**UNIVERSITE PAUL CEZANNE AIX-MARSEILLE III**

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# ECOLOGIE, DYNAMIQUE DE POPULATION, COMPORTEMENT ET IMPACT D'UN RONGEUR INTRODUIT *RATTUS RATTUS* SUR LES ILES DE MEDITERRANÉE

THÈSE
pour obtenir le grade de

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*Somewhere over the rainbow*
*Way up high*
*And the dreams that you dreamed of*
*Once in a lullaby ii ii iii*
*Somewhere over the rainbow*
*Blue birds fly*
*And the dreams that you dreamed of*
*Dreams really do come true ooh ooooh*
*Someday I'll wish upon a star*
*Wake up where the clouds are far behind me ee ee eeh*
*Where trouble melts like lemon drops*
*High above the chimney tops that where you'll find me oh*
*Somewhere over the rainbow bluebirds fly*
*And the dream that you dare to, why, oh why can't I? i iiii*

***Over the Rainbow, E.Y. Harburg***

*"Rather than look down our noses at scientists whose interest, methods or philosophies don't coincide with our own, it's time that we all unplug, sit around the same camp-fire, pass the botle, and swap lies. We may not solve the world's problems but'll all learn a lot, and after the fire has died out and were're back home staring at computers, our research programs will improve".*

*"We are all trying to understand nature. That is a privilege to treasure and perserve."*

***R. Steadman***

*A mes parents,*

*Flo, et mes deux grand-mères.*

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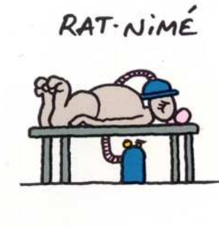

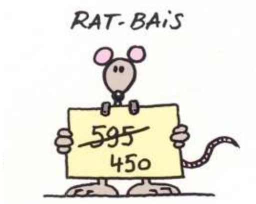

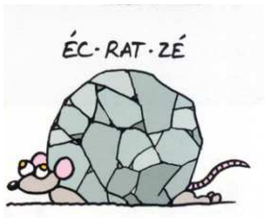

Il y a énormément de personnes à remercier ici, mais je vais prendre soin de n'oublier personne.

La toute première personne que je souhaiterais remercier ici, c'est bien toi Eric, avant tout pour m'avoir confié « ton bébé », ce gros projet qui, je sais, te tenait à cœur. Même si on en sort aujourd'hui avec encore une kyrielle de nouvelles questions, on en aura appris des choses et on se sera bien marrés aussi ! Un grand merci à toi pour m'avoir fait confiance pour mener à bien ce projet. J'ai bénéficié d'un appui hautement appréciable de ta part au cours de ces trois années, tu as été un véritable pilier dans l'accomplissement de ce travail car tu as toujours su à la fois te rendre disponible, réactif et dynamique, à l'écoute et intéressé, tu as toujours accordé un fort intérêt à échanger, conseiller, orienter, transmettre…et également su trouver les bons mots lors de petites baisses de moral. J'ai également bénéficié, grâce à la confiance que tu as accordé dans mon projet, de conditions de travail de haute qualité, avec un avantage certain dans le monde de la recherche qui est de pouvoir se déplacer dans les labos extérieurs, assister aux conférences internationales et rencontrer d'autres chercheurs pour échanger et collaborer. Et enfin, merci à toi (ainsi qu'à notre PE international !) pour m'avoir embarquée dans cette aventure cinématographique très palpitante par l'intermédiaire de ce petit documentaire animalier et de ses aventures insulaires. C'est donc avec un grand enthousiasme que j'ai travaillé sur ce projet sous ta tutelle.

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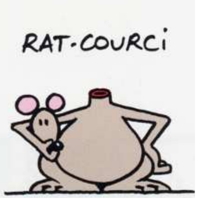
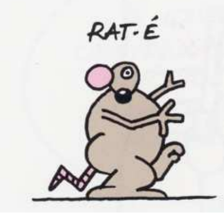




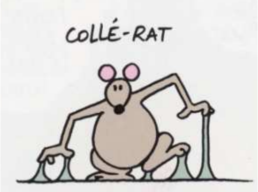
Sur le terrain, tous ces gens qui ont contribué au bon déroulement de ces travaux :

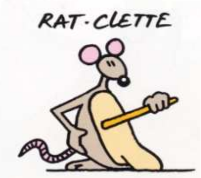
La structure du Parc National de Port Cros pour m'avoir accueillie dans les locaux du parc et m'avoir autorisée à mener mes travaux. Toute l'équipe du parc, que j'ai côtoyé pendant plus de trois années et envers qui je serai éternellement reconnaissante. Hervé, un grand merci à toi pour avoir toujours fait de ton possible pour que je puisse mener à bien mon terrain ; Armel, Sylvain, Gilles, Olivier, Céline, ce sont des milliers de services rendus et des bonnes parties de rire aussi! On a vécu de sacrés moments, j'espère beaucoup que l'on se recroisera dans d'autres aventures ; et puis, Bernard K., Bernard R., Pascal, Isa, Sabrina, Donia, Elodie, Cyrielle P., Cath, Daniel, vous qui avez toujours été présents pour un service, un sourire, un échange, des moments toujours très agréables partagés…

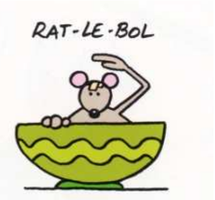
P.-E., le caméraman de l'univers intergalactique tout terrain (mais, les sabots « crocs » aux pieds c'est mieux :) Sur Bagaud, sur Europa, on en aura vécu des aventures, et ce film vraiment splendide, c'était une sacrée expérience ! Agathe, l'assistance modèle, efficace, qui ne recule devant rien ! J'ai adoré ta compagnie et j'espère que l'on aura l'occasion de se recroiser sous d'autres horizons. Cathy & Isa, on aura fait un sacré boulot ensemble lors des premières sessions de captures ! Je n'en reviens toujours pas de l'aide que vous m'avez apportée, c'était génial les filles; Géraldine & Amandine (Géraldine, ton appareil photo est toujours coincé dans les murs du fort, c'est pour quand les prochaines fouilles sur Bagaud ??) ; Ade, ma Grande Amie, je t'en ai fait bavé, ma pauvre, les dernières nuits de terrain auront été rudes…mais je crois savoir que tu auras passé de supers moments, non ? ;-) Aude (quelle joie quand je t'ai vu arriver un soir de décembre aux « Pontons », le temps était vraiment moche, et je crois que j'aurais sombré dans une petite déprime sans toi !) ; Mathilde (on s'est vraiment bien marrées toutes les deux, tu as fait une excellente assistante de terrain !) ; Sylvie (qui n'a pas peur des scolopendres dans le duvet sur le toit du fort !), Diane & Lola (Diane, souviens toi au début t'étais pas très fière pour manipuler ces petites créatures, qui pourtant n'ont plus de secret pour toi aujourd'hui ! Souviens toi aussi de la tente canadienne…et de la vilaine branche de lentisque qui aura valut une bonne douche chaude à ton fidèle assistant !) ; Fab et Alban (les sauveurs de mes premiers jours de terrain seule sur Bagaud !) ; Joss (la peur de ma vie la nuit où tu as débarqué sur Bagaud sans prévenir !) ; Karen & Sylvain (c'était super sympa cette dernière nuit de terrain tous ensemble ; merci encore pour le layon de la batterie Nord Sylvain !) ; Vincent (je crois que tu m'en voudras toute ta vie pour ces tests comportementaux de nuit sur PC !) ; Jérôme & Lucie, toujours partants pour des petits aller-retours en zod' ; Cyrielle H. (il faut que tu me racontes ton tour du monde !) ; Jean-Louis C., j'ai appris l'art subtil du maniement de l'antenne VHF grâce à toi !

Merci à tous les rats noirs de Bagaud (>600 individus marqués, triturés, manipulés, auscultés) qui ont bien voulu se prêter au « jeu » ! Il faut dire qu'à la fin, la capture en valait la chandelle :

du bon beurre de cacahuète, un joli transpondeur sous-cutané « à la mode » et un splendide collier dernier cri ! Merci à mon duvet chaud, mes chaussures imperméables et mon lecteur mp3… Eléments indispensables afin d’affronter ces 113 nuits sur Bagaud, soit quasiment 4 mois passés sur cette île aux premiers abords inhospitalière, mais qui s’apprivoise avec le temps…Les splendides couchers et levers de soleils, véritables baumes au cœur, en valaient tellement le coup!







Autour du labo, il y a bien évidemment tout mon entourage proche :

Olive, en tant que parfait colocataire et ami, toujours à l’écoute et disponible pour n’importe quel coup de main. J’ai énormément apprécié tout ton soutien (jusqu’à la relecture dernière minute des parties de ma thèse et la vérification des références alors que j’étais au bout du rouleau; un vrai travail de fourmis !!). Finalement, on aura survécu dans ce bureau aux conditions climatiques quelque peu « drastiques » ! A ton tour maintenant, c’est la dernière ligne droite !

La fine équipe de puffinologues avertis, Karen, Elsa et Diane. Ces Drôles de Dames, comme dirait le Chef ;-) Karen, tu as été un autre pilier de ma thèse, tu m’as fait découvrir ces étranges créatures nocturnes que sont les puffins. Ces ambiances obscures, parfois très humides, perchés sur un minuscule bloc rocheux en falaise, à l’affût de retours d’oiseaux aux terriers, ont toutes été plus extraordinaires les unes que les autres. Même si la chasse n’était pas fructueuse (ces puffins peuvent parfois se montrer très discrets !), on rentrait toujours l’esprit paisible. Toutes ces longues discussions et la transmission de ton panel de connaissance sur ces oiseaux m’ont énormément enrichie. Un énorme merci à toi ! Elsa, même si nos travaux de terrain ne se sont que trop peu croisés, je garde en tête ta grande disponibilité, ton enthousiasme constant, et ces mots de soutien que tu as toujours su m’adresser quand il le fallait. Diane, voilà que tu prends la relève de nous toutes ! J’ai eu un très grand plaisir à travailler avec toi, et je garde d’excellents souvenirs de nos escapades de terrain, pleines de parties de rire et très souvent ponctués d’imprévus ! Ton grand intérêt pour la recherche et tes capacités indétrônables te conduiront très loin, ma Grande.

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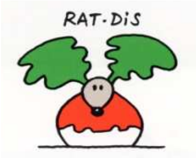
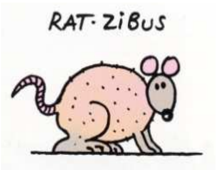
Autour d’une table, d’un thé ou au détour d’un couloir, il a toujours été très agréable d’échanger avec vous tous : Laurence, Erik & Marielle (la petite équipe de « fourmicologues » chevronnés), Annabelle R. (ma première colloc’ de bureau !), Jérémy, Elise, Fred G., Daniel, Philippe T., Mathieu, René, P.J. & Annabelle, Clémentine, Camille, Alex B, Pascal.





Et puis tous les amis, d’ici et d’ailleurs…

Les gars du Ch’Nord, expatriés aux quatre coin de la France et d’ailleurs, chez qui un clic-clac était toujours disponible pour m’héberger: Ade la lilloise ; Elo & David les parisiens (on reconnait les vrais amis lorsqu’ils vous hébergent, vous et vos 550 tubes de bouts de rats séchés pendant 3 semaines ;-) merci les amis, je viendrais à Bruxelles, promis, mais avec une bonne bouteille cette fois !) ; Audrey & Virgile et leur toute petite Cécile du Nord, le VRAI ! (il faudra que je lui apprenne quelques locutions locales du Sud à cette petite) ; Meuh & Guillaume les amiénois ; Bruns & Céline les bretons ; Anaïs, Elo & Cédric restés nordistes… Merci pour tous ces supers moments les amis, il y en aura encore beaucoup d’autres !

