91) for the two categories combined. Comparisons of the survival functions showed that captive-bred snails released from a soft procedure had a significantly lower survival rate than those from the hard release ($X^2= 4.38$, $df=1$, $p<0.05$).

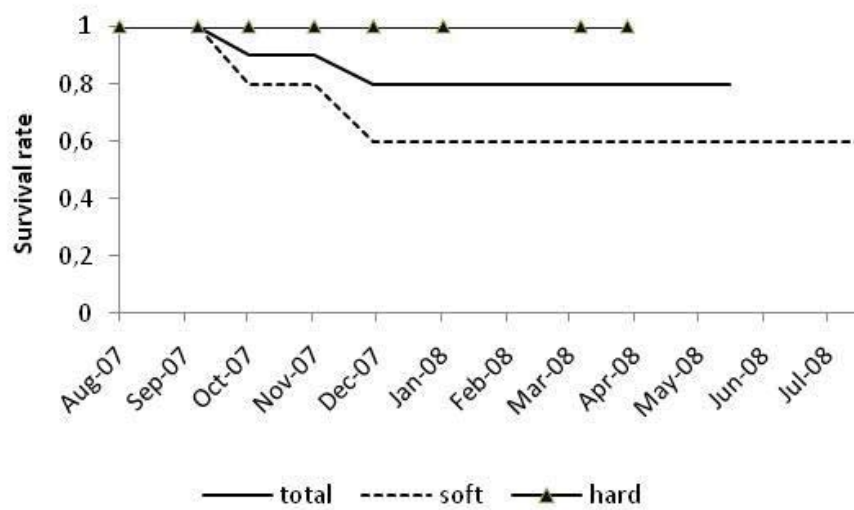


Figure 9.2: Survival graphs based on Kaplan-Meier estimates of the survival rate of captive-bred *Placostylus* for the soft-release and hard-release protocols.

9.3.3 Changes in body mass and growth

Snails intended for soft- and hard-release did not differ in their initial height, weight and aperture lip before the acclimation period (two-sample t-tests, $P > 0.05$, Table 9.1). Figure 9.3 shows the change in mean aperture lip size (A) and weight (B) of captive-bred snails before and after they were released into the forest. After the acclimation period, snails intended for a soft release had lost about 17% of their weight and snails intended for a hard release were significantly heavier (two-sample t-tests, $p < 0.01$).

Table 9.1: Characteristics of captive-bred snails intended for soft and hard release, one month before their release and on the day of release. Data are means \pm 95% CI.

	Fate of snail	Weight (g)	Height (mm)	Lip (mm)
A month before release (June 2007)	Soft release (n= 7)	50.45 \pm 2.31	78.8 \pm 1.7	5.81 \pm 0.75
	Hard release (n=14)	49.32 \pm 2.23	79.2 \pm 2.1	5.99 \pm 0.81
Day of release (July 2007)	Soft release (n= 6)	42.16 \pm 3.21	78.9 \pm 1.8	5.82 \pm 0.78
	Hard release (n=12)	50.58 \pm 2.84	79.4 \pm 2.3	6.02 \pm 0.85

However, 25 months of study, there were no differences in growth of the aperture lip or weight gain between the hard- and soft-released snails (Wilcoxon paired sample t-tests, $p > 0.05$). The mean lip thickness steadily increased in snails in both release protocols. Weight varied through time, dropping in the hot season (November to December) and during droughts in the dry season (June to July). During the month following release, hard released snails on average lost about 8% of their initial weight while the soft released snails increased their weight by 6%.

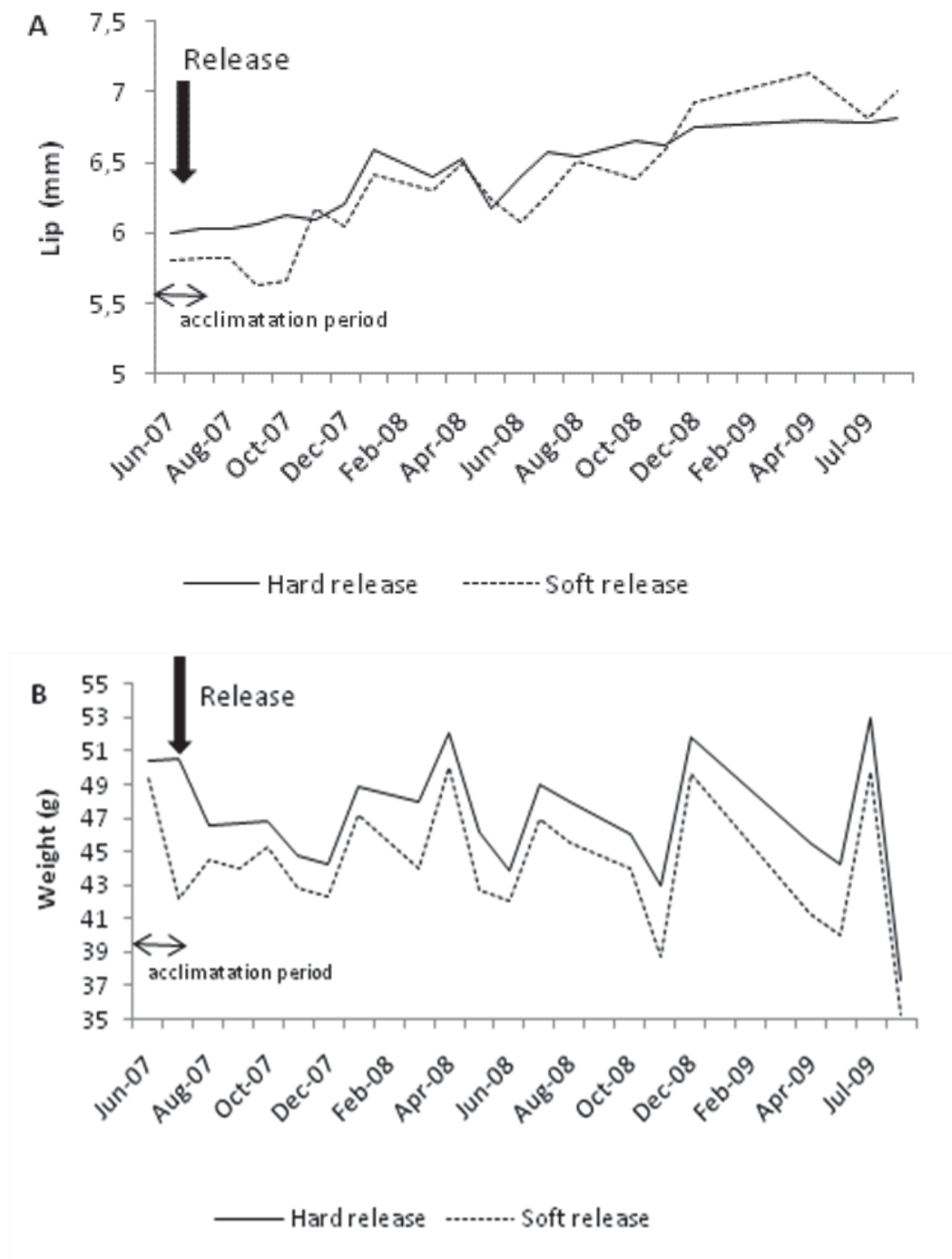


Figure 9.3: Variation of (A) mean lip aperture and (B) weight of snails released in Mépouiri in July 2007 according to their soft or hard release protocols.

9.3.4 Distances travelled and dispersal movements

The mean daily distances travelled, calculated monthly from each snail's current and previous position, did not differ significantly between soft-released and hard-released snails, and did not vary with any of the parameters tested (release type, time elapsed and season) (Table 9.2, Analysis of Variance, $F_{3,38}=1.060$, $p>0.05$). Overall, the mean daily distance travelled between two positions was 0.28 ± 0.09 m ($n=38$, Figure 9.4).

Table 9.2: Results of the Univariate ANOVA of factors (release type and season) affecting daily distance between two positions and distance from the release point. Elapsed time was measured from the day of release.

Source of variation	Daily distances between two positions			Distances from the release point		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Release type	1	0.035	0.852	1	1.684	0.203
Time elapsed	1	3.145	0.085	1	8.510	0.006
Release type x Season	1	0.031	0.861	1	0.014	0.907

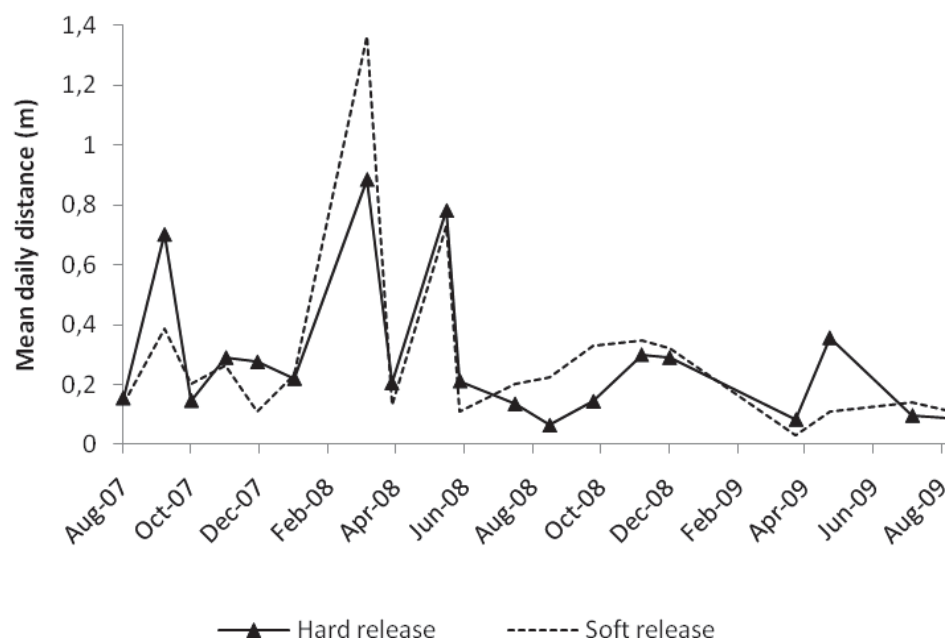


Figure 9.4: Mean daily distance travelled (m) between recapture locations over two years of study of both soft released and hard released snails.

The linear distances travelled from the release point were used as a measure of each animal's site fidelity (Figure 9.5). Site fidelity differed significantly between the two release groups (Table 9.2, Univariate Analysis of Variance, $F_{3, 38}=5.189$, $p<0.01$). After two years the mean distance travelled from the release point was 20.56 ± 2.16 m ($n=19$) for hard-released snails and 16.04 ± 2.91 m ($n=19$) for soft-released snails.

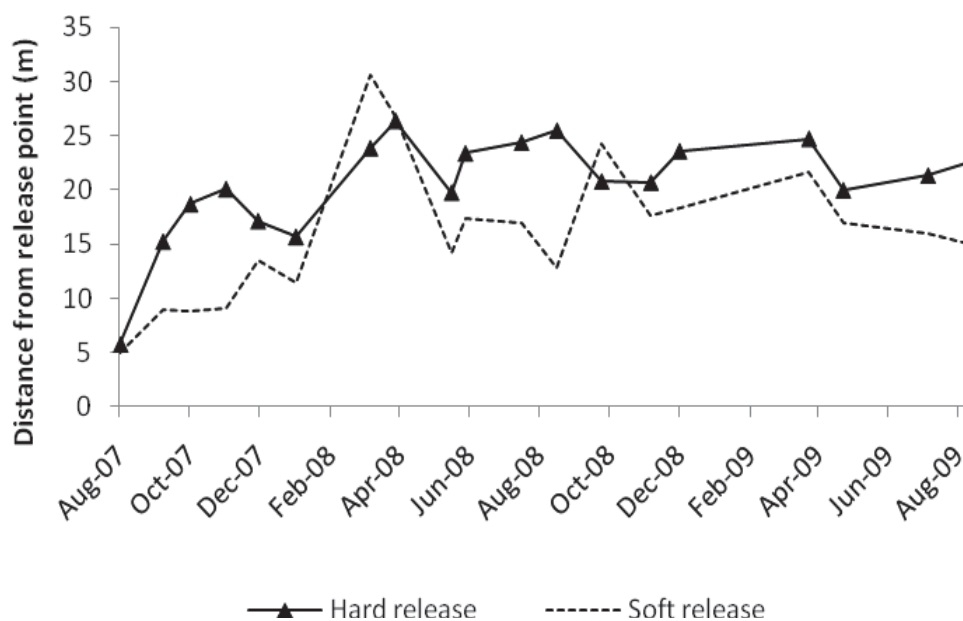


Figure 9.5: Variation of the linear distance travelled (m) from the release for soft released and hard released snails.

A linear regression indicated a significant increase in distance travelled from the release point with time since release for the hard-released snails ($\text{Distance}=0.011 \times \text{Time} + 16.38$; $r^2= 0.305$; $F=7.452$; $p<0.01$) but not for the soft-released snails ($\text{Distance}=0.011 \times \text{Time} + 12.190$; $r^2= 0.143$; $F=7.452$; $p>0.05$).

Snail movements showed a random distribution without any directional preferences regardless of release procedure (Watson's U_2 test, $P>0.05$) and season (Rayleigh Tests, $P>0.05$, Figure 9.6).

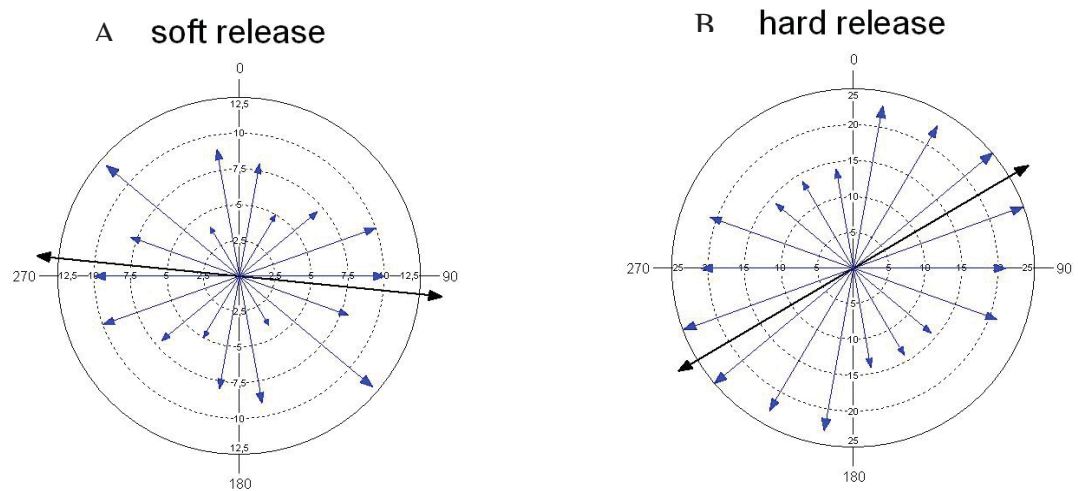


Figure 9.6: Circular histogram of directions followed by released snails between recaptures in M  pouiri, all seasons combined. A. soft-released snails, B. hard-released snails. Concentric circles describe the number of observations in each bin; the means vectors are connected to the 95% confidence interval on the plot circumference.

9.3.5 Behaviour patterns

Snails from the two release procedures did not differ in their daytime position on the ground. In nearly 100% of the observations for both release procedures, snails were found with the front of their shell buried in the soil under the leaf litter. On one occasion a released snail was found alive but, surprisingly, 2.5 m off the ground up in a tree where it was clearly transported by a rat; it was in the junction of two branches amidst the rest of a rodent's meal (e.g. damaged seeds and African snail shells). Also, both the transponder and the glue used to adhere it to the snail's shell showed evidence of rat chewing. Twice, a captive-bred snail was found within 0.5 m of a wild *Placostylus*.

9.4 Discussion

Results from this first attempt to release captive-bred *Placostylus* snails into a New Caledonian dry forest are encouraging and show that the idea is feasible and has considerable potential as a conservation management tool for these snails.

Hard- versus Soft-release

Despite the small sample sizes involved, this study revealed that there was a difference in survival between soft- and hard-released snails, with an unexpected

higher survival rate for those that were hard-released. Based on our observations of the same rate of growth but better survival of the hard-released snails, we could argue that an acclimation period prior to release is not necessary. In mammal and bird translocations, Bright *et al.* 1994 suggested that animals acclimated to a novel site before release show higher performance and survival. Here, all the snails had been subject to favourable conditions of captivity since birth and it is possible that the acclimation period was too short for full acclimation before the environmental conditions changed suddenly and became hard to tolerate. An increase in the time spent under acclimation conditions may have reduced stress factors. Nevertheless, the hard-release group showed some sign of suffering from their new environment and had lost weight a month after released despite showing greater survival. Also, the soft-released snails travelled shorter distances than the hard-released snails and showed greater site fidelity in the forest. Hard-released snails appeared more erratic in their movements and this behaviour increased as distance travelled increased through time. This may be of significance in supplementation releases because excessive dispersal from the initial point of release may compromise establishment of cohesive populations and the effectiveness of post release monitoring. Bright *et al.* 1994 observed a similar response in translocated dormice and partially explained this as the hard-releases possibly dispersing further to a suitable area to obtain sufficient food, or becoming disoriented as a result of the translocation. However, if disorientation when translocated was the main cause, we would expect the soft released snails should have shown the same behaviour as the hard released snails but they did not.

In the future, longer acclimation periods should be tested, but even if higher mortality of soft-released snails is confirmed, this procedure may still be preferable if it leads to a higher likelihood of successful establishment in the area initially planned since the soft-release technique seems to lead to captive-raised snails settling close to the release site. This difference in dispersal between soft-and hard-released snails averaged just 5 m after two years in this very small patch of dry forest but it might be higher elsewhere e.g. in a larger continuous dry forest.

Stringer & Grant (2003) reported an unsuccessful transfer of captive-bred New Zealand *Placostylus* land snails (three adults, three juveniles and one sub-adult) to an outside cage protected from mammalian predators. The seven snails survived less than one year and starvation and dehydration were thought to be responsible for their

deaths. In a second attempt, Stringer & Parrish (2008) released 11 captive-bred *P. hongii* (4 adults and 7 juveniles) using a hard-release procedure. All eleven snails died in a period from 4 months to 19 months after release. The snails remained within 3 m of the small grove of trees (230 m²) surrounded by grasses where they had been released and moved 0.3-11.1 m from their previous positions between recaptures between November 2002, January 2003, August 2003, November 2003 and 24 March 2004).