Les gars du Sud : ma Clairounette, Laure, Juju & Toinou et leurs petit Jedi (les copains de toujours - de la Galline ! - toujours partants pour une petite soirée, un apéro en terrasse après le boulot) ; Eve & Stephane et leurs bambins, Karine, Mel, Steph, Jypé, Jérém & Joseph (les copains de la fac, toujours de supers moments passés ensemble et j’espère encore beaucoup d’autres !) ; les cousins-cousines : Guillaume, Benja & Guylaine. Je vous adore tout simplement !

Ceux de l’Entre-deux : ma Puffinette (que de rigolade depuis que l’on se connait ! Et il y en aura encore, ma Belle. Va falloir qu’on monte notre propre labo, n’oublie pas), Marinouille, Emilie. Et Yann, tu as toujours été d’une grande écoute, tu as beaucoup apporté à ce travail, je n’ai pas perdu une miette de tous tes conseils ! Merci pour tout l’Ami !

Vient la famille : Mamounette & Papounet, Flo, Mamie Dédé et Mamie Jo, je vous dédie cette thèse, c’est en quelque sorte la votre. Je vous serai éternellement reconnaissante pour tout votre soutien, votre enthousiasme dans mes projets, les élans de motivation que vous m’avez insufflés lorsque les batteries étaient à plat, et tout simplement pour avoir été présents depuis que l’aventure a commencé, il y a 3 ans ½, et aussi durant ces 25 dernières années ! A la maison, la porte a toujours été grande ouverte, le week end, en semaine, c’est quand tu veux Ma Fille ! Toute cette bonne humeur qui règne à la maison, cette solidité des liens qui nous unit et cette sincérité ont contribué à former une famille synonyme d’amour, d’entre-aide, d’échanges et d’aventures !

Enfin, Vincent… l’avenir entier est devant nous, plein de délicieuses aventures…

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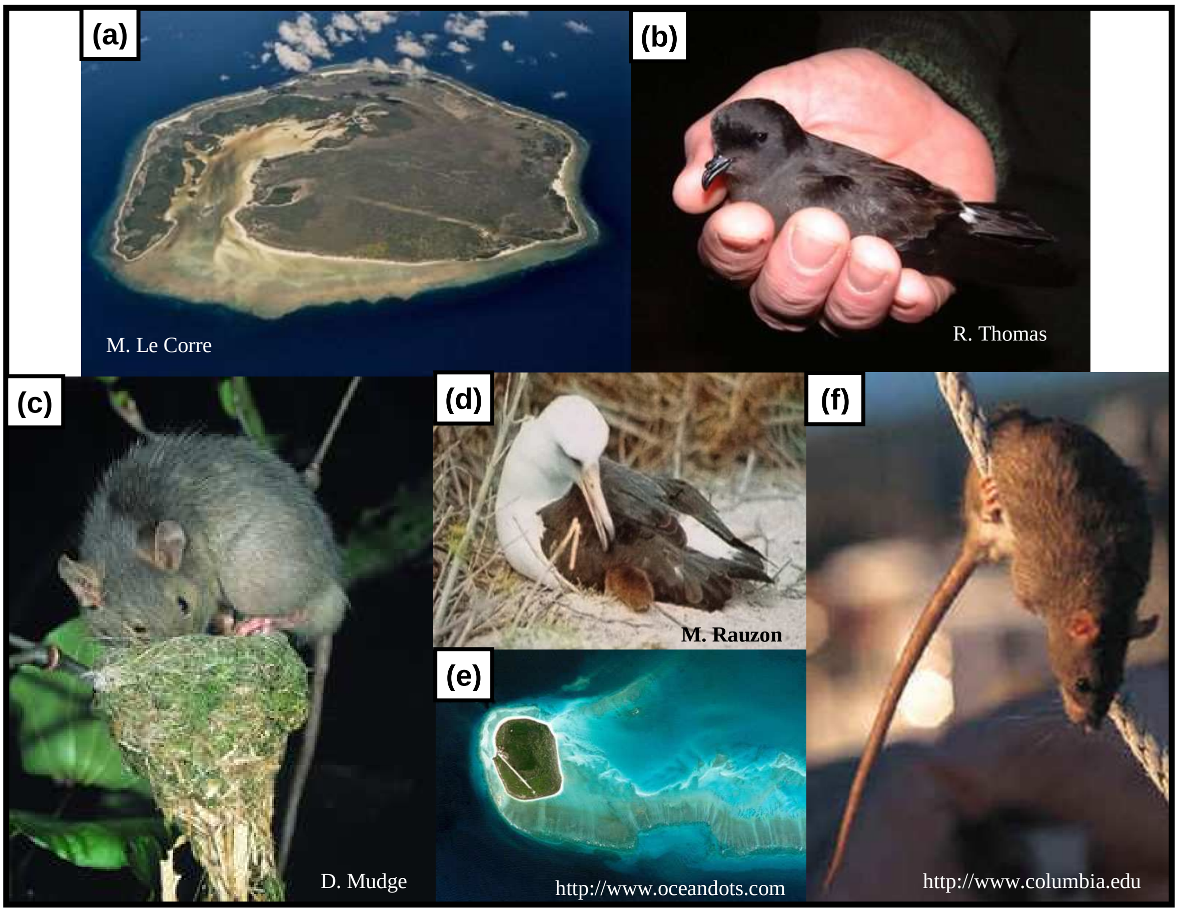
## INTRODUCTION GÉNÉRALE



(a) Ile Europa, Océan Indien ; (b) Océanite tempête *Hydrobates pelagicus*; (c) rat noir *Rattus rattus* ; (d) rat du Pacifique *R. exulans* s'attaquant à un albatros de Laysan *Diomedea immutabilis* sur l'île Midway ; (e) Ile de Grande Glorieuse, Océan Indien ; (f) rat surmulot *R. norvegicus*.

# 1. INTRODUCTION

## 1.1. Les invasions biologiques, une composante majeure du changement global

### 1.1.1. Définition et généralités

La référence à l'« Ère Homogocène » popularisée par Gordon Orians il y a plus de 20 ans est devenue aujourd'hui évocatrice d'une homogénéisation globale des écosystèmes, et le fruit d'une redistribution sans précédent des espèces à l'échelle mondiale (MacKinney & Lockwood 1999 ; Mack *et al.* 2000). L'essor considérable des échanges commerciaux et humains depuis plusieurs millénaires a permis aux espèces de franchir des barrières géographiques qui leur auraient été insurmontables sans l'aide de l'Homme, et contribue à l'accroissement des probabilités d'invasion d'espèces allochtones (Pascal *et al.* 2006). Une invasion biologique provoquée par l'Homme résulte de l'introduction délibérée ou non d'une espèce dans un milieu dont elle n'est pas naturellement originaire. Cette espèce doit alors pouvoir se reproduire de manière pérenne et autonome, se propager dans son nouvel environnement et occasionner des perturbations au fonctionnement de son écosystème d'accueil pour qu'elle soit considérée comme « invasive » (« invasive species », selon la définition de l'ISSG) ; on parle aussi d'espèce « alien ». Soixante ans après que Charles Elton (1958) a fait émerger les premières mises en garde face aux « méfaits » environnementaux engendrés par les invasions biologiques, l'intérêt pour ce phénomène en pleine expansion s'est accru, si bien que les invasions biologiques font partie des cinq composantes majeures du changement global (Sala *et al.* 2000) et sont considérées à l'heure actuelle comme la seconde cause d'érosion de la biodiversité à l'échelle mondiale (Vitousek *et al.* 1997 ; Mooney & Cleland 2001 ; Clavero & Garcia-Berthou 2005).

### 1.1.2. Quels sont les facteurs qui prédisposent les espèces à l'invasion ?

Toutes les espèces introduites par l'Homme ne deviennent pas envahissantes et n'occasionnent pas des dommages aux communautés indigènes (Williamson & Fitter 1996). Définir et prédire les traits biologiques qui prédisposent une espèce à réussir une invasion reste cependant difficile, notamment du fait de la méconnaissance des causes de la majorité des cas d'échecs. Face à la complexité des processus qui gouvernent le succès d'invasion d'une espèce dans un nouvel environnement (e.g. Colautti *et al.* 2004), les recherches se sont jusqu'alors plus longuement attardées à identifier des facteurs corrélatifs au succès ou à l'échec d'une invasion (e.g. Williamson & Fitter 1996 ; Veltman *et al.* 1996). Ainsi, certaines caractéristiques intrinsèques des espèces semblent être liées à l’amplitude de leur niche écologique (i.e. capacité à exploiter des ressources, habitats et environnements variés ; Vazquez 2005 ; Jeschke & Trayer 2006 ; Blackburn *et al* . 2009), la plasticité écologique (Sol *et al*. 2002) et/ou trophique (Caut *et al*. 2008) des individus (i.e. capacité à changer de préférences alimentaires ou d’habitats), des stratégies de reproduction adaptées à une expansion rapide (Drake *et al*. 1989), le comportement exploratoire du nouveau territoire (Russell *et al*. 2010), la variance génétique de la « population » nouvellement arrivée (Baker & Stebbins 1965 ; Lee 2002), et enfin les capacités des espèces à répondre rapidement aux pressions de sélection naturelle (Lee 2002). D’autres facteurs extrinsèques ont été identifiés comme favorisant l’invasion, à savoir l’absence de prédateurs, compétiteurs et pathogènes dans l’environnement nouvellement colonisé (Brooke *et al*. 1995 ; Cincotta *et al*. 2009).

### 1.2. Vulnérabilité des écosystèmes insulaires aux invasions biologiques

Les îles, d’origine océanique ou continentale, ont évolué en isolement pendant des dizaines, centaines de milliers voire millions d’années. Ces systèmes hébergent une richesse spécifique faible, un fort taux d’endémisme ainsi que des réseaux trophiques simplifiés (Cronk 1997 ; Denslow 2001 ; Drake *et al.* 2002). Ces trois particularités confèrent aux îles une grande vulnérabilité aux invasions biologiques et notamment aux extinctions d’espèces de vertébrés autochtones (Amori *et al*. 2008 ; Sax & Gaines 2008 ; Berglund *et al*. 2009). En effet, les invasions biologiques sont rendues responsables de près de la moitié des extinctions de vertébrés survenues depuis 1600. Parmi elles, 90% des 30 espèces de reptiles et amphibiens (Honegger 1981), 93% des 176 espèces et sous-espèces d’oiseaux (King 1985) et 81% des 65 espèces de mammifères (Ceballos & Brown 1995) reconnues éteintes durant cette même période étaient des formes insulaires.

Les organismes adaptent leurs traits d’histoire de vie et leurs comportements en fonction de signaux environnementaux (e.g. caractéristiques des sites de reproduction, risque de prédation, interactions intra- et inter-spécifiques), qui les guident vers la sélection d’habitats de bonne qualité, maximisant ainsi leur succès reproducteur et leur survie (Schlaepfer *et al*. 2002). Dans certains cas, l’altération brusque de certains facteurs environnementaux par l’Homme n’engendrerait pas automatiquement de réponse adaptative des individus pour faire face à cette nouvelle menace (Schlaepfer *et al*. 2002 ; Battin 2004 ; Robertson & Hutto 2006). Cela peut ainsi générer des « pièges évolutifs » chez les espèces qui subissent ces changements dont le comportement et les traits d’histoire de vie deviendraient subitement mal adaptés au nouveau contexte environnemental et mettraient en péril leur persistance sur le long terme. Les espèces insulaires sont particulièrement vulnérables à ces pièges évolutifs causés par les espèces invasives (Schlaepfer *et al*. 2005) car elles ont souvent évolué en l'absence de fortes contraintes de compétition, prédation, herbivorie ou parasitisme. C'est pourquoi la plupart d'entre elles n'ont pas développé de capacités de dispersion élevées ni de systèmes de défense contre les prédateurs ou pathogènes, et ont adopté des stratégies de reproduction lentes avec une fécondité réduite (Williamson 1996). Par exemple, chez les espèces d'oiseaux marins qui se reproduisent exclusivement sur des îles, ces zones insulaires constituaient par le passé un refuge contre les prédateurs terrestres que l'on pouvait rencontrer sur le continent. Leur degré de fidélité aux sites de reproduction et partenaires étant donc forts et leurs capacités de défense contre les prédateurs limitées (Burger & Gochfeld 1994), ces oiseaux, surtout les pétrels et puffins, apparaissent fortement enclins aux pièges évolutifs (Igual *et al*. 2007).