Stringer and Parrish (2008) suggest that *P. hongii* snails are best released as either large juveniles or as adults, because small juveniles may experience a higher mortality in the wild. However, the low growth rates of *Placostylus* (*P. fibratus*) mean that rearing sub-adults requires almost two years (Brescia *et al.* 1998) and thus rearing costs (labour, artificial food, containers) are relatively high. Releasing younger stages if they succeed would certainly be more cost effective. Ewen & Armstrong (2007) recommend that monitoring of reintroductions should primarily aim to assess the suitability of the habitat for supporting the species in the long term rather than the short-term effects of different release strategies (e.g. soft- versus hard-release) and to test the extent to which habitat factors such as food and predators limit population viability. In New Caledonia, *Placostylus* recruitment suffers severely from introduced rodent predation and in dry forests we found that the mean shell height size damaged by rodents was 29.6 ± 1.4 mm (n=110; min=15 mm; max=50 mm) (Chapter 4) which correspond roughly to six month-old snails. We found here evidence of a rat attack on an adult *Placostylus* where the snail was transported up into a tree. No rodent control programmes exist in mainland populations in New Caledonia currently, but supplementation with captive-bred snails would probably be more effective management strategy if predators are removed prior to release, and intensive and sustained rodent control is maintained. Hadfield and Saufler (2009) describe the successful introduction of 10 arboreal snails *Partulina redfieldi* in Hawaii, but report that this translocated population suffered the same depredation from rats (at least 75% disappeared) as the natural snail population.

Clearly in New Caledonia, where only 1% of sclerophyllous forests remains, supplementations or reintroductions into areas where snails have already vanished should be done in conjunction with reforestation to ensure that suitable future habitat exists for the snails.

The behaviour of captive-bred snails appeared unaffected by the release and they appeared able to adapt quickly to natural conditions; for example, they did not lose their ability to avoid water loss by burying into the soil. They were occasionally found together with wild snails suggesting that mating with the wild population would be possible. Evidence of reproduction would reinforce the utility of restocking wild populations with captive-bred snails to boost small breeding populations. According to Caddy and Defeo (2003), Allee effects that cause reproductive success to drop in small sparse populations in many invertebrates, and thus invertebrate restocking should aim to restore relatively dense, discrete, breeding populations (Purcell and Kirby, 2006). Mace *et al.* (1998) in developing a general conservation programme for tree snails (Partulidae), and Pearce-Kelly *et al.* (1995) when discussing the release of zoo-bred *Partula taeniata*, an endangered species of Polynesian tree snail, highlighted the need to establish a genetic management protocol in breeding programmes to retain the natural genetically-based adaptations of snails and to minimize their genetic adaptation to captive conditions.

From a conservation perspective, the supplementation of dry forests of New Caledonia with captive-bred *Placostylus* snails is now clearly possible and could be used to augment a residual population provided that factors that caused the original decline have been removed or at least heavily reduced (such as habitat loss or degradation and predation by introduced rodents). Further studies should focus on determining an optimal number of snails to release for cost-effective supplementation, and on investigating what length of the acclimation period during soft releases is most favourable for snail survival and for the establishment of cohesive populations.

9.5 Acknowledgements

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CHAPTER 10

GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS



10.1 Overview

The objective of this thesis was to investigate the biology and ecology of *Placostylus* land snails of New Caledonia, with a view to providing conservation and management strategies. The thesis focused on two endemic species. The first, *P. lacostylus porphyrostomus*, is now restricted to small, very isolated populations mostly in dry forests and is highly threatened by introduced rodent predation and habitat fragmentation and loss. The second, *Placostylus fibratus*, is a patrimonial species (i.e. a flagship species with cultural importance). It has a sparse but wide distribution, but its strong-hold is now the Isle of Pines. Here, it is over-collected for commercial purposes and management and harvest guidelines are needed urgently.

Prior to this research being undertaken, the threats to New Caledonian *Placostylus*, population structure and demography parameters, population trends, and the impact of human harvest were unknown. Thus, to achieve the aim of the thesis, research focused on answering three main questions:

- What are some of the life history traits of two species of New Caledonian *Placostylus* snails (Chapters 4, 5 and 6)?
- What were population changes through time and the impact of human collection on snails of the Isle of Pines (Chapter 3), and what will be the fate of these populations if current population management and harvest regimes remain unaltered (Chapter 7)?
- Can we develop conservation tools to restore threatened populations of New Caledonian *Placostylus* (Chapters 8 and 9)?

For the purpose of discussion the following section is split into three parts illustrating the significance of the research:

1. Main ecological findings and fate of New Caledonian *Placostylus* populations
2. Opportunity and feasibility of restoration operations
3. Recommendations for management

Finally suggestions for further work are made based on this research.

10.2 Main ecological findings and fate of New Caledonian *Placostylus* populations

Here I present the main results of the different studies conducted during the thesis; these results have already been discussed at the end of each chapters but they are presented here as a compilation of my principal findings and I have updated them in light of the results from the population modelling chapter that presents a rather pessimistic outlook for the likely fate of the snail populations if steps are not actively taken to change current management and harvest practices. A coherent overview of the life history of New Caledonian *Placostylus* is presented and several new points raised for discussion.

Snail density and population structure

In Chapter 4, I found that *P. fibratus* densities on the Isle of Pines, in a well preserved humid forest, were greater than for *P. porphyrostomus* in dry forests where the snail populations are far more scattered and isolated. Historical records indicate that all species of New Caledonian *Placostylus* were more abundant and widespread than they are today, and the widespread and frequent presence of old shells in forests throughout New Caledonia, often in areas where no living snails exist today, attests to this (Pisier 1985; Pöllabauer 1995; Brescia and Pöllabauer 2005; Philippe Bouchet, pers. comm. 1999). Empty shells are more common than live snails since empty shells can persist for many years on the forest floor (I estimate that an empty shell can persist for up to 37 years for *P. fibratus*, and for 80 and 9 years for *P. porphyrostomus* respectively on Isle of Pines and in dry forest). Even if the presence of old *Placostylus* shells in forest does not provide reliable information about past densities, it remains proof of the existence of past populations. Surveying these old populations more extensively than I have done here would provide valuable information on their previous distributions, and would help identify locations into which snails could be reintroduced in the future if the likely causes of their local extinction can be determined and mitigated.

Data presented here indicate that the age structure of *Placostylus* populations appears to be changing, with many populations now comprising mostly adults. For both species, recently-hatched or juvenile snails are rarely found in the field. Moreover, when they are found a high proportion of hatchlings and non-hatched eggs are dead, suggesting that the eggs and hatchlings are very susceptible to desiccation or predation. However, I did not explore these aspects in detail here because methods to

investigate the fate of hatchlings are likely to be very time-consuming and difficult. The shell of hatchlings is very thin and fragile making individuals difficult to mark and identify and making the accurate determination of mortality rates and causes of mortality (predators or natural death) problematic; shells typically disappear completely (the snail is eaten entirely by the predator or the shell degrades rapidly) or only tiny fragments of shell are found. The arboreal behaviour of the young snails presents an additional challenge since it means that finding the live animal is difficult.

The population structure of New Caledonian *Placostylus* species was similar to those of the New Zealand taxa reported by Choat & Schiel (1980), Penniket (1981), and Stringer *et al.* (2004), where populations appear to be maintained by a pool of large and long-lived adults (Choat & Schiel 1980), but the New Caledonian populations are far smaller with densities several times less than reported for the New Zealand species (0.06 and 0.02 snails/ m² respectively for *P. fibratus* on Isle of Pines and *P. porphyrostomus* in dry forest versus 0.78/m² (Stringer *et al.* 2004), 1.9/m² (Choat & Schiel 1980) and 8.1/m² (Penniket 1981) for *P. hongii* and 0.15 to 0.35 /m² (Brook and Laurenson 1992) for *P. bollonsi* in New Zealand).

This highlights the urgent need to undertake conservation and management actions that will counteract the rapid and ongoing degradation of the remaining habitat by feral ungulates. Also, in terms of composition, I found that the pestiferous giant African snail was between three and seven times more abundant than *P. porphyrostomus* in dry forests, and it was the second most abundant species, after *P. fibratus* found in quadrats in the 2006-2008 survey on Isle of Pines, both for live and empty shells. The introduced giant African snail (*Achatina*) competes directly with *Placostylus* for suitable microhabitat by searching for humid shelters. *Achatina* snails were introduced into New Caledonia in 1972 and rapidly became a serious pest for the environment and for agriculture (Gargominy *et al.* 1996). I did not explored the life history traits of the giant African snails in detail here because the main method of surveying for *Placostylus* snails used here relied on searching quadrats on the ground but *Achatina* are often buried deep in the soil or are up high in trees, so I would most likely have greatly under estimated their abundance.

Growth rate and lifespan

My data showed that growth of *Placostylus* is slow, with the lowest rates of growth occurring as the snail approaches maturity which they do not reach until about four years of age. I estimated that the lifespan of *P. fibratus* snails varies between 19 and 30 years. Observations from New Zealand on other species of *Placostylus* suggest a long lifespan for the genus, of between 20 and 30 years (Parrish *et al.* 1995; Stringer *et al.* 2004; Choat and Schiel 1980).

Survival, fecundity and mortality

New Caledonian *Placostylus* populations appeared to be maintained by a pool of large and long-lived adults which produce many juveniles that have a low likelihood of reaching adult size (Choat and Schiel 1980). Once they reach adulthood survival for both species was relatively high and I found that fecundity can be very high for *P. fibratus*, but variable for *P. porphyrostomus* in dry forest. Results suggested that the eggs and hatchlings are very susceptible to desiccation and predation, with rodent predation appearing to be the primary cause of mortality of juveniles. I found that ship rats *Rattus rattus* and Polynesian rats *Rattus exulans* are both very abundant in the sclerophyllous and evergreen forests of New Caledonia, and densities were far higher than reported in New Zealand (Chapter 5). The house mouse *Mus musculus* was also found but in evergreen forest only and then only in low numbers. In this study I highlighted the original situation of New Caledonia hosting three species of rodent in the same habitat; on other sites on the mainland, I have also found the Norway rat *Rattus norvegicus* to be sympatric to the three other species, which is particularly worrying for the persistence of *Placostylus* populations in these areas (F. Brescia, pers. obs. 2009). On the New Zealand mainland, populations of all four species of rodent have never been recorded in any one location or habitat (Roberts 1991, Atkinson & Towns 2001), except possibly on the Chatham Islands (King 2005), so the finding of three-to-four species living sympatrically in New Caledonia is both unusual and raises serious concerns about the viability of the populations of snails in these sites. The high level of rodent predation in New Caledonia seriously jeopardizes recruitment into the snail population, which was particularly true in dry forests where populations are small and very isolated.

The impact of the introduced little fire ant *Wasmannia auropunctata* on *Placostylus* snails was investigated. Little fire ants had a negative impact on

Placostylus growth, but I found no direct evidence of ant predation on snails with snail survivorship being unaffected by the presence of the ants under semi-natural conditions (Chapter 6). I saw no evidence from either semi-natural conditions or in the field that little fire ants directly attack healthy *Placostylus* snails in the wild. Rather, I observed that little fire ants might have a positive impact on *Placostylus* snail populations as they may control Carabidae (predators of snails) and influence the spatial distribution of rodents and possibly large introduced ungulates like feral pigs (*Sus scrofa*) which also prey on snails, and rusa deer *Cervus timorensis russa* which are responsible for severe modification of habitat but seem to avoid ant-infested areas. Time and financial constraints precluded more detailed study of these apparently inverse spatial associations, and pigs were localised and deer completely absent from the Isle of Pines.

Life-history traits and harvest regimes for *P. fibratus* on Isle of Pines render them vulnerable and it is likely that at some critical point, ongoing harvesting could trigger a population collapse. I showed evidence for change in the total population of *Placostylus fibratus* snails on the Isle of Pines between 1993 and 2008 (Chapter 3), with a particularly apparent decline in the population of juveniles from 2001 to 2008. In 2003, 52,986 snails were collected for marketing from the wild, 56,897 snails in 2005 and in 2006 it was 66,227 snails. Also, $42,624 \pm 26,208$ snails are estimated to be eaten annually by Kuniés. Thus, the actual annual harvest represents approximately 6% of the estimated wild adult stock (ca. 2,5 million snails) and I considered that the sustainability of this harvest, in the actual context of significant decline of populations, needs serious consideration. Repeated harvests for decades in certain districts of Isle of Pines may have already led to local population extinction or population reduction to unsustainably low densities.

The stage-structured population dynamics model I developed (Chapter 7) based on my findings of the life history traits was used to investigate the fate and persistence of the populations and to assess population trends under different management options. If the actual harvest rate is maintained, simulation predicts that the population has a significant risk of declining to very low levels within the next 50 years. If the harvest rate increases, the decline is accelerated. Sustainable exploitation is predicted to be attained at a 3% harvest rate (c.a. 70,000 snails per annum); this rate would preclude any further collection for commercial purposes and would allow collection solely for

daily consumption by locals on Isle of Pines. However, the model is very sensitive to rodent predation and predicts that small changes in rodent predation rates make the difference between *Placostylus* populations recovering or going extinct within the next 50 years. Unfortunately, poison-based rodent control operations on Isle of Pines have little likelihood of being approved because of opposition from local people, tourists, and local government alike. Publicity about the negative impact of rodents on these snails is required urgently if attitudes are to be changed and a political will to intervene is to be kindled. Also, decisions to further limit or cease the collection of snails will depend largely on the Kuniés.

Critical data are still lacking for some of the life history traits of *P. porphyrostomus* on the Mainland, so I was not able to model population trends for this species. Nevertheless, given the high level of fragmentation of dry forests and degradation of habitat by ungulates, coupled with the high levels of rodent predation occurring there, there is no doubt that the Mainland populations of *P. porphyrostomus* are in serious decline and require urgent conservation intervention. With this objective in mind, I undertook restoration trials.

10.3 Opportunity and feasibility of restoration trials

Conservation biology- a relative new multidisciplinary science- has two goals: first, to investigate human impact on species, communities and ecosystems, and second, to develop practical approaches to prevent extinction of species and, if possible, to reintegrate them into a properly functioning ecosystem (Primack 1998). In New Caledonia, several attempts are currently being made to restore ecosystems, mainly after intense nickel mining activities. However, these programmes are focused solely on restoration of the flora by replanting and soil restoration. Except for a small number of rodent control trials on some offshore islets, or very locally for the flightless bird Cagou (*Rhynochetos jubatus*), no fauna restoration operations have been conducted in New Caledonia, and for this reason, the data presented here are both original and innovative.

10.3.1 A rodent control programme by continuous poisoning

Controlling rodents

In order to try to restore a remnant *Placostylus* snail population in a dry forest patch, I experimentally poisoned rodents on a relatively large scale on the mainland of

New Caledonia (Chapter 8). I successfully controlled rodent populations for 22 months by continuous poisoning in 5 ha of dry forest.

Following periods when bait stations had not been replenished, the indices of rodent abundance increased rapidly. This demonstrated that rodent control programmes in New Caledonian dry forest need to be sustained or carried out over large areas to be effective. And it needs continuous financial support from authorities. With regards to my trial, I thus tried to evaluate costs and field expenditures in order to provide useful guidelines for managers for future large-scale poisoning programmes in New Caledonia.

Field expenditures for the poisoning control

In the first nine months of poisoning I used 170 kg rodenticide (diphacinone) in the 125 bait stations (comprising losses and amount consumed by rodents). Assuming the grid and transects were already in place, placing bait on the 125 bait stations and monitoring rodent abundance on 45 tracking tunnels required 10 hours of labour per month for an mean effective poisoning area of 18 ha [13.4 to 22.5 ha (depending on whether the New Zealand or New Caledonian home range estimates are used)]. The inputs required for the study which used a 1-ha 25 m poisoning grid (not including the time taken to mark out the grid and transects) were 9.4 kg of poison per year and 10 hours of labour per month. This represents USD \$70 a year per hectare for the poison and \$10.95 monthly per hectare for labour. Costs for equipment and supplies were incurred mostly in the first year and dropped in subsequent years.

Nelson *et al.* 2002 in Hawaii found that a combination of rodenticide baiting and snap-trapping effectively controlled rodents and they calculated that in the first year, the cost was 2.5 times higher for baiting than for snap-trapping, and in subsequent years cost was eight times higher for baiting than for snap-trapping because of the annual cost of bait. They recommended increasing the distance to 100 m between stations could reduce costs.

Impact of poisoning on snail populations

After 15 months, the poisoning I did was sufficient to have reduced and maintained rodent activity at low levels but I was unable to conclusively demonstrate a significant recovery of *P. porphyrostomus* after this time. Considering the special life history traits of New Caledonian *Placostylus*, this suggests that the control may need to

be continued for several years to yield benefits. Also, I considered that supplementation of these populations by adding captive-bred snails may speed recovery in rodent-poisoning areas.

10.3.2 A captive-bred snail supplementation programme

The Institut Agronomique néo-Calédonien (IAC) has been actively developing farming methods for the snails. Captive breeding of snails may help to allow the exploitation of the resource to continue (a topic of great concern for inhabitants of Isle of Pines) by supplementing or replacing the harvest from the wild, as well as facilitating the preservation of natural populations especially in dry forests where only 1% of the original cover remains. Successful farming of snails may also enable the restocking of small populations of *Placostylus* in areas where they are now rare or extinct. A successful farming method has now been developed for New Caledonian *Placostylus* following many years of trials (Appendix 2).

Results from the first attempt to release captive-bred *Placostylus* snails into a New Caledonian dry forest are encouraging and show that this approach is feasible and has considerable potential as a conservation management tool for these snails (Chapter 9). Nevertheless, Ewen & Armstrong (2007) recommended that monitoring of reintroductions should primarily aim to assess the suitability of the habitat for supporting the species in the long term rather than the short-term effects of different release strategies (e.g. soft *versus* hard release), but also to test the extent to which habitat factors such as food and predators are limiting population viability.

Thus, supplementation with captive-bred snails would be an efficient management strategy only if predators have been removed from the suitable sites, and this kind of operation needs to be accompanied by intensive and sustained rodent removal. Also, clearly in New Caledonian sclerophyllous forests, supplementations or reintroductions into areas where snails have already vanished should be done in conjunction with reforestation to ensure suitable habitat and food for snails.

The need for the establishment of a genetic management protocol in breeding programmes to retain the natural genetically based adaptation of snails and minimize their genetic adaptation to captive conditions has been highlighted in previous attempts at invertebrate restocking (Caddy and Defeo 2003; Mace *et al.* 1998; Purcell and Kirby 2006). Classification of New Caledonian *Placostylus* remains uncertain (Chapter 2;

Appendix 1); reintroduction, supplementation or translocation operations require that the genetic status of the target populations is known in order to prevent the risk of genetic pollution. Thus, during the thesis I also contributed to a study that increased our knowledge of the diversity and phylogeny of these snails (Appendix 1). Interestingly, evidence of recent hybridisation was found; this pattern of exchange might be explained by movement of snails by people.