Les mammifères figurent parmi le groupe d'espèces qui ont été largement introduites sur les îles de la Planète par l'Homme, à des fins alimentaires (e.g. porcins, bovins, ovins, cervidés, rat du Pacifique), de contrôle d'autres espèces envahissantes (e.g. chats, mustélidés), de loisirs pour la chasse (cervidés, lapins), en tant qu'animal de compagnie (e.g. chats, chiens), ou de manière involontaire (e.g. rats, souris), et représentent ainsi une menace majeure pour les espèces indigènes des îles (Courchamp *et al*. 2003). L'exemple frappant de l'introduction volontaire de deux chats sur l'archipel des îles Kerguelen qui conduisit en 30 ans au développement d'une population de chats de 3500 individus, et à l'élimination de 1,2 millions d'oiseaux par an (Pascal 1980) illustre parfaitement l'ampleur de la menace que représentent les prédateurs introduits pour les espèces animales indigènes. Les effets des invasions peuvent être relativement simples (e.g. prédation directe sur l'espèce indigène) ou très complexes (e.g. synergie entre plusieurs espèces introduites, cascades trophiques). Ainsi la compréhension des mécanismes d'impact des espèces introduites, la prédiction des effets des invasions biologiques et la mise en place d'opérations de conservation adaptées et efficaces dépendent étroitement de la complexité des réseaux trophiques « envahis », c'est-à-dire le nombre d'espèces introduites et la nature des interactions qu'elles ont tissées avec les espèces indigènes mais aussi avec les autres espèces introduites (Rayner *et al*. 2007 ; Witmer *et al*. 2007 ; Caut *et al*. 2009 ; Dowding *et al*. 2009).

## 1.3. Les rongeurs introduits du genre *Rattus* : écologie, répartition géographique, dynamique de population et impacts sur les écosystèmes insulaires

### 1.3.1. Description générale

Sur les 66 espèces de rats du genre *Rattus* (famille Muridés, sous-famille Murinés) décrites à ce jour, cinq d'entre elles ont été introduites sur les îles par l'Homme : *R. rattus* (Linné 1758), *R. norvegicus* (Berkenhout 1769), *R. exulans* (Peale 1848), *R. praetor* (Thomas 1888), *R. tanezumi* (Temnick 1844). La taxonomie est souvent rendue compliquée par l'existence de nombreuses dénominations associées à ces cinq espèces (e.g. 49 pour *R. exulans*, plus de 150 pour *R. rattus* et *R. tanezumi* réunis; Musser & Carlton 2005). D'autres espèces de rongeurs ont également été introduites au cours de l'histoire de colonisation des îles par l'Homme, mais, mis à part *Mus musculus*, elles n'ont pas largement été répandues sur les îles de la Planète (Aplin *et al*. 2003). *R. rattus* (rat noir, rat des champs, « ship rat »), *R. norvegicus* (rat brun, rat des villes, rat surmulot, « Norway rat ») et *R. exulans* (rat du Pacifique, rat polynésien, « kiore ») sont les trois espèces de rats considérées comme ayant le potentiel envahissant le plus fort, et qui occasionnent de sévères dommages aux faunes et flores insulaires des îles où ils ont été introduits (Atkinson 1985 ; Courchamp *et al*. 2003 ; Jones *et al*. 2008).

### 1.3.2. Ecologie des *Rattus* spp. introduits sur les îles

Les trois espèces de rats introduits du genre *Rattus* présentent des écologies relativement distinctes. Sur les îles, elles occupent des milieux très variés comme les milieux agricoles, forestiers, côtiers, de pelouse, de mattoral, perturbés et urbains (Musser & Carlton 2005). Le rat noir (son poids adulte excède rarement 230-250g) est considéré comme l'espèce la plus généraliste dans la sélection de son habitat (Harper *et al*. 2005), avec cependant une préférence pour les milieux secs et tempérés. C'est un rongeur arboricole très agile, mais qui adopte facilement un mode de vie terrestre en nichant, s'abritant et se reproduisant dans des terriers ou sous des buissons bas (Musser & Carlton 2005). En région méditerranéenne, où la température extérieure reste douce durant l'année, il vit en dehors des habitations et a établi des populations strictement non commensales (Cheylan 1988 ; Faugier & Pascal 2006). Cette espèce possède également un spectre alimentaire très large (Fall *et al*. 1971 ; Daniel 1973 ; Clark 1981 ; Campbell *et al*. 1984 ; Moors 1985 ; Miller & Miller 1995 ; Quillfeldt *et al*. 2008) et une plasticité alimentaire qui a été fortement suggérée comme favorisant sa survie sur les petites îles, où les contraintes trophiques sont souvent drastiques (Clark 1981 ; Cheylan 1988 ; Caut *et al.* 2008). Ainsi, il a été montré, sur certaines îles, que le rat noir pouvait changer de ressources de manière opportuniste afin de compenser l'absence temporaire d'une ressource principale (e.g. oiseaux marins ; Fleet 1972 ; Caut *et al.* 2008).

Le rat surmulot (poids adulte : 350-450 g), quant à lui, affectionne les milieux humides et sa présence sur les îles est plus nettement liée à la présence permanente d'eau douce (Musser & Carlton 2005). Ce rongeur affectionne particulièrement les milieux urbanisés, où il a trouvé une « niche écologique » en étroite proximité des habitations. Enfin, le rat du Pacifique (poids adulte < 130 g) préfère les milieux bien végétalisés et drainés, où il est étroitement associé aux activités humaines (Marshall 1977). Rats noirs et surmulots se rencontrent dans des écosystèmes contrastés et à des latitudes très variées, à l'exception de l'Antarctique, alors que le rat du Pacifique reste cantonné à l'Asie du Sud Est et sur les îles du Pacifique, de la Mélanésie à l'île de Pâques en passant par l'archipel d'Hawaii. 12% des groupes majeurs d'îles mondiaux hébergent simultanément les trois espèces (Atkinson 1985). Leur présence conjointe sur les îles et leur coexistence au sein de mêmes habitats semblent être fortement régies par des relations interspécifiques de compétition (Russell & Clout 2004).

### 1.3.3. Histoire de colonisation des îles et répartition géographique actuelle

Plus de 80% des principaux groupes d'îles de la Planète hébergent au moins une des trois espèces de rats introduits (Atkinson 1985). Leur diffusion par l'Homme sur les îles de la Planète a débuté à des périodes distinctes et selon des schémas différents pour chaque espèce. Le complexe *R. rattus* comprend plusieurs lignées phylogénétiques, toutes issues du sud et sud-est de l'Asie (K. Aplin non publié[1]). De la forme asiatique ancestrale ($2n = 42$ chromosomes) ont évolué plusieurs lignées composées de deux autres formes caryotypiques ($2n = 40$ et $2n = 38$ chromosomes ; Yosida 1980 ; Baverstock *et al.* 1983). Seules les populations à $2n = 38$ (forme océanique) et $2n = 42$ (forme asiatique) ont été introduites par l'Homme sur un grand nombre d'îles. Une des formes asiatiques, *R. r. tanezumi*, a probablement été introduite à la période préhistorique aux Philippines, au Japon (îles Amami), en Indo-malaisie (îles Sulawesi),

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[1] Aplin K. Prehistory of the world's greatest pest, the black rat (*Rattus rattus*), based on a global survey of its mitochondrial DNA. Résultats presents à la Conference ANU Archaeological Science 2008 à l'Université Nationale Australienne, Camberra, non publié.

Micronésie et Nouvelle Guinée (Matisoo-Smith & Robins 2004), et récemment élevée au rang d'espèce (*R. tanezumi* ; Musser & Carlton 2005). La forme océanique, originaire du sud de la péninsule indienne (Sri Lanka) correspond, quant à elle, aux populations de rats noirs qui ont été introduites sur la plupart des îles des trois principaux océans (Yosida 1980). Bien qu'un représentant de la forme océanique datant de 20 000BP ait été identifié au Moyen Orient (Tchernov 1968), le rat noir ne semble pas avoir atteint le pourtour méditerranéen avant 8 000BP pour la Palestine (Tchernov 1986 ; mais cette date est toujours en débat ; Armitage *et al.* 1984 ; Audouin-Rouzeau 1999) ou 3500BP pour la Mésopotamie (Ervynck 2002). Puis, durant la période romaine, et profitant de l'essor des échanges humains et commerciaux, il aurait été largement transporté sur les rivages et les îles de l'ensemble du bassin Méditerranéen (Ruffino *et al.* sous presse ; voir aussi **Partie 2.1.**), ainsi qu'en Europe continentale, jusqu'en Grande Bretagne (Armitage 1984 ; Audouin-Rouzeau & Vigne 1996), en voyageant « clandestinement » par bateaux. L'implantation du rat noir en Europe occidentale semble prendre son essor dès le XI$^{ème}$ siècle, période à laquelle les évènements les plus ravageurs de la peste sévirent (Audouin-Rouzeau 1999). Sa diffusion depuis l'Europe vers les océans atlantique et indien débuta sporadiquement à la fin du XV$^{ème}$ siècle avec la période des grandes découvertes, puis s'intensifia, notamment dans le Pacifique, dès le milieu du XIX$^{ème}$ siècle pour atteindre son apogée au milieu du XX$^{ème}$ siècle (Atkinson 1985).

Le rat polynésien semble trouver son origine dans la région indo-malaise (Matisoo-Smith & Robins 2004). Bien que l'histoire de colonisation des îles de l'Océanie Proche par l'Homme se soit amorcée très tôt, dès 40 000BP (Green 1991), aucun indice de présence du rat du Pacifique sur ces îles n'est identifié avant l'Holocène (Flannery 1995). Son introduction sur les îles vers l'Est du Pacifique ne débuta visiblement qu'il y a environ 3 500 ans, en relation avec les mouvements des peuples de culture Lapita et de langue austronésienne (Matisoo-Smith *et al.* 1998). Les restes archéozoologiques de rats du Pacifique apparaissent dans tous les contextes archéologiques correspondant aux peuples Lapita et polynésiens, même au niveau des contextes les plus anciens (Matisoo-Smith *et al.* 1998 ; Matisoo-Smith & Robins 2004), notamment sur les archipels des Samoa, Tonga et Fidji (~3 000BP), puis sur les îles Marquises et Hawaii (1 000-800BP), et sur l'île de Pâques (800-600BP ; Barnes *et al.* 2006). Durant les premières phases de colonisation des peuples Lapita et polynésiens, le rat du Pacifique aurait été volontairement introduit (Matisoo-Smith & Robins 2004), probablement en tant que source de nourriture comme l'ont été d'autres espèces (coqs, cochons ; Matisoo-Smith *et al.* 1998).

L'introduction du rat surmulot sur les îles a débuté bien plus tard que pour les deux autres espèces de rats. Cette espèce est originaire d'une région voisine du sud de la Sibérie et du nord de la Chine. Son arrivée en Europe centrale est tardive, vers le début du XVIII$^{\text{ème}}$ siècle (Atkinson 1985). Cependant, une fois implanté dans les ports européens, il fut transporté par les bateaux sur un grand nombre d'îles des trois océans majeurs.

### 1.3.4. Dynamique de population des *Rattus* spp. sur les îles

Chez la plupart des espèces opportunistes à stratégies de reproduction rapide, comme les rongeurs généralistes, les fluctuations de dynamique de population sont régulées à la fois par le contrôle exercé par un ou plusieurs prédateur(s) (forces dites « top-down »), et par la variation de la disponibilité et de l'abondance des ressources (forces dites « bottom-up ») (Korpimaki & Norrdahl 1998 ; Blackwell *et al.* 2001 ; Efford *et al.* 2006). Sur les îles où, en l'absence de prédateurs, les trois espèces du genre *Rattus* figurent parmi les consommateurs de dernier ordre, la disponibilité et l'abondance des ressources conditionnent fortement la dynamique de population des rats. En particulier, plusieurs auteurs comme Clark (1980) et Moller & Craig (1987) remarquent l'influence récurrente et forte de la saisonnalité sur certains paramètres populationnels comme l'abondance des populations ou la période de reproduction. En zone tempérée, la saisonnalité de la dynamique des populations insulaires de rats est marquée par l'arrivée de conditions printanières plus clémentes et l'apparition concomitante de ressources abondantes (Cheylan & Granjon 1985 ; Miller & Miller 1995). En zone tropicale ou aride, l'apport d'eau douce par les fortes précipitations saisonnières, en accroissant notamment la productivité primaire du milieu, est reconnu pour être un facteur déclenchant la reproduction chez *R. rattus* (Clark 1980). Par ailleurs, les capacités des populations insulaires de rats noirs à répondre rapidement à une augmentation soudaine de l'abondance des ressources ont récemment été démontrées de manière expérimentale par Harris & MacDonald (2007). Ainsi, l'apport artificiel de ressources supplémentaires dans le milieu s'est traduit chez les populations de rats noirs des Galapagos par un accroissement de leurs abondances, une augmentation de la masse corporelle des femelles et un allongement de la période de reproduction. Globalement, trop peu d'études s'appuient sur un suivi des populations insulaires de rats sur le long terme (i.e. plusieurs saisons ou années) afin d'identifier les facteurs influençant leurs variations spatio-temporelles. Par contre, l'apport épisodique de ressources exogènes induit par les précipitations intenses (Madsen & Shine 1999 ; Brown & Ernest 2002), ou endogènes, par les « pluies de graines ou de fruits » (Choquenot & Ruscoe 2000) et émergences d'insectes (Marcello *et al.* 2008) ont été identifiées pour avoir un effet significatif sur les populations d'autres rongeurs introduits (*M.*

*musculus*) ou de petits mammifères non introduits (e.g. *Peromyscus* spp., *Rattus* sp., *Dipodomys* spp., *Tamiasciurus* sp., *Sciurus* sp.).

### 1.3.5. Impacts des rats sur la biodiversité insulaire

Du fait de leur comportement opportuniste, leur régime polyphage et leur répartition ubiquiste, les trois espèces de rats introduits ont exercé et exercent toujours de lourds impacts sur les communautés de faunes et flores indigènes des îles où ils ont été introduits. Les rats sont des prédateurs d'un large spectre de groupes d'espèces, comme les invertébrés (Clout 1980 ; Ruffaut & Gibbs 2003 ; Myer & Shiels 2009), reptiles (Towns 1994 ; Towns *et al.* 2007), amphibiens (Whitaker 1978), oiseaux terrestres (Penloup *et al*. 1997 ; Robinet *et al*. 1998 ; Innes *et al*. 1999) et marins (Jones *et al*. 2008), ainsi que les mammifères volants (Fellers 2000). Leurs impacts sur la faune indigène des îles se manifestent également au travers de processus de compétition pour les ressources avec les communautés de petits mammifères (Harris 2009) et d'oiseaux (Clark 1981), et la transmission de pathogènes contre lesquels la faune indigène n'est pas adaptée (Wyatt *et al*. 2008). La flore indigène des îles est affectée par le comportement herbivore des rats (Clark 1981; Grant-Hoffman & Barboza, sous presse), via notamment la prédation sur les graines et l'altération de la régénération des plantules (Allen *et al*. 1994 ; Shaw *et al*. 2005). Les effets délétères des rats sur les communautés insulaires peuvent être favorisés et accentués par la présence d'une source de nourriture alternative qui permettrait aux rats de survivre sur les îles lorsque la proie indigène principale est temporairement absente (cas des lapins introduits sur Whale Island, Nouvelle Zélande : Imber *et al*. 2000 ; cas des émergences de tortues vertes sur l'île Surprise, Nouvelle Calédonie : Caut *et al*. 2008).

Les effets des rats sur les faunes insulaires prennent parfois une ampleur dramatique, conduisant très rapidement certains taxons endémiques à l'extinction totale. L'un des exemples les plus frappants est représenté par le cas de Big South Cape Island en Nouvelle Zélande (Atkinson 1985). Arrivé accidentellement en 1964, le rat noir causa en deux années la disparition de plus de 40% de l'avifaune locale ainsi que l'extinction complète d'une espèce et une sous-espèce de chauve souris. De même, l'invasion de Lord Howe Island, à l'est de l'Australie, par le rat noir, suite à l'échouage d'un paquebot en 1918, engendra en cinq ans l'extinction locale de cinq espèces d'oiseaux forestiers (Atkinson 1985). En 1943, deux espèces d'oiseaux disparurent définitivement de l'île de Midway, 18 mois après l'arrivée du rat noir par cargo militaire (Atkinson 1985). Les rats ont provoqué ou contribué aux disparitions locales d'autres taxons animaux, notamment de vertébrés. Cependant, même si la relation de cause à effet entre l'arrivée du rat et l'extinction d'espèces insulaires apparait claire dans les trois exemples cités, la plupart des cas d'extinctions locales imputés aux rats restent circonstanciels et basés sur la découverte de restes subfossiles et la comparaison de patrons de distribution passés et présents (Towns *et al.* 2006 ; Ruffino & Vidal, en préparation ; voir aussi **Partie 3.4.**). De plus, les taux d'extinctions d'invertébrés liées pour partie ou intégralement aux effets des rats sont certainement sous-estimés du fait d'une mauvaise connaissance des faunes invertébrées sur certaines îles et du manque de données sur les patrons de distribution de la plupart des espèces invertébrées. Globalement, la compréhension des déterminismes d'extinctions est rendue compliquée par les effets synergiques et cumulatifs d'autres facteurs de risque (e.g. effets d'autres prédateurs ou compétiteurs introduits, impact de l'Homme, changement climatique ; Steadman 2006)

### 1.3.6. Impacts des rats sur l'avifaune marine des îles

En échos à la crise d'érosion de la biodiversité insulaire, et au regard du statut de conservation UICN alarmant des oiseaux marins (Butchard *et al.* 2004), un intérêt croissant a porté sur l'identification des facteurs de menaces et de risques majeurs d'extinction des oiseaux marins (Burger & Gochfeld 1984 ; Atkinson 1985 ; Butchard *et al.* 2004). Une littérature extensive existe notamment sur les effets négatifs des rats sur les oiseaux marins (voir la synthèse de Jones *et al.* 2008). Ainsi, Jones *et al.* (2008) ont répertorié 61 îles réparties dans tous les océans du monde, excepté l'Arctique et Antarctique, où au moins l'une des trois espèces de rats affecte ou a affecté au moins une espèce d'oiseau marin. Les trois espèces de rats introduits sont reconnus pour avoir un spectre d'impact sur les oiseaux marins très large, depuis des espèces de très petite taille et « cryptiques » comme le pétrel tempête (*Hydrobates pelagicus*, poids moyen = 23-29g) jusqu'à des espèces beaucoup plus massives comme l'albatros de Laysan (*Phoebastria immutabilis*, poids moyen = 2 855g). Le degré de vulnérabilité de l'oiseau dépend étroitement de la propension des rats à affecter tous les stades démographiques (œuf, poussin, adulte) et notamment le stade adulte. Ainsi, un oiseau de taille équivalente ou de plus petite taille que celle d'un rat serait fortement vulnérable à la prédation et plus enclin à un déclin majeur de ses populations (Imber 1984). De plus, il arrive fréquemment que les parents laissent leur unique œuf ou leur jeune poussin vulnérable sans surveillance dans leur terrier pour aller se nourrir. La prédation exercée par les rats est un phénomène cryptique, qui se déroule en général la nuit, souvent au fond de terriers ou cavités profondes. De ce fait, son observation et sa quantification sont rendues particulièrement difficiles. L'estimation de l'intensité avec laquelle les rats affectent les populations d'oiseaux marins est alors facilitée par la comparaison de paramètres démographiques des populations d'oiseaux avant et après éradication ou contrôle local des populations de rats de l’île (Towns *et al.* 2006 ; Ruffino & Vidal, en préparation). Par exemple, le succès reproducteur du pétrel de Cook *Pterodroma cookii* passa de 0.05 poussin.couple$^{-1}$ avant éradication du rat du Pacifique à 0.53 poussin.couple$^{-1}$ l’année suivant l’éradication (Rayner *et al.* 2007). La suppression du prédateur introduit peut également conduire à la recolonisation de sites délaissés par les oiseaux (Whitworth *et al.* 2005). Enfin, l’effet négatif des rats sur les populations d’oiseaux marins peut également avoir des répercutions en chaine sur les autres compartiments de l’écosystème, à savoir les communautés végétales littorales (Kurle *et al.* 2008) ou d’insectes (Towns *et al.* 2009) inféodées aux apports de nutriments d’origine marine transportés par les oiseaux marins, en réduisant ces apports extérieurs, et bouleversant ainsi l’équilibre trophique des communautés insulaires.

### 1.4. Problématique et plan de la thèse

Comme le soulignent les précédents éléments, les trois espèces de rats introduits figurent aujourd’hui en ligne de mire des gestionnaires, scientifiques, et tous autres acteurs de la lutte pour la conservation de la biodiversité insulaire menacée, et en particulier des oiseaux marins. L’impact généralisé et largement accepté des trois espèces de rats introduits sur les oiseaux marins fait échos aux estimations de risques d’extinction annoncées par l’UICN pour lesquels les rats sont identifiés comme un facteur de vulnérabilité majeur et de risque d’extinction chez 70% des espèces de pétrels et puffins (Famille des Procellariidae) classées par l’UICN en 2008 comme « globalement menacées » (effectif total = 40 espèces oiseaux). Ainsi, à l’heure actuelle, les rats portent clairement l’étiquette de prédateurs très efficaces et néfastes d’oiseaux marins. Or, le fonctionnement des populations insulaires de rats ainsi que les facteurs favorisant leurs impacts sur les îles restent encore mal connus. De plus, les rats sont avant tout des animaux crépusculaires ou nocturnes, et le phénomène de prédation en lui-même, tout aussi élusif que fugace, est rarement observé en milieu naturel, et difficilement quantifiable, notamment pour certains groupes d’oiseaux marins aux mœurs très discrètes, nichant dans des zones peu accessibles, en falaises abruptes et à l’intérieur de terriers ou cavités profondes. De ce fait, malgré la variété de cas d’étude (contextes insulaires et expérimentaux) dont nous disposons sur les effets négatifs des rats sur les oiseaux marins, de récents questionnements ont émergé relatifs aux lacunes de nos connaissances portant sur les mécanismes réels d’impact du rat, et sur les difficultés rencontrées dans une évaluation robuste de l’intensité de cet impact sur des oiseaux aux mœurs aussi discrètes que certains oiseaux marins.

L’idée générale de ce travail de thèse s’inscrit dans la nécessité d’une meilleure compréhension de l’écologie, de la dynamique des populations des rongeurs introduits mais aussi des mécanismes d’impact du rat sur les oiseaux marins et de leurs interactions, afin de contribuer à la construction de bases scientifiques solides en vue d’une meilleure évaluation du degré de vulnérabilité des espèces et de la mise en place de stratégies de conservation pertinentes et efficaces. Parmi les pistes de recherche qui ont été jusqu’à présent peu approfondies, pourtant susceptibles de conduire à une amélioration de la qualité de nos connaissances et estimations, nous avons identifié trois axes majeurs visant à : (1) mieux comprendre les effets des introductions anciennes de rats sur le long terme, et plus particulièrement les mécanismes favorisant la persistance de certaines espèces d’oiseaux marins en présence de rats, (2) éclaircir les patrons d’interactions entre rats et oiseaux marins et mieux évaluer les déterminismes et mécanismes du phénomène de prédation, (3) accorder plus d’intérêt au fonctionnement des populations de rats insulaires, et notamment leurs écologie et dynamique de populations, afin d’identifier les facteurs intrinsèques et extrinsèques susceptibles de favoriser leur maintien sur des îles où les ressources sont souvent imprédictibles et dont la disponibilité varie dans le temps et l’espace.