10.4 Recommendations for management

The key findings of the thesis presented above have direct implications for the conservation and management of New Caledonian *Placostylus*. I deliberately organized this section in a practical manner in order to make the thesis of direct use and value to managers and locals by presenting explicit guidelines for recovery of both *Placostylus fibratus* and *P. porphyrostomus* snails in the foreseeable future. I thus decided to organized and integrate management recommendations made at the end of each chapter (reorganized and prioritized) into a recovery plan by highlighting urgent actions that need to be undertaken for each species of New Caledonian *Placostylus*.

Long-term goal of the recovery plan for New Caledonian *Placostylus*:

To preserve and enhance populations of New Caledonian *Placostylus* in their natural geographical and genetic range

10.4.1 Recovery Plan for *Placostylus fibratus fibratus* on Isle of Pines

Distribution and description

The species is not endemic to Isle of Pines but is found throughout the whole of New Caledonia including the Loyalty Islands. On Isle of Pines, *P. fibratus fibratus* is the type species. Generally, a large snail (height up to 12 mm) with a heavy dark brown to yellowish background shell, fusiform aperture relatively short, not exceeding the length of the spire. Aperture usually internally tinted with red, the colour may be reduce to a narrow red line around the inner rim of the peristome leaving a creamy white inner aperture. Adult growth restricted to the apertural region leading to heavy lip calluses and apertural incrustations (Neubert *et al.* 2009).

Habitat

They are mostly found under leaf litter between coral rocks in the evergreen forest of Isle of Pines. They are attracted to and feed under trees with large canopies and/or with broad leaves such as fig and banyan trees (*Ficus* spp.), *Ficus habrophylla* Bennett & Seeman, 1865), Kohu (*Intsia bijuga* (Collebrooke) Kuntze, 1891), *Elaeocarpus hortensis* Guillaumin, 1931, *Meryta macrocarpa* Baillon, 1878, but also under the ferns *Asplenium nidus* Linnaeus, 1753 and *Microsorium punctatum* Copeland, 1929.

Short term goal:

To prevent the extinction of populations on Isle of Pines, maintain the sustainability and protect cultural aspects of the species.

Cause of decline and threats

- 1- Intense human collection of adult snails for commercial purposes (around 120,000 adults snails per year annually)
- 2- Predation by introduced mammals including rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*) and pigs *Sus scrofa*
- 3- Habitat destruction and modification by humans (forest clearing, fire), by domestic or feral browsers and grazers (cattle *Bos taurus*, pigs *Sus scrofa*, goat *Capra hircus*)

Current conservation status and conservation efforts

International status: Vulnerable (1996) (IUCN Red List, November 2010). In this thesis (Chapter 2), given the estimated population decline due to the habitat degradation and the levels of exploitation and other factors implicated in the population decline, I proposed to revise this status to Endangered.

Local protection: Regulated under law (Province Sud). In 1994, the Délibération 50–94/APS regulated the collection and the transportation of *P. fibratus* on the Isle of Pines. It became illegal to collect snails from 1st May to 30th September (during the breeding season), and illegal to transport live snails out of the Isle of Pines at any time (only cooked snails could be sent to restaurants and supermarkets on the

mainland). In 2000, the Assembly revised the law (Délibération 26-2000/APS), adding an amendment that allowed the collection of *Placostylus* throughout the year on the Isle of Pines but the prohibition of export to the mainland became applicable to both live and cooked snails. Since then cooked snails from the Isle of Pines thus could only be eaten in restaurants and by locals on the island but not at all on the mainland.

Objectives for the next 10 years

Stop the observed decline and maintained populations

Objective 1

Limit the number of snails collected annually for commercial purposes

Actions required

Reinforce the law to limit the collection of snails for commercial purposes. My studies showed that an increase in the harvest rate will led to the decline of populations within 50 years; a complete stop of the commercial harvest would halt the population decline and allow for a 3% rate of harvest (i.e. of around 70,000 adults snails annually based on the 2008 estimated stock). During the next 10 years, the most efficient conservative measure would require a complete ban on commercial collection and would allow only locals to eat the snails. As a precaution, for social and economic reasons, and after discussions with locals, if a total ban was not acceptable, the number of snails collected should not exceed the current rate of 120,000 adults snails collected annually.

Objective 2

Survey population trends

Actions required

Continue to monitor snail abundance. The monitoring of snail abundance on Isle of Pines started in 1993 and has continued almost annually till now. Annual surveys need to be continued so as to assess how the snail population responds to management measures imposed in the future. The recommended method is to survey

10 x 10 m quadrats every three months (four times a year), with five districts being sampled on an rotational basis (see Chapter 3, Section 2. Methods). Reducing the frequency of surveys to every two years would further reduce costs whilst still helping to assure the long-term continuity of the monitoring programme.

Objective 3

Involvement of the local people

Actions required

Organize meetings with locals, authorities in charge of the environment and scientists to presents results of the studies and the management options required. Techniques for sustainable harvesting and monitoring should be taught beforehand to the Kuniés. Involvement of local people who are directly involved in managing collection of the snails would facilitate more responsible approaches to resource use and would enhance acceptance of the necessary restrictions. Kuniés could also be involved in the monitoring programme that eventually could be devolved to them by local authorities. Involvement of the local population is a requirement of the traditional land ownership rights.

Objective 4

Protect snail populations

Actions required

Control or eradicate predators: simple control measures such as hunting and improving fence quality to limit the number of domestic ungulates escaping and surviving in the forest. This applies to pigs, which are snail predators, and to cattle and goats that contribute to the degradation of suitable habitat and also trample snails.

Establish a systematic harvesting plan: if the decision to continue to harvest for commercial purposes was preferred by locals and managers, the management of *Placostylus* snail collection would benefit from a more rigorously organised regime in the spatial pattern of harvesting to avoid depletion. Indeed, the current system has allowed repeated collecting in the same districts for decades rather than spreading harvests more evenly. To enable populations to recover, alternating the collection in specific areas would be an efficient way to use the resource more

sustainably as well as facilitating a more equitable income in each district. The establishment of “no-take areas” could also be implemented to maintain a source population for recruitment into the surrounding area.

Objective 5

Substitute wild snails with captive snails for commercial purposes

Actions required

Develop farming methods: the production of snails in captivity would allow continuous sustained exploitation of the resource. The Institut Agronomique néo-Calédonien (IAC) has been actively developing farming methods for snails to reduce the reliance on the wild population for harvest and to provide a source for restocking wild populations. A successful farming method has now been developed for *P. fibratus*; this knowledge needs now to be transferred to Kuniés.

Objective 6

Undertake research on priority topics

Actions required

The actions required for this objective are the general recommendations I made in paragraph 5 of this chapter for future research prospects.

10.4.2 Recovery Plan for *Placostylus porphyrostomus* on dry forests

Distribution and description

Placostylus porphyrostomus is considered to comprise four sub-species (*P. p. porphyrostomus*, *P. p. smithii*, *P. p. mariei*, *P. p. monackensis*), which show a considerable degree of variation between them. It is the most common species on the west coast of the Mainland, where sclerophyllous forests dominate. Throughout its range, it can be found living sympatrically (and often syntopically) with the local subspecies of either *fibratus* (on Isle of Pines) and *bondeensis*, or *caledonicus* and *scarabus* (Neubert *et al.* 2009).

Generally a medium snail (height up to 80 mm) with a particular form of the columellaris which is a strong and elongated lamella which is usually uplifted as far as the peristome. Another distinctive character is the carmine-red colour of the interior of

the aperture, which is not found in any of the other taxa. This colour can be very extensive and can extend to an overall pinkish colouration of the shell beneath the periostracum.

Habitat

In the dry forests of the mainland, the favoured habitat and environmental conditions have been described for *P. porphyrostomus* by Brescia and Pöllabauer (2005). The snails appear to seek out areas with deep leaf litter, where the cover of understorey trees is high (> 75%). In general, they are found in shady places with low light levels (ca. 800 lux), and where environmental conditions are cooler (on average, 2–3°C less than points 1 m radius away from the snail). Important components of the habitat of *Placostylus* of dry forests are the understory trees of *Codiaeum peltatum* (Labillardière) Green (1986), *Carissa ovata* Brown 1810, and *Fontainea pancheri* (Baillon) Heckel 1870. In these forests the snails are generally found under leaf litter or close to fallen logs. The sclerophyllous forest is currently the most threatened of the Caledonian biomes due to deforestation and habitat modification by feral ungulates: only 1% of its original surface remains in the form of very small and isolated patches of forest (Programme Forêt Sèche 2007).

Short term goal:

Prevent the extinction of populations in dry forest and maintain the genetic diversity

Cause of decline and threats

- 1- Habitat destruction and modification by humans (clearing, fire) and by domestic or feral browsers and grazers (rusa deer *Russa timorensis*, cattle *Bos Taurus* and pigs *Sus scrofa*)
- 2- Predation by introduced mammals including rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*) and pigs *Sus scrofa*
- 3- To a far lesser extent, human collection is sometimes recorded

Current conservation status and conservation efforts

International status: Vulnerable (1996) (IUCN Red List, November 2010). Given the estimated population decline due to habitat degradation and the levels of exploitation and other factors implicated in the population decline, I proposed to revise this status to Endangered (Chapter 2).

Local protection: on the Mainland, in the “Code de l’Environnement” of South Province, all species of *Placostylus* are classified as protected; it is forbidden to destroy, collect, transport and market them (only the collection of *P. fibratus* on Isle of Pines is regulated). No such law is in force yet in the North Province which includes several important remnant populations.