Dans le cadre de ces recherches, nous nous sommes focalisés sur le bassin méditerranéen qui présente plusieurs caractéristiques favorables. Tout d’abord, le bassin méditerranéen représente un vaste secteur insulaire aux contextes biogéographiques variés, où l’introduction du rat noir, espèce considérée comme l’une des espèces de mammifères les plus dévastatrices sur l’avifaune marine, a été ancienne (datant de l’époque romaine) et généralisée. En outre, il s’agit d’une région d’étude hautement privilégiée car, contrairement à d’autres régions insulaires susceptibles d’avoir été précocement colonisées par le rat noir au cours de sa diffusion depuis le sous-continent indien (e.g. archipels du sud et sud-est de l’Asie), de nombreuses données sont disponibles en Méditerranée, non seulement sur la présence ancienne du rat noir et des oiseaux sur les îles, mais aussi sur leurs statuts actuels. Par ailleurs, de manière intrigante au regard du statut critique mondial des Procellariidés, les quatre espèces de pétrels et puffins endémiques et sous-endémiques de Méditerranée semblent s’être maintenues sur le long terme, au moins sur une partie des îles, malgré une introduction ancienne du rat noir. Enfin, le bassin Méditerranéen, comme beaucoup d’autres secteurs insulaires au monde, subit depuis les dernières décennies une intensification des activités humaines, qui mettent en péril, de manière directe (destruction d’habitats, dérangement, chasse) et indirecte (introduction multiple d’espèces, favorisation de l’accroissement démographique de certaines pestes écologiques), les espèces natives des îles, et plus particulièrement les oiseaux marins.

Les différents chapitres de la thèse s’articulent de la manière suivante :

La prise en compte de la dimension temporelle des introductions sur les îles est cruciale pour une meilleure compréhension des interactions observées entre espèces natives et introduites, des processus d’extinctions d’espèces passés mais aussi des mécanismes mis en jeu dans leur persistance, et fournit ainsi des éléments de comparaison et de prévention de risques futurs (Morrison 2002 ; Steadman 2006 ; Strayer *et al.* 2006). C’est pourquoi, l’une des premières étapes de cette thèse a été de réunir l’ensemble des informations disponibles (essentiellement archéozoologiques) sur l’arrivée ancienne du rat noir sur les îles méditerranéennes afin de mettre en avant l’intérêt fort que représente le contexte insulaire méditerranéen pour l’évaluation des effets sur le long terme des rats introduits sur les communautés indigènes de ces îles (**Partie 2.1.**).

L’analyse des patrons de distribution des espèces à une large échelle permet d’éclaircir leurs patrons d’interactions et de pointer du doigt les facteurs déterminants la répartition géographique des espèces (Yom-Tov *et al.* 1999 ; Martin *et al.* 2000 ; Russell & Clout 2004 ; Deleon *et al.* 2006). Dans la partie 2 du chapitre 2, nous avons travaillé à l’échelle du bassin méditerranéen occidental où nous avons abordé les interactions entre rats et oiseaux marins par un bilan complet des connaissances qui étaient disponibles sur la distribution du rat noir, la distribution et les abondances des quatre espèces et sous-espèces de puffins et pétrels endémiques de méditerranée sur environ 300 îles et îlots, et également par une synthèse bibliographique des mentions d’impact de rats sur les quatre taxa d’oiseaux en Méditerranée. Les principaux objectifs de ce volet d’étude ont été (1) d’identifier si, après une présence ancienne et prolongée du rat noir sur les îles, sa présence actuelle constituait un facteur limitant dans la présence ou les abondances d’oiseaux à l’échelle du bassin méditerranéen occidental, et (2) de bénéficier de l’existence de contextes insulaires variés pour chercher à mettre en évidence des zones de cantonnement des populations d’oiseaux marins sur des sites qui permettraient de limiter les interactions avec les prédateurs introduits (**Partie 2.2.**).

Le troisième chapitre s’attache à mieux comprendre les mécanismes d’interactions aux terriers d’oiseaux marins, les capacités de prédation des rats et leurs impacts au travers de différents axes de recherche. Dans le cadre des deux premières parties de ce chapitre, nous nous sommes focalisés sur l'étude fine des interactions entre rats noirs et une espèce de puffin endémique de Méditerranée à nidification hypogée, le puffin yelkouan *Puffinus yelkouan*, sur une île (Parc National de Port-Cros, sud-est de la France) où les abondances de population de cet oiseau semblent être relativement stables depuis une vingtaine d'années (Vidal 1985 ; IMEP données non publiées), malgré une présence ancienne supposée du rat noir. L'étude des interactions aux terriers entre rats et puffins s'est effectuée dans deux contextes écologiques différents : (1) au démarrage d'une opération de contrôle d'un prédateur apical introduit, le chat haret *Felis catus*, sur l'île de Port-Cros, et en situation de densités modérées de rats noirs sur l'île (**Partie 3.1.**), et (2) après le contrôle du prédateur apical sur Port-Cros, où l'on suppose un changement des abondances de rats ou de leur comportement de prédation (Courchamp *et al*. 1999 ; Hugues *et al.* 2006 ; Rayner *et al*. 2007), et donc de la nature et intensité des interactions avec les puffins (**Partie 3.2.**).

La prédation par les rats est souvent un phénomène cryptique, difficilement observable et quantifiable. La compréhension des déterminismes et mécanismes de prédation est alors facilitée par la mise en place d'expérimentations en situation contrôlée (Prieto *et al*. 2003 ; Meyer & Shiels 2009). Ainsi, par l'utilisation de tests comportementaux sur individus sauvages, nous avons évalué la capacité des rats noirs à casser et consommer des œufs dont la taille et l'aspect étaient assimilables à ceux d'oiseaux marins de petite et moyenne taille, en mesurant les effets relatifs à la taille de l'œuf et son état, la masse corporelle des rats, leur sexe ainsi que leur habitat d'origine (**Partie 3.3.**).

Dans le cadre de la quatrième partie de ce chapitre 3, nous nous sommes attachés à réunir et analyser les articles scientifiques publiés depuis les 30 dernières années portant sur l'impact des trois espèces de rats introduits sur les oiseaux marins des îles de la Planète, dans le but de faire le point sur l'ensemble des méthodologies employées pour évaluer l'impact des rats, de pointer du doigt les faiblesses associées à chaque méthodologie ainsi que les manques dans notre recherche, et enfin de préconiser des perspectives de recherche dans le but d'améliorer la compréhension des mécanismes d'impact et sa quantification (**Partie 3.4.**). Même si la littérature foisonne de mentions et études d'impact des rats introduits sur les communautés d'oiseaux marins, les mécanismes mis en jeu et l'intensité des interactions sont souvent encore mal connus (Towns *et al.* 2006). Pourtant, dans le but de prévenir et freiner le déclin généralement annoncé des communautés d'oiseaux marins, il est nécessaire de disposer d'estimations les plus robustes possibles en termes de degré de vulnérabilité et risques d'extinction. Cela passe avant tout par l’utilisation de méthodologies appropriées permettant d’établir de manière assez fiable les processus d’impact.

Bien que le rat noir a été introduit précocement sur les îles méditerranéennes, la nature et l’intensité de son impact sur les communautés insulaires est susceptible d’évoluer depuis quelques décennies. En effet, des changements récents dans le fonctionnement trophique des îles sont survenus en Méditerranée, par l’intermédiaire d’apports de nutriments et ressources d’origine allochtone favorisés par les activités humaines (Vidal *et al*. 1998 ; Hulme 2004). Au travers de ce quatrième chapitre, nous avons tenté de mieux comprendre le rôle de ces ressources allochtones et de leur distribution spatiale sur les îles dans l’écologie, la dynamique et le maintien des populations insulaires de rats noirs, afin de mieux évaluer l’impact qu’ils peuvent engendrer à l’heure actuelle sur les communautés insulaires. Les trois études suivantes se sont déroulées sur l’île de Bagaud, réserve intégrale au sein des eaux du Parc National de Port-Cros. Cette île présente la particularité de recevoir saisonnièrement des apports de nutriments allochtones d’origine anthropique, par l’intermédiaire d’une colonie de goélands leucophée *Larus michahellis* nicheuse et d’une plante envahissante produisant des figues charnues, *Carpobrotus* spp. Les rats introduits, et plus particulièrement le rat noir, sont reconnus pour être des espèces généralistes et plastiques dans leurs choix alimentaires et d’habitats (Clark 1981 ; Caut *et al*. 2008). Ainsi, dans le cadre d’un premier volet (**Partie 4.1.**), nous avons étudié à la fois la plasticité de l’espèce mais aussi celle des individus face aux variations spatio-temporelles de la qualité et de la nature des ressources, au travers d’une étude basée sur une complémentarité de méthodologies : des analyses de régime alimentaire sur contenus fécaux et en isotopes stables ont été couplées à une étude approfondie des patrons de déplacements des individus, à la fois sur le long terme (capture-marquage-recapture sur 24 mois) et sur un plus court terme (radio-télémétrie).

Les apports épisodiques d’eau douce par l’intermédiaire d’évènements intenses de précipitations sont connus pour avoir une nette influence sur le fonctionnement des communautés insulaires sur les îles oligotrophes (Stapp & Polis 2003 ; Anderson *et al*. 2008). Les deux parties suivantes ont porté sur le rôle des variations intra- et inter-annuelles des conditions climatiques dans la modulation des effets des ressources allochtones sur la dynamique de populations des rats noirs, à savoir les densités, les paramètres reproducteurs, les taux de croissance des individus et la masse corporelle (**Partie 4.2.**). Les effets des précipitations et des ressources d’origine allochtone ont également été testés sur la survie des individus grâce au développement d’un modèle mathématique bayésien basé sur 14 sessions de capture-marquage-recapture (**Partie 4.3.**).

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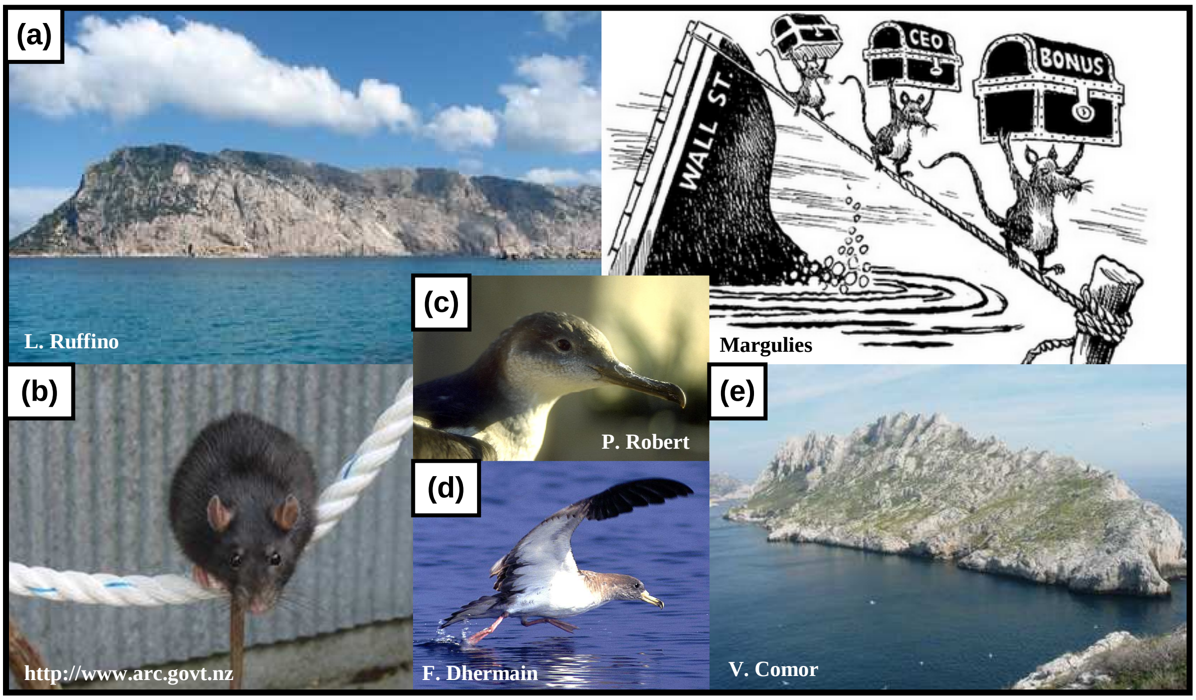
# Chapitre 2.