Objectives for the next 10 years

Preventing the extinction of recognized subspecies, and maintaining and increasing the existing populations

Objective 1

Protect existing colonies and compile an inventory of past populations

Actions required

Survey of present and past colonies: the survey of patches of dry forests hosting live snails is urgently needed to help to identify priority sites. Also, the survey and mapping of past colonies, which are easily identified by the presence of fossil shells on the ground would be useful to help identify suitable areas for reintroduction operations after the causes of local extinction are redressed.

Fence to protect snail colonies against pigs and stock: already some patches of dry forest where remnant populations of live snails were identified have been fenced (Mépouiri and Nékoro in Poya) and are now pig- and deer-proof. Fencing of other sites where snail populations remain need to be urgently considered.

Control or eradicate predators: eradication of pigs by direct hunting on areas around *Placostylus* colonies needs to be pursued and intensified. Also, eradication and control methods for rodents need to be developed on the Mainland.

Objective 2

Survey population trends

Actions required

Monitor population trends at selected snail colonies: in areas where management operations has been carried out (such as fencing against introduced ungulates), the monitoring of snail colonies need to be undertaken to evaluate the success of operations.

Objective 3

Protect and enhance quality of suitable snail habitat

Actions required

Protect by fencing and restoration by re-vegetating with local species that provide appreciate shelter and food for the snails would enhance suitable habitat and help maintain existing populations, as well as creating sites suitable for future translocation/reintroduction or supplementation operations.

Eradication or control feral ungulates: rusa deer, pigs, domestic stock and also, to a lesser degree, the giant African snail *Achatina fulica* are responsible for degradation of the habitat in dry forest by removing leaf litter and altering the understory essential for *Placostylus*. The removal of feral ungulates and African snails in areas around *Placostylus* snail populations is urgently needed.

Limit the impact of humans: many of the remaining patches of dry forest are on private properties. Development of the awareness of land owners is required to prevent forest clearing for pasture or crops by destruction and fire.

Objective 4

Maintain captive populations

Actions required

Develop captive breeding of very rare populations: the maintenance and rearing of the most threatened races in captivity must also be pursued for future translocations and population supplementations.

Objective 5**Involvement of land owners****Actions required**

Continue the collaborative work with landowners initiated by the “Dry Forest Programme” and continue to develop their involvement: the promotion and signing of collaborative agreements between farmers and local authorities in charge of the environment are required to compensate farmers for the cost of fencing off patches of dry forest and/or eradication feral ungulates from their properties.

Provide them with information about the scarcity of *Placostylus* snails in dry forest and the very real risk of causing local extinction if they harvest snails illegally.

Objective 6**Pursue research on priority topics****Actions required**

The actions required for this objective are the general recommendations I made in chapter 10.5 of the thesis for future research prospects.

10.4.3 Recovery Plan for poorly-known *Placostylus*

In addition to *P. fibratus* and *P. porphyrostomus*, four other species of *Placostylus* are present in New Caledonia (Neubert *et al.* 2009). They are mostly located in the far north of Grande-Terre, where the biome is not at such great risk as is dry forest. They have not been harvested commercially, but their populations have never been studied. In the absence of more specific data, the recommendations for the conservation and management of these species are relatively similar to the ones establish for *P. porphyrostomus* in dry forest.

Distribution and description (Neubert *et al.* 2009)

Placostylus scarabus lives in the northern part of New Caledonia (Poum, Baie de Néhoué and Belep Islands, Ile Pott and Ile Art and several small island in the coral reef lagoon just offshore the Mainland). The shell is elongated to almost oval, smaller

than the *fibratus* group. The aperture is internally of blood-red colour; dentition is almost missing.

Placostylus eddystonensis (*P. e. eddystonensis*, *P. e. savesi* and *P. e. bavayi*) is native to the central mountainous area of New Caledonia (from Ouémou in the North to Mont Mou in the South). It is often found to living sympatrically with other *Placostylus* species. The shell is of medium size, fragile and an aperture broadly elongate usually bright orange-red to yellow; periostracum is deep brown but erodes easily and eroded shell often show a pinkish colour.

Placostylus bondeensis (*P. b. bondeensis* and *P. b. rossiteri*) is restricted to the north-western mountains and hills of Grande-Terre (Kaala-Gomen and Taom regions and Mt Tiebaghi). The shell is thick and heavy. The aperture interior is bluish to yellowish or deep reddish. The periostracum is chestnut brown in colour which contrasts strongly with the colour of the interior aperture.

Placostylus caledonicus is restricted to the northern part of Grande-Terre. The shell is slender and conical with an elongated aperture and narrowed by the usually strongly developed labial callus. The periostracum is uniformly olive to greenish.

Habitat

No information or literature is available about the preferred habitat of these species. Nevertheless, personal observations indicate that, like *P. fibratus* and *P. porphyrostomus*, these species are relatively specific in their habitat requirements. They are found in humid evergreen native forests of the east coast and the central mountain of the mainland, and in more dry and mesophyllous native coastal forests in the west and on offshore islets.

Short term goal:

Prevent the extinction of populations and maintain the genetic diversity

Cause of decline and threats

- 1- Habitat destruction and modification by humans (clearing, fire), by domestic or feral browsers and grazers (rusa deer *Rusa timorensis*, cattle *Bos taurus*, pigs *Sus scrofa* and goats *Capra hircus*)
- 2- Predation by introduced mammals including rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*) and pigs *Sus scrofa*
- 3- To a far lesser extent, human collection was sometimes recorded

Current conservation status and conservation efforts

International status: of these four species considered here, only *P. eddystonensis* have an international status and it is listed as Vulnerable (1996) (IUCN Red List, November 2010). Given the estimated population severe decline due to the severe habitat loss and degradation and other factors such as introduced ungulates implicated in the population decline, I propose (Chapter 2) to revise this status to Critically Endangered, and also to give this status to *P. caledonicus*, *P. bondeensis*, and *P. scarabus*.

Local protection: on the Mainland and in the South Province only, the “Code de l’Environnement” protects all species of *Placostylus* (it is forbidden to destroy, collect, transport and market them (only the collection of *P. fibratus* on Isle of Pines is regulated)). Nevertheless, the poorly-known species of *Placostylus* concerned by this recovery plan are located in the North Province, and no specific local law protects them there currently.

Objectives for the next 10 years

Preventing the extinction of recognized subspecies, maintaining and increasing the existing populations

Objective 1

Protect existing colonies and inventory of past populations

Actions required

Survey of present and past colonies: the survey of forests hosting live snails is urgently needed to help to identify priority sites. Also, the survey and mapping of past

colonies (easily identified by the presence of fossil shells on the ground) would be useful to help identify suitable areas for reintroduction operations once the causes of the local extinction have been managed.

Fence to protect snail colonies against pigs and stock: fencing sites where snail populations remain needs to be urgent consideration because no snail populations in the far north of Grande-Terre have been given this protection.

Control or eradicate predators: eradication of pigs by direct hunting on areas around *Placostylus* colonies needs to be initiated and methods of eradicating and controlling rodents on the Mainland need to be developed.

Objective 2

Survey population trends

Actions required

Monitor population trends at selected snail colonies: in areas where management operations will be carry out (such as fencing against introduced ungulates), the monitoring of snail colonies will need to be undertaken to evaluate the success of operations.

Objective 3

Protect and enhance quality of snail suitable habitat

Actions required

Protect by fencing and restore by revegetation with local species that provide appreciate shelter and food for the snails would enhance suitable habitat and help maintain existing populations, as well as creating sites suitable for future translocation/reintroduction or supplementation operations.

Eradication or control of feral ungulates: rusa deer, pigs, goats and stock are mostly responsible for degradation of the habitat in these forests by removing the leaf litter and altering the understory essential for *Placostylus*. The removal of feral ungulates in areas around snail populations is urgently needed.

Limit the impact of humans: some of the forest remnants suitable to host these *Placostylus* species are localised on private property or in traditional Melanesian areas (tribes). Development of the awareness of people living near snail colonies is required to prevent forest clearing for pasture or crops by destruction and fire.

Objective 4

Maintain captive populations

Actions required

Develop captive breeding of very rare populations: the maintenance and amplification of the most threatened races in captivity must also be pursued for future translocations and population supplementations.

Objective 5

Involvement of land owners and Melanesian Tribes

Actions required

Initiate collaborative work with landowners and Tribes similar to what is done for dry forests by the “Dry Forest Programme” and develop their involvement: signature of collaborative agreements with authorities in charge of environment to find compensation measures for fencing patches of dry forest in their properties or traditional lands, and/or encouraging ungulates eradications must be pursued.

Give them information about the scarcity of *Placostylus* snails in dry forest and explain to them the danger of harvesting in these small populations.

Objective 6

Pursue research on priority topics

Actions required

The actions required for this objective are the general recommendations I made in chapter 10.5 of the thesis for future research prospects.

10.5 Research prospects

In this section I outline gaps in our knowledge that future research should address to enhance the management and conservation of New Caledonian *Placostylus*.

10.5.1 Some aspects of the life history traits

Further work is required to enhance our knowledge of the life history of New Caledonian *Placostylus*; in particular, a more exact understanding is needed of causes

and rates of mortality of the newborn stages. In the model I constructed, some parameters such as natural mortality rates for eggs and newborns were “best-guess” estimates based on observations in captivity and need to be investigated if a more robust model is to be developed.