## HISTOIRE D’INTRODUCTION DU RAT NOIR SUR LES ILES DE MÉDITERRANÉE

## EFFETS D’UNE INTRODUCTION ANCIENNE SUR LA STRUCTURATION ACTUELLE DES POPULATIONS DE PROCELLARIIDÉS



(a) Ile de Tavolara, Sardaigne ; (b) *R. rattus* ; (c) Puffin yelkouan *Puffinus yelkouan* ; (d) Puffin cendré *Calonectris diomedea* ; (e) Ile de Maïre, Archipel de Riou, France.

# - Partie 2.1. -

## 2.1. EARLY COLONIZATION OF MEDITERRANEAN ISLANDS BY *RATTUS RATTUS*: A REVIEW OF ZOOARCHEOLOGICAL DATA

2.1. Colonisation ancienne des îles de Méditerranée par *Rattus rattus*: une synthèse bibliographique de données archéozoologiques

**Résumé :**

Les effets des espèces envahissantes sur les communautés indigènes des îles après une introduction ancienne sont suceptibles de changer sur le long terme, du fait notamment de changements dans la nature des interactions biotiques et abiotiques, et des processus évolutifs mis en oeuvre. Ainsi, dater l'arrivée d'espèces dans un nouvel environnement permet de mieux comprendre les patrons actuels de répartition des espèces, leurs interactions, mais aussi les phénomènes d'extinctions et de persistance d'espèces. Le rat noir, *Rattus rattus sensus stricto*, est l'espèce de rongeur qui a été la plus largement introduite par l'Homme sur les îles de la Planète. Alors que sa diffusion sur les archipels mondiaux a considérablement augmenté au cours des 150 dernières années, le bassin méditerranéen a connu une introduction bien plus ancienne du rat noir. Dans le cadre de ce travail, nous avons réuni l'ensemble des données archéozoologiques disponibles attestant de la présence du rat noir sur les îles et le pourtour méditerranéen avant le 14$^{e}$ siècle afin de mieux appréhender les effets d'une introduction ancienne (~2 000 ans) et généralisée de ce prédateur sur les communautés indigènes des îles. Les plus anciennes traces de rats noirs trouvées en Egypte datent de 400 BC. Les données archéozoologiques pour le bassin levantin restent très rares ; cependant il ne semble pas que le rat noir figurait parmi le cortège d'espèces commensales introduites sur les îles par les premiers hommes néolithiques. Pour le bassin occidental, les restes les plus anciens sont datés de manière très fiable de 400-200 BC. La diffusion généralisée du rat noir sur les îles de Méditerranée a été favorisée par l'intensité des échanges commerciaux et humains durant la période romaine, pour atteindre son apogée au Haut Moyen Age. Les îles méditerranéennes sont au cœur d'un des 34 hotspots de biodiversité mondiaux, et hébergent une faune et une flore hautement sensibles à l'action des rongeurs introduits. Ainsi, nous suggérons que le bassin méditerranéen représente un lieu d'étude priviliégié pour analyser les effets sur le long terme de l'introduction ancienne du rat noir sur les communautés insulaires indigènes après 2 000 ans de présence de rats. Plus particulièrement, cette situation originale d'introduction ancienne offre d'intéressantes perspectives de recherche sur les mécanismes ayant permis aux espèces indigènes de se maintenir en dépit d'une présence ancienne d'un prédateur aussi dévastateur que le rat noir.

**Cette partie correspond à l'article *sous presse* suivant :**

**Ruffino L. & Vidal E. Early colonization of Mediterranean islands *by Rattus rattus*: a review of zooarcheological data. Sous presse dans *Biological Invasions*.**

### 2.1.1. Introduction

Dating the arrival of invasive species in a new region and reconstructing their colonization processes and routes serve multiple research goals. They help us to understand the dynamics of species' introduced range expansion (Hingston *et al*. 2005), to trace movements of people and elucidate the history of their settlement especially when the introduced species are commensal or domestic (Matisoo-Smith *et al*. 1998; Matisoo-Smith and Robins 2004; Searle et al. 2009), and to explain the spread of zoonotic diseases across regions (Audouin-Rouzeau 2003; Duplantier & Duchemin 2003). Moreover, elucidating the history of species introductions allows us to understand processes and to measure rates of evolutionary (Strauss *et al*. 2006) and ecological changes, such as species extinctions (Steadman 2006) or distribution shifts or changes in species abundance, in response to invasions (e.g. Ebenhard 1988; Lodge 1993; Morrison 2002). In the particular case of longstanding invasions, the long-term effects of invasive species on native communities should change over time, as invasive species interact with their novel environment and alter invaded communities (Strauss *et al*. 2006; Strayer *et al*. 2006).

Among the 65 species of the genus *Rattus*, only three (*R. rattus* Lineaus 1758, *R. exulans* Peale 1848, *R. norvegicus* Berkenhout 1769) have been widely scattered by humans throughout the world, sometimes with very old histories of invasion (Atkinson 1985). The *R. rattus* complex can be divided into two main cytogenetic groups (the Asian type [$2n = 42$] and the Oceanic type [$2n = 38$]; Baverstock *et al*. 1983; Yosida 1980). Recent phylogenetic research has revealed that the *R. rattus* complex includes several lineages, all of them originating from south or southeast Asia (K. Aplin unpublished[2]). The dispersal of the Asian type (*R. r. tanezumi*) to islands has been limited to a few island groups of southeast (Philippines, New Guinea, Indo-Malaysia, Micronesia) and east Asia (Japan), and this taxon has recently been recognized as a true species (*R. tanezumi*, Musser & Carlton 2005). The Oceanic type, the black rat or ship rat, *R. rattus sensus stricto*, is native to the southern Indian peninsula and has been introduced to most islands around the world (Ervynck 2002). This species is recognized as one of the world's ten worst invasive species (Lowe *et al*. 2000),

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[2] Aplin K. Prehistory of the world's greatest pest, the black rat (*Rattus rattus*), based on a global survey of its mitochondrial DNA. Results presented at the ANU Archaeological Science 2008 Conference at the Australian National University, Camberra, unpublished.

having triggered rapid extirpations and extinctions of native island species, especially birds (Atkinson 1985). The history of colonization of islands by the ship rat varies among regions of the world and reflects the different routes and periods of human settlement. Although this rodent species has greatly expanded its introduced range throughout the world's oceans in the last 150 years (Atkinson 1985), some regions, such as the Mediterranean basin and its many islands, have undergone a longstanding invasion (i.e. beginning about 2,000 years ago). The Mediterranean basin is one of the world's 34 biodiversity hot spots (Myers *et al*. 2000), and Mediterranean islands feature outstanding animal and plant biodiversity with high conservation interest (Delanoë *et al*. 1996; Médail & Quézel 1997), including several taxa that are considered endangered because of invasive species, especially ship rats (Igual *et al*. 2006; Palmer & Pons 1996, 2001; Pascal *et al*. 2008; Penloup *et al*. 1997). Here, we provide a comprehensive review of zooarcheological evidence of ship rat occurrence in the different regions of the Mediterranean basin before the Middle Ages to emphasize its longstanding and widespread introduction on Mediterranean islands. With tens of thousands of various biogeographical island contexts (Arnold 2008), we suggest that the Mediterranean basin provides a unique opportunity to investigate the long-term effects of pervasive invasive rats on native island communities.

### 2.1.2. Methods

We searched the literature for reliable zooarcheological data on *R. rattus* in the Mediterranean region before the High Middle Ages (1,100-1,300 AD), which was the upper chronological limit of our research period because after this period, 90% of zooarcheological contexts in Europe revealed ship rat remains (Audouin-Rouzeau & Vigne 1994). We specifically focused on the oldest and most reliable existing records on Mediterranean islands and continental margins.

### 2.1.3. Results and discussion

#### 2.1.3.1. Arrival and dispersal of ship rats to eastern Mediterranean coasts and nearby islands

The exact period when the ship rat spread out of its native range and reached the extreme eastern Mediterranean basin remains unknown. Some dates, still under debate (Armitage *et al*. 1984; Ervynck 2002), have been proposed for the Middle East as early as the Upper Pleistocene (17,000-12,000 BP; Tchernov 1968) and around 8,000 BC in Palestine (Tchernov

1986; Figure 1). Ship rat arrival in the eastern and southern Mediterranean coasts may have occurred by two different routes: (1) terrestrial or sea-trade with Mesopotamia, where the ship rat is recorded as early as 3,500 BC in Syria (Ervynck 2002; Figure 1), and (2) sea-trade across the Indian Ocean to the Red Sea ports of Egypt, where rat remains were found in the stomach of a mummified cat dated to around 0-200 AD at Quseir el-Qadim, Egypt; this was the Roman port of Myos Hormos, whose translation from Greek could be “Port of the Rat” (McCormick 2003; Von den Driesh & Boessneck 1983). Moreover, in Egypt, a number of partially digested ship rats have been discovered in mummified birds of prey, some of them dated from Roman times, others probably from the Ptolemaic period (i.e. 400 BC, Armitage *et al*. 1984). There is no doubt that the ship rat was already present in the southeastern part of Mediterranean basin during Roman times, although reliable data remain patchy. Some other zooarcheological studies mention the occurrence of rat remains in ancient Egypt, but these suffer from possible misidentifications, probably caused by confusion of the rat with other rodent species (Ervynck 2002; A Charron pers. comm.).

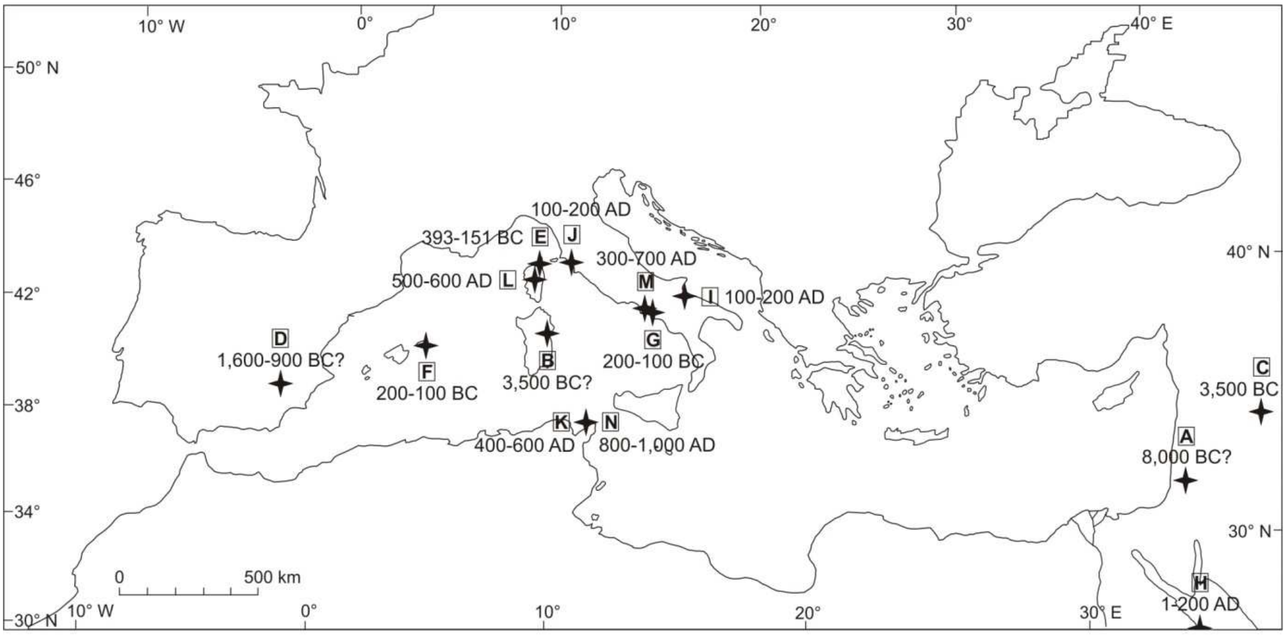

**Figure 1**: Rat (*R. rattus*) bone remains found in zooarcheological sites recorded in the Mediterranean basin before the High Middle Age (1,100-1,300 AD).