10.5.2 Feasibility of restoration trials

In order to make rodent control operations feasible on the Mainland of New Caledonia or in inhabited areas (such as Isle of Pines), future research into reducing costs for controlling rodents by combining rodenticide baiting and snap-trapping should be examined. Further studies should focus on determining an optimal size for cost-effective supplementation with captive-bred snails and investigating what length of the acclimation period during soft releases would be most favourable for survival and the establishment of cohesive populations.

10.5.3 Interactions with introduced species

Suitable methods for monitoring the introduced African snails need to be developed. Also, it would be useful to try to enhance our knowledge of how the composition of rodent species changes after poisoning and other aspects of rodent biology including home ranges competitive interactions with other rodents, and the foraging strategies of each species. A better understanding of rodent ecology should help in the development of efficient rodent control techniques adapted to the New Caledonian context of very high rodent abundances.

I suggested that little fire ants might have a positive impact on *Placostylus* snail populations but it would be useful to understand how they may control Carabidae, and influence the spatial distribution of rodents and possibly large introduced ungulates like feral pigs (*Sus scrofa*) and rusa deer (*Cervus timorensis russa*).

An understanding of the impacts of pulsed rodent control on population trends and on sustainable harvest rates on Isle of Pines should be investigated further.

10.5.4 Knowledge on genetic differentiation between populations

The genetics work initiated on Appendix 1 needs to be extended to include snails from more districts of the Isle of Pines, but also from other sites of the Mainland to enhance the taxonomy of New Caledonian *Placostylus* currently based on anatomical characteristics and analysis of shells (Neubert *et al.* 2009).

10.6 Conclusion

In this study, I have reported and discussed the main finding of some of the life history traits, ecology, human impacts and population trends of two endemic species of New Caledonian *Placostylus* that are either overexploited (*P. fibratus* and *P. porphyrostomus* on Isle of Pines) and/or very isolated with small populations and threatened by habitat loss and predation (*P. porphyrostomus* in dry forests).

Also, I have undertaken restoration operations for a threaten *Placostylus* species by controlling rodents and supplementing the wild population with captive-bred snails.

This work has provided a much firmer foundation of scientific knowledge for the species, and has enabled me to formulate recommendations for the conservation and management of the New Caledonian *Placostylus* and the development of recovery plans.

The results presented in this thesis are original and innovative because they:

- i) deal with an exploited species of considerable economic, social and traditional value
- ii) provides practical conservation and management guidelines that can be implemented by government authorities and local people
- iii) constitutes the first attempt at achieving effective management and recovery of endemic terrestrial New Caledonian species (this is the first case of fauna restoration and the first case of rodent control in Mainland Island situation in New Caledonia)

This research involved working closely with local communities and actively encouraging their input; as such, this approach should serve as a good model for further studies on other exploited elements of the New Caledonian wildlife such as the over-hunted flying-foxes (Brescia 2007; Kirsh *et al.* 2000), and the notou pigeon *Ducula goliath* (de Visscher 2001).

10.7 References

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APPENDICES

APPENDIX 2

A REARING METHOD FOR *PLACOSTYLUS* (RESEARCH NOTE)



An adult P. fibratus and newborns in captivity

Land snails of the genus *Placostylus* (Family Bulimulidae) are found only in few islands of the South West Pacific. In New Caledonia, the endemic snail species (6 endemics) are favoured as food, and are threatened by over-exploitation where it represents an important traditional economic activity for locals. Also, modification and destruction of habitat by feral ungulates, and predation by rodents are also responsible for dramatic declines and sometimes the local extinction of populations in some areas (Brescia *et al.* 2008). Measures designed to limit the number harvested have been imposed by local authorities. In parallel with the passing of these laws that control the numbers of *Placostylus* harvested from the wild, the Institut Agronomique Néo-Calédonien (IAC) has been actively developing farming methods. Captive breeding of snails may help to allow the exploitation of the resource to continue (a topic of great concern for inhabitants) by supplementing or replacing the harvest from the wild, as well as facilitating the preservation of natural populations. Successful farming of snails may also enable the re-stocking of small populations of *Placostylus* in areas where they are now rare or extinct.

The initial attempts, based on typical rearing methods for European snails, were not encouraging and it appeared that these snails were going to be very difficult to maintain in captivity (Salas *et al.* 1997). They are large (up to 15 cm long), slow moving, slow developing (sexually mature after 4 years) and long-lived snails (15-25 years) making it difficult to make quick assessments of the potential of different rearing techniques.

In New Zealand, where *Placostylus* snails are mainly threatened by introduced species, the techniques needed for successful captive breeding have not yet been developed (Parrish *et al.* 1995). However, researchers at Massey University managed to keep a small number of *Placostylus* adults in captivity until they laid eggs and raised them successfully to adulthood (Stringer and Grant 1992, 2007).

Ecological and behavioural studies of the New Caledonian snails in their natural environment and studies in captivity under semi-natural and regulated conditions have helped improve understanding of their needs (Pöllabauer, 1993; Brescia 2005, 2006). This has led to refined handling methods through systematic testing of alternative farming methods.

Placostylus snails are essentially nocturnal (between 7 pm to 6 am) and are photophobic. Activity is higher at dusk (8 pm) and in the middle of the night (3-4 am) when humidity is high (90 –95%) and temperatures cooler (18-20°C). Newborn snails are tree-dwelling. Adults and juveniles are almost always hidden under a thick layer of dead leaves. They are mostly found on CaCO₃ rich soil (coral forests). Snails are inactive more than 80 % of the time, and show a very low dispersal rate (0.9 to 1 m per night).

We explored the possibility of mass-rearing of New Caledonian *Placostylus* snails and we describe here the farming technique developed for these snails. Each year, from 1995 to 2000, 50 adult *Placostylus* were collected in the forest, individually identified with a number engraved on the shell and placed in captivity. We observed annual reproduction rate and survival of 10 groups of 15 newborns each year.

General husbandry conditions

From 1995 to 1997

Adult snails collected in the wild were placed in enclosures with a humus-rich soil for substrate, with a stocking rate limit of 5 kg/m². Wheat bran supplemented with calcium carbonate (20% of dry weight) was provided *ad libitum* in small troughs, and was changed every 1-3 days. When adults laid eggs, clutches were placed in separate small enclosures (15 x 10 x 10 cm) with humus-rich soil and were watered daily. No leaf litter was provided for either adults or newborns. Newborns were fed with the same diet as the adults.

From 1997 to now

Placostylus are maintained in plastic boxes with an artificial substrate of coco-fibre compost supplemented with calcium carbonate. Humidity is maintained by daily watering. A thick layer of leaves (papaya, banana) is used as a cover to maintain moisture, to reduce the light reaching the snails, and to limit the climbing behaviour of hatchlings and the associate energy losses.

An artificial diet has been developed as a substitute to the natural diet of decaying forest leaves. Specific diets have been developed to suit the different age classes of snails. Adult and juvenile snails are fed with a dry, very thin mix, of cereal flour (80% of dry weight) supplemented with calcium carbonate (20%). Hatchlings are

fed with a more energy-rich thin powder of cereal flour (50%) and calcium carbonate (20%) supplemented with milk powder (30%). A large number of feeding dishes and water-troughs are set out in different areas of the enclosures to improve access for these relatively sedentary snails. Also, dishes with *ad libitum* calcium carbonate are placed in the enclosures and enable snails to cover their needs for the formation of their heavy shell. To maximise reproductive productivity, adult snails have been collected from the forest during the breeding season and maintained in captivity under the conditions described above, with a stocking rate limit of 5 kg/m².

Each day, a search is conducted for egg clutches. When found, they are collected with great care using a tea spoon (the eggs are very fragile because they lack a calcified layer), and placed in nursery boxes (15 x 10 x 10 cm) on a substrate of humid coco-fibre/soil mix. Hatching under these conditions occurs after 10 to 45 days. A fine brush is then used to transfer them into new clean nursery boxes. In the first weeks, a thin layer of artificial food is spread manually on some leaves of the litter and is thus accessible to newborns as they move around.

Reproduction and survival

The mean reproduction rate of captive snails (number of clutches / mean number of adults expressed as a percentage) varied from 31% in 1996, 23% in 1997, 65% in 1998, 271% in 1999 and 156% in 2000. At the start of these trials in 1995, only about 0.16 egg-clutches per adult per year was obtained. Now, we achieve more than 10 times this rate (1.5 to 2.7 egg-clutches per adult per year).

In 2000, 72% of the adults in captivity laid at least one clutch per year (28.0% never laid eggs, 34.0% laid a single clutch, 23.4% laid twice, 12.5 three times and 2.1% five time a year).

For the whole period 1995 to 2000, the mean hatching success per clutch remained relatively high and averaged 72% overall (n=203 clutches; SD=19) and the mean number of eggs per clutch was 182 (SD=85, min=58, max=312). The mean hatching time was 47 days (SD=21, min=15, max=45).

Survival of the hatchlings to one month in the nursery now approaches 70% whereas in earlier farming attempts in 1995 it was only 10% (Salas *et al.* 1997; Brescia *et al.* 1998); and 68% of juveniles now survive to eight months (vs. 5% in 1995). We

observe the best growth rates of juveniles when the stocking rates are maintained at a low level, around 1.5 to 2.0 kg/m² (Brescia 2000). Juveniles grown under higher stocking rates give rise to small adults and even dwarf forms. Adult size (and sexual maturity) in captivity is reached in two years under these conditions, compared to five years in the wild (Pöllabauer 1995).