A: Palestinia, date must be confirmed; B: Su Guanu, Sardinia, Italy, date must be confirmed; C: Mesopotamia; D: Cerro del Real, Galera, Spain, date must be confirmed; E: Monte di Tuda, Corsica, France; F: Taula Torralba d’en Salort, Menorca, Spain; G: Pompei, Italy; H: Quseir el-Qadim, Red Sea coast, Egypt; I: Ordona, Italy; J: Sette, Grosetto, Italy; K: Zembra, Tunisia; L: Castellu, Corte, Corsica, France; M: Naples, Italy; N: Zembra, Tunisia.

Zooarcheological data on eastern Mediterranean islands remain very scarce and uncertainty persists for the period of the first introduction of ship rats on eastern islands (J-D Vigne pers. comm.). However, some evidence suggests that despite its early introduction, the ship rat was probably not the first commensal species that accompanied human colonization of eastern Mediterranean islands. Indeed, in Crete and Cyprus, some species of shrews (*Crossidura suaveolens* and *Suncus etruscus*; Vigne 1988a) have been found associated with Neolithic pioneers, while house mouse *Mus musculus domesticus* remains have been found within human commensal assemblages from the late Bronze Age (2,500-1,000 BC) and the early Iron Age (~1,000 BC) (Cucchi *et al*. 2005). Despite very rich small mammal assemblages from excavations, these periods (Neolithic, Late Bronze Age, and early Iron Age) have not revealed any black rat remains on Crete and Cyprus (J-D Vigne pers. □wart.).

#### 2.1.3.2. Dispersal of ship rats towards the western Mediterranean basin

Early human settlement on the main western Mediterranean islands dates from ca. 9,000-8,000 BC on Corsica (the first true colonization by modern man; Vigne & Desset-Berset 1995) and from 3,000 BC in the Balearics (Bover & Alcover 2003). However, ship rats do not appear to have been transported with humans at that time (Vigne 1988a). So far, the oldest and most reliable ship rat remains recorded in the western Mediterranean basin date from 2,400-2,200 years ago. On Corsica, analyses of the diet of the barn owl *Tyto alba* indicated that ship rats were absent until 393 BC to 151 BC (Vigne & Valladas 1996). The spread of ship rats on western islands is demonstrated from records found in Minorca dated from 200-100 BC (Saunders & Reumer 1984; Figure 1) and in coastal Italy during the same period (Pompei: 200-100 BC; Hirst 1953; Figure 1). Older records have sometimes been suggested, in Spain (Late Bronze Age; Boessneck 1969) and Sardinia (2,500 BC; Sanges & Alcover 1980), but these remain unconfirmed (Armitage *et al*. 1984; Audouin-Rouzeau & Vigne 1994). Subsequently, the expansion of the Roman Empire and the increase in human population in several cities, especially Rome, generated huge trade flows that probably facilitated rat transport across countries and islands, since the intense military and trade activities of the Roman Empire linked the Near East (Syria, Judea) and the northern African coast (Egypt, Cyrenaica) to western provinces. Transportation of rats on grain and military ships inevitably facilitated their introduction onto Mediterranean islands and around the continental margins of the basin (McCormick 2003). On the continent, most Roman rat remains occurred within 10 km of the coast (Audouin-Rouzeau & Vigne 1994). For example, old zooarcheological records have been found in Italy during the early centuries AD (Rome:

0-200 AD, De Grossi Mazorin 1987; Ordona: 200 AD; Grosetto: 100-200 AD; Naples: 400-500 AD, Armitage *et al*. 1984; Ervynck 1988-1989; Figure 1). Remains have also been found on islands during the same period on Corsica, France (Corte: 500-600 AD, Vigne & Marinval-Vigne 1985; Figure 1) and in Tunisia (Zembra Island: 400-600 AD, Vigne 1988b; Figure 1).

#### 2.1.3.3. Rates of rat spread within and around the Mediterranean basin

The spread of the ship rat throughout the Mediterranean basin, especially on islands, and towards western continental Europe has been progressive since its first arrival in the Mediterranean. Between Antiquity (pre-0 AD) and the Upper Middle Ages (0-1100 AD), respectively 30% and 40% of zooarcheological excavations, where microfauna was analyzed on Mediterranean islands and in continental Europe, have revealed ship rat remains (Audouin-Rouzeau & Vigne 1994). Then, from the 11th century AD, the occurrence of ship rat remains approached a saturation point with up to 90% of the zooarcheological excavations containing the species, and then up to 100% from the 14th century AD (Audouin-Rouzeau & Vigne 1994). While spreading across continental Europe, ship rats remained in coastal and riverside towns and villages during the first millennium AD, in close proximity to humans. However, within the Mediterranean region, ship rats are not strictly commensal. Once they were introduced on islands, the mild Mediterranean climate (mean annual temperature: 11°C) may have facilitated their spread out of human settlements and away from coasts (e.g. Castellu, Corsica: 500-600 AD; Vigne & Marinval-Vigne 1985; Figure 1) and their establishment on islands without permanent human settlement. Nowadays, very few Mediterranean islands remain ship-rat free, and in the western basin 99% of islands > 30ha are invaded by rats (Ruffino *et al*. 2009). Finally, the widespread establishment of rats on Mediterranean islands for 1,000 to 2,000 years has been facilitated by (1) the longstanding intensity of human activities on islands and (2) the close proximity of most islands and islets to the continent (Ruffino *et al*. 2009), which may also have favored natural dispersal by rats (Russell *et al*. 2008).

#### 2.1.3.4. How are dating ship rat introduction on Mediterranean islands and integrating its long-term effects on native communities of interest for conservation?

Dating species arrival in a new environment facilitates understanding of the mechanistic causes of species extirpations and extinctions (Steadman 2006). For example, the exact dating of ship rat introductions on Big South Cape, Lord Howe and Midway islands has contributed to establishing reliable relationships between rat invasions and the sudden extirpations and extinctions of many native bird, bat, and reptile species (Atkinson 1985). However, most of the time, especially for prehistoric extinctions, causes of extinction and extirpation are poorly documented and it is often difficult to identify unequivocal cause-and-effect relationships. Extinction processes are often complicated by other stochastic and intrinsic factors acting synergistically or in addition to rats to accelerate species decline and increase extinction risk (e.g. human impact, climate change, introduction of other species; Steadman 2006). In the Mediterranean, estimation of the most likely period (i.e. Roman times) of ship rat introduction in the different parts of the basin has allowed us to rule out the role of rats in the extinctions of some small mammals, reptiles, and birds that occurred during the Pleistocene and early Holocene (Cinzia Maria 2005), such as *Puffinus nestori* which disappeared before rat arrival in the Balearics (Zotier *et al*. 1999).

For species that have managed to persist despite the longstanding presence of invasive predators or competitors, the patterns of distribution of their populations, their population sizes, and their behavioral, physiological and morphological traits should reflect the long-term effects of invasive species (Strayer *et al*. 2006; Strauss *et al*. 2006). This is why understanding of the current effects of invasive species on native populations can be improved by including the temporal dimension of the invasion. In the Galápagos, Harris *et al*. (2007a,b) showed that 400 years of interference competition pressure from black rats strongly restricted the spatial distribution of the endemic rodent *Nesoryzomys swarthy* on Santiago Island, whose persistence may have been facilitated by *Opuntia* refugia (Harris *et al*. 2006; Gregory & Macdonald 2009). In the Mediterranean, the longstanding and widespread introduction of ship rats on islands may have played a role in shaping the current distribution patterns of birds (Martin *et al*. 2000; Ruffino *et al*. 2009), reptiles (M Delaugerre pers. comm.), insects (Palmer & Pons 1996), and also plants (Palmer & Pons 2001). Research into behavioral and ecological mechanisms enabling native species to persist despite the long-term presence of invasive predators is not well investigated (but see works from Hoare *et al*. 2007), yet it is crucial to avoid misinterpretations of native species responses to introduced species removal and hence to formulate adequate conservation strategies. In this sense, the early and widespread introduction of ship rats on the various biogeographical island contexts of the Mediterranean should provide a great opportunity to study the long-term effects of ship rats on native species and to better understand the mechanisms involved in the long-term persistence of some of the natives.

Overall, zooarcheological data of ship rat occurrence remain patchy on Mediterranean islands and scarce for the Levantine basin (which includes thousands of islands). The colonization processes and routes of ship rats from their Asian origin and throughout the Mediterranean basin should gain clarification and precision with the use of phylogenetic analyses. Analyses of mitochondrial DNA polymorphism is a useful tool to identify evolutionary lineages within taxa and some closely allied species and to track their geographic dispersal from prehistoric to modern times, especially for widespread commensal rodents (Hingston *et al*. 2005; Matisoo-Smith & Robins 2004; Robins *et al*. 2007, 2008; Searle *et al*. 2009;  K. Aplin unpublished).

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# - Partie 2.2. -

## 2.2. INVASIVE RATS AND SEABIRDS: A REVIEW AFTER 2,000 YEARS OF AN UNWANTED COEXISTENCE ON MEDITERRANEAN ISLANDS

2.2. Rats introduits et oiseaux marins: une synthèse après 2000 ans d’une coexistence non désirée sur les îles de Méditerranée

### Résumé :

Les rats introduits représentent à l’heure actuelle l’une des plus lourdes menaces pour les faunes insulaires, notamment les oiseaux marins pour lesquels ils sont reconnus responsables du déclin et de l’extinction d’un grand nombre de populations. Dans le bassin méditerranéen, le rat noir (*Rattus rattus*) a été introduit sur la plupart des îles et îlots il y a environ 2 000 ans. Malgré une présence ancienne et généralisée du rat noir sur ces îles, la persistance des quatre espèces et sous-espèces d’oiseaux marins (famille des Procellariidés) endémiques de Méditerranée représente un intrigant paradoxe. L’analyse par modèles linéaires généralisés d’une base de données concernant environ 300 iles et îlots du bassin méditerranéen occidental a permis (1) d’identifier les facteurs physiques, géographiques et anthropiques influençant la présence du rat sur les îles après une colonisation ancienne, et (2) de déterminer comment les caractéristiques des îles et la présence du rat gouvernaient la présence actuelle et les abondances des quatre espèces de puffins et pétrels. Nos résultats montrent, qu’à l’heure actuelle, la plupart des îles du bassin méditerranéen occidental hébergent des populations de rats noirs. A une échelle régionale, la présence du rat noir ne semble conditionner que les abondances de l’espèce d’oiseau marin la plus petite, l’océanite tempête *Hydrobates pelagicus*, alors que la présence et les abondances des trois espèces de puffins ne paraissent être influencées que par les caractéristiques physiques des îles. Ainsi, nous émettons l’hypothèse que la persistance des Procellariidés de Méditerranée sur le long terme, malgré une présence de rats ancienne, a pu être facilitée par la diversité des contextes insulaires.