It is now possible to produce *Placostylus* snails on mass in captivity. The farming method has been validated for different species of *Placostylus* from New Caledonia (Brescia and Pöllabauer 2004, 2005). However, the cost of production needs to be reduced for it to become commercially viable (extensive methods). Amplification of threatened *Placostylus* populations is now feasible and this makes *Placostylus* snails far less vulnerable to extinction. Conservation trials based on the release of captive snails for re-introduction, supplementation or translocation are now conceivable, but this requires further research on methods that will maximise survival in the wild after release, and on the genetic structure taxonomic status of wild populations to avoid genetic pollution.

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APPENDIX 3

TWO POSTERS PRESENTED AT THE WORLD CONFERENCE OF MALACOLOGY- PERTH 2004



New Caledonian *Placostylus* land snails reared in captivity - Impact for their conservation -

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Land snails of the genus *Placostylus* (BULIMULIDAE Family) are found only in few islands of the South West Pacific. In New Caledonia, the endemic snails species are favoured as food, and are threatened by over-exploitation (important traditional economic activity). Modification and destruction of habitat by feral ungulates, and predation by rodents are also responsible for the dramatically decline and sometimes the local extinction of populations, in some areas. Measures designed to limit the amount of harvested have been imposed by local authorities. In parallel with these control measures, development of farming methods has been explored. It would allow exploitation of this natural resource to continue, as well as the preservation of wild snail populations. In addition, successful farming would enable the production and restocking of small populations of *Placostylus* in areas where they are almost extinct.

- RESEARCH QUESTION and CHALLENGES -

The aim of this study is to explore the possibility of mass-rearing of *Placostylus* snails and to develop farming techniques. These snails are very difficult to maintain in captivity : 90 % mortality rate of new born snails after one month, high adults mortality rate and extremely low reproductive rate in captivity, very slow growth rate (4-5 years for sexual maturity, but a long-life span: 15-30 years)

- METHODS -

Ecology and behavioural studies in their natural environment and studies in captivity under semi-natural and regulated conditions have helped improve understanding of their needs. This research was conducted to improve farming methods.

- BIOLOGICAL AND ECOLOGICAL REQUIREMENTS -

Placostylus snails are essentially nocturnal (between 7 p.m to 6 a.m) and are photophobic. Activity is higher at dusk (8 p.m.) and in the middle of the night (3-4 a.m.) when humidity is high (90 –95 %) and temperatures cooler (18-20 °C). Newborn snails are tree-dwelling. Adults and juveniles are almost always hidden (80 % of cases) and under dead leaves mainly (61 %). They are mostly found on CaCO₃ rich soil (coral forests). Snails are inactive more than 80 % of the time, and show a very low dispersal (0.9 to 1 m per night). For comparison, the giant African snail, *Achatina fulica* can do more than 50 m per night!

- PLACOSTYLUS SNAILS FARMING METHOD -

An artificial diet

Different artificial diets have been tested on growth and reproduction performances.

Adult and juveniles diet : cereal flour (80 % of dry weight) supplemented with calcium carbonate (20 %).
New-borns diet : cereal flour (50 %) with powder milk (30 %) and calcium carbonate (20 %).



Substrate

A neuter substrate, a coco compost supplemented with calcium carbonate. Humidity is maintained by daily watering. A thick layer of leaves (papaya, banana...) to keep humidity high and limit the quantity of light, and the arboreal behaviour of new-borns.

Reproduction

Placostylus snails in reproduction enclosures (biomass level: 5 kg/m²) lay eggs (about 200 at a time) at almost any time of year (Figure 1), but roughly 2 peaks can be identified in April-May (cold season) and October-November (beginning of dry season). These two peaks correspond to the natural reproduction period.

At the beginning of the study in 1995, only 0,31 (31%) laying by adult and by year was obtained. Now, it is more than 8 times more (1.5 to 2.7) – (Table 1)-. About 72% of adult snails lay at least once per year in captivity.

Hatching and survival of newborn in nursery

70% survival rate of newborns at 1 month are now obtained vs. 10% in the past, then 68% at 8 months. These results have to be related to the improvement of the conditions (temperature, humidity and diet) in the enclosures.



Growth rate

Best growth performances are obtained when biomass is maintained at a low level (1.5 to 2.0 kg / m²). Adult size and sexual maturity in captivity are reached at two years (vs. 5 in the forest): the aperture lip becomes thick and snails can be consumed

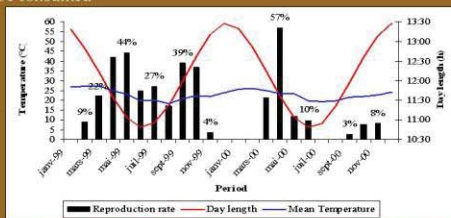


Figure 1: Evolution of reproduction rate for captive *Placostylus* (number clutches / mean number adults), according to temperature and day length, from January 1999 to December 2000

Reproduction period	Mean number of captive adult snails	Number of clutches	Reproduction rate (number of clutches / mean number of adults)
1995 – 1996	16	5	31 %
1996 – 1997	35	8	23 %
1997 – 1998	40	26	65 %
1998 – 1999	38	103	271 %
1999 – 2000	39	61	156 %

Table 1: Evolution of annual reproduction rate for captive *Placostylus* from 1995 to 2000



- CONCLUSIONS AND IMPACT FOR CONSERVATION -

It is now possible to produce *Placostylus* snails in mass in captivity. The farming method has been validated for different species of *Placostylus* from New Caledonia. The cost of production must be diminished for commercial farming (extensive method?)

Amplification of threatened *Placostylus* populations is feasible and it makes *Placostylus* snails no longer vulnerable to extinction. Conservation snails based on the release of captive snails for re-introduction, supplementation or translocation are now conceivable, but this requires acquisition of necessary information to maximise survival in the wild, and to take into consideration the taxonomic status of animals to avoid genetic pollution.

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South Province of New Caledonia (DRN- Direction des Ressources Naturelles) and French Ministry of Environment for their financial support to the project

Ecology and population trends in the New Caledonian *Placostylus* land snail populations - a PhD Thesis -



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Land snails of the genus *Placostylus* are found only in the Western Pacific (on a few islands between New Zealand and Melanesia). This ancient genera is a relict of the Gondwanaland. *Placostylus* lives on the ground in native forest and can grow large (10-15 cm long and about 100 g). In New Caledonia, these endemic snails (6 species) are favoured as food and marketed. It is also an important part of Melanesian culture and traditions (traditional food, jewellery and medicinal properties).

The harvesting of wild snails in some parts of New Caledonia for consumption is an important traditional economic activity. The number of snails harvested has increased over years (700 000 in 1993) and recent surveys indicated a dramatically decrease in the number of wild snails (a drop of 40 % in 7 years), a situation which is probably due to over-exploitation. In dry forests (also known as sclerophyllous forests- the most endangered habitat in New Caledonia), modification and destruction of habitat by feral ungulates, and predation by rodents are also responsible for the dramatic decline, and sometimes the local extinction of *Placostylus* snail populations.

Placostylus are slow moving, slow developing and long-lived. The species found in New Zealand are protected under the Wildlife Act of 1953, and are currently endangered. Massey University and the Department of Conservation (DoC) have worked on the conservation of these snails for more than 20 years now. Only one species of New Caledonian *Placostylus* snails has been the subject of scientific research, but the lack of information on particular points of ecology and biology is harmful to their conservation.

- RESEARCH QUESTION -

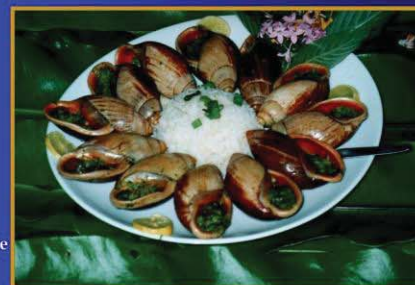
WHEN CONSERVATION MEETS SUSTAINABLE USE

The thesis will:

- Contribute to the conservation and the sustainable exploitation of New Caledonian *Placostylus* snails (by determining maximum sustainable yield and providing advice to decision-makers).
- Investigate the ecology and the dynamics of populations, and identify and quantify threats

In a wider scientific context, the thesis will:

- Constitute a prime study model with regard to the evolution of exploited species with small populations that are subjected to miscellaneous pressure factors.
- Contribute to the development of tools for use in the field of Conservation and Restoration Biology



- GOALS, METHODS AND EXPECTED RESULTS -



- A literature review on *Placostylus* snails will give an overview on the state of knowledge on the genus
- The survey of wild stocks (quadrats method) will give information on status of populations (counts and population structure)
- The survey on removals will give information on the market (survey by enquiries to (i) restaurants to quantify the number of snails collected for the market and by enquiries (ii) to locals to quantify what is collected for consumption as bush meat).
- Impact of predation (rodents and little fire ants (*Wasmannia auropunctata*) mainly) on *Placostylus* snail populations : predator exclusion methods *in situ* and trials in captivity with captive bred snails will provide information on the vulnerability of snails to predation (which stages are affected and to what extent ?)

- Demography and dynamic of populations: (mark and recapture studies in fixed quadrats with transponders to access basic population parameters such as mortality, growth, and reproduction rates)
- Computer simulations will assist in the development of sustainable exploitation models for *Placostylus* snails.

- CONCLUSION -

The study will contribute to a better knowledge of New Caledonian *Placostylus* snails, and contribute to its sustainable use.

The originality of this study is that not only biological considerations are taken into account but also socio-economic realities. The full agreement and participation of locals are needed to succeed.

- ACKNOWLEDGMENT -

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