**Cette partie correspond à l’article publié suivant :**

**Ruffino L., Bourgeois K., Vidal E., Duhem C., Paracuellos M., Escribano F., Sposimo P., Baccetti N., Pascal M. & Oro D. (2009) Invasive rats and seabirds: a review after 2,000 years of an unwanted coexistence on Mediterranean islands. *Biological Invasions* 11: 1631-1651.**

### 2.2.1. Introduction

For thousands of years, island colonization by humans and intense exploitation of native biotas have triggered catastrophic species extinctions on islands worldwide (Steadman 1995; Alcover *et al*. 1998; Roberts *et al*. 2001; Steadman & Martin 2003; Burney & Flannery 2005). As they keep moving further and faster, humans have scattered a large number of species beyond their natural ranges and have been responsible for an unprecedented ecological turnover on islands (Vitousek *et al*. 1997; Chapin *et al*. 2000; Rosenzweig 2001). Rats (*Rattus* spp.) have been successfully introduced on more than 80% of the world's major islands and are known to negatively affect island biota, especially birds (Atkinson 1985; Courchamp *et al*. 2003; Towns *et al*. 2006; Jones *et al*. 2008). Evidence of rapid bird extinctions soon after rat arrival has been documented on several islands (e.g. Big South Cape Island in New Zealand, Midway Island in Hawaii and Lord Howe Island; Atkinson 1985; Towns *et al*. 2006). Seabirds in particular are extremely sensitive to rat impact as they have generally evolved in the absence of mammalian predators and thus have not developed any defense mechanisms (Burger & Gochfeld 1994; Blackburn *et al*. 2004). Consequently, numerous cases of breeding failures, sharp decreases in breeding populations and local extirpations of seabird colonies have coincided with rat introduction on islands (Atkinson 1985; Towns *et al*. 2006). Most seabird species worldwide are negatively affected by the impact of rats, especially the smallest species and those nesting in burrows or cavities (Imber 1976; Atkinson 1985; Martin *et al*. 2000; Jones *et al*. 2008). Therefore, today, rats are identified as a leading cause of extinction risk in 70% of the world's Procellariiform seabirds (e.g. petrels and shearwaters, except albatrosses; IUCN 2008).

Except bats, two endemic shrews and an endemic mouse, all terrestrial mammals currently present on Mediterranean islands have been introduced by man and the native mammal fauna found on islands during the Pleistocene has been extinct since the Early Holocene (large mammals), or slightly later (small mammals) (Vigne 1992; Pascal *et al*. 2006). The Pleistocene mammal fauna was poor and disharmonic. Most species were shrews and vegetarian rodents and very few if any of these native species were likely to be potential seabird predators (Vigne 1992; Marra 2005; Gippoliti & Amori 2006). With more than 10,000 islands and islets, the Mediterranean Basin comprises one of the largest groups of islands in the world, with exceptional biodiversity (Delanoë *et al*. 1996; Médail & Quézel 1997; Myers *et al*. 2000). This island system has been early and widely colonized by ship rats (*Rattus*

*rattus*) since their spread from the Indian peninsula (Audouin-Rouzeau & Vigne 1994; Masseti 1995; Vigne & Valladas 1996). The oldest reliable ship rat remains recorded in the North-Western Mediterranean islands date back to Roman times (Corsica: 393-151 BC, Vigne & Valladas 1996; Menorca: 200-100 BC, Audouin-Rouzeau & Vigne 1994), although older records are possible (Audouin-Rouzeau & Vigne 1994). However, despite the long-standing and widespread rat introduction and human presence on Mediterranean islands, no seabird species extinction has been reported in the Mediterranean Basin since rat introduction (Alcover *et al*. 1992; Milberg & Tiberg 1993; Vigne *et al*. 1997; Zotier *et al*. 1999), although local extirpations have occurred on some islands (Martin *et al*. 2000; Bourgeois & Vidal 2008). The globally extinct *Puffinus nestori*, formerly restricted to the Balearic Archipelago, vanished during the late Pliocene before humans introduced rats on islands. Among the nine seabird species currently breeding in the Mediterranean islands, the four endemic Procellariiformes have been present since the Pleistocene (Alcover *et al*. 1992; Zotier *et al*. 1999). The survival of these endemic long-lived seabirds on Mediterranean islands, despite thousands of years of ship rat presence, constitutes an amazing conservation paradox, since this group of birds is known to be negatively affected by the introduction of alien predators worldwide (Atkinson 1985; Jones *et al*. 2008; IUCN 2008).

The Mediterranean Basin may thus constitute a key site for studying the long-term interactions between introduced rats and seabirds on islands. This paper focuses on three main aims: (1) to identify factors likely to explain ship rat presence on Western Mediterranean islands; (2) to account for how ship rat presence and island characteristics may have driven the presence and abundance of the four Mediterranean Procellariiformes at the scale of the Western Mediterranean Basin, and (3) to review documented data of rat impact on Mediterranean seabird communities.

### 2.2.2. Methods

#### 2.2.2.1. Datasets

We focused our study on the Western Mediterranean Basin because it has been more studied than the Eastern part. The Western Mediterranean Basin stretches from the Gibraltar Strait (West) to the Adriatic Sea (East), covers about one third of the 3,081,880 km$^2$ Mediterranean Sea and comprises *ca.* 700 islands and islets. Although available, data about island characteristics, seabirds and rats have never been compiled and analyzed on such a wide scale (but see Martin *et al*. 2000). The data used in this review were collated from published sources (including grey literature), unpublished reports, notes and personal communications from nature reserve managers, conservationists and researchers, who were specifically contacted.

Data on seabird presence and abundance, island characteristics and ship rat presence were collected for 292 islands (Figure 2; Annexe 1). Only the most recent and reliable census on breeding seabird populations was used. For each of these islands, five potential explanatory variables for rat presence and seabird presence and abundance were also collected (Table 1). Because they possess life-history traits likely to make them particularly sensitive to introduced mammal predators (Jones *et al*. 2008), we focused seabird analyses on the four Mediterranean Procellariiform taxa: the Yelkouan shearwater (*Puffinus yelkouan*) and the Balearic shearwater (*P. mauretanicus*), which are Mediterranean endemic species, and two Mediterranean endemic subspecies, the Mediterranean Cory's shearwater (*Calonectris diomedea diomedea*) and the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*). The Cory's shearwater is the largest species (500-800 g) and its distribution encompasses the entire Mediterranean Basin (57,000-76,000 breeding pairs, Zotier *et al*. 1999). Its breeding colonies on islands range from small (< 20 breeding pairs) to large (e.g. 25,000 breeding pairs on Zembra Island, Tunisia; Isenmann & Moali 2000). The distribution of the Yelkouan shearwater (350-500 g) is sparse and the world population may be limited to only a few thousand breeding pairs (Bourgeois & Vidal 2008). Yelkouan shearwater colonies are generally quite small but can reach up to 1,300-8,600 pairs on Tavolara-Molara islands, Sardinia (G. Spano & N. Baccetti, pers. comm.). The Balearic shearwater (349-416 g) is restricted to the Balearic Archipelago (< 2,000 breeding pairs; Ruiz and Martí 2004) and usually breeds in small- (< 30 breeding pairs) and medium-sized colonies (e.g. 250-300 breeding pairs on main Menorca Island, Balearic Archipelago, R. Triay, pers. comm.). The storm petrel, the smallest species under study (25-29 g), is widely distributed throughout the basin (> 15,000 breeding pairs, Zotier *et al*. 1999) and usually breed in small islands where colonies can sometimes reach thousands of pairs (e.g. 6,550 breeding pairs on Filfla (2 ha), Maltese islands, Borg & Sultana 2002).

Ship rats were considered present on a particular island if mentioned, either continuously or occasionally, and absent if not found despite thorough investigation. When ship rats were eradicated from islands, we used seabird abundance assessed before eradication. Two main island substrates were distinguished (i.e., limestone and non-limestone; Table 1) according to the nature of the dominant substrate. A limestone substrate may provide deeper and more abundant cavities (caves, crevices) than non-limestone subtrates (Martin *et al*. 2000). For rat distribution analysis, we considered continents and islands ≥ 5 ha as potential sources of permanent rat populations since 86 % of islands ≥ 5 ha housed ship rats in our dataset.

We reviewed studies reporting ship rat impact on Mediterranean Procellariiformes throughout the entire basin by collecting data from published works, unpublished reports and personal communications. Finally, we collected data on the breeding success of Cory's and Balearic shearwaters in three situations (Table 1): (1) rat-inhabited islands, (2) islands where rats have been controlled within shearwater colonies, and (3) rat-free islands (either absent or eradicated). Unfortunately, for the two other Procellariiform species (storm petrel and Yelkouan shearwater), reliable data on the breeding success were too sparse to be used.

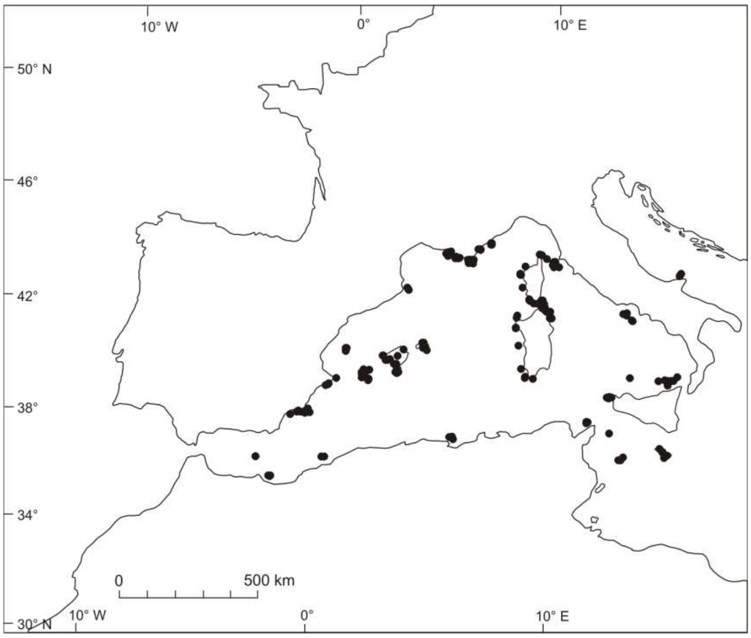

**Figure 2**. Map of the Western Mediterranean and location of the 292 islands studied.

### 2.2.2.2. Statistical analysis

In order to highlight factors likely to explain ship rat presence on Western Mediterranean islands, we constructed a Generalized Linear Model (GLM, binomial distribution, LOGIT link function) for a set of 257 islands and islets (Table 1, Appendix 1). For seabirds, GLMs (binomial distribution, LOGIT link function) were first performed to explore how seabird presence on islands may be influenced by the *a priori* selected explanatory variables for each seabird species (*P. yelkouan*: *n* = 135 islands; *C. diomedea*: *n* = 179 islands; *P. mauretanicus*: *n* = 69 islands; *H. pelagicus*: *n* = 101 islands; Table 1, Appendix 1). We performed one model for each seabird species since the four species did not share the same geographical distribution and reliable data on breeding status were not available for each species on all islands. Then, GLMs (normal distribution, IDENTITY link function) were used to evaluate which variables may explain seabird abundance on islands where they breed (*P. yelkouan*: *n* = 30 islands; *C. diomedea*: *n* = 79 islands; *P. mauretanicus*: *n* = 13 islands; *H. pelagicus*: *n* = 23 islands; Table 1). Finally, the effects of rat impact (rat presence, local control and rat absence), year of study and geographical region on the breeding success of Cory's shearwaters were investigated through GLM analysis (normal distribution, IDENTITY link function). Due to the lack of data on Balearic shearwater breeding success (*n* = 13), we only investigated the effect of rat impact through a non-parametric Kruskal-Wallis ANOVA (Table 1).

All continuous variables (i.e., size, distance, elevation and abundance) were $\log_{10}$-transformed to remove right skew distribution and increase normality of their distribution (Sokal & Rohlf 1995; Russell & Clout 2004). Cory's and Balearic shearwater breeding success were arcsin-square-root transformed (Sokal & Rohlf 1995). Before constructing GLMs, we used Spearman rank correlations to identify collinearity between explanatory variables. Even though island area and island elevation were correlated ($r^2$ = 0.73), we kept the two terms in the models since these two factors are known to be potential predictors of seabird presence and abundance (Schramm 1986; Brandt *et al.* 1995; Muller-Dombois 1999; Lomolino 2000; Sullivan & Wilson 2001; Catry *et al.* 2003). Furthermore, explanatory value would be lost by arbitrarily dropping one of the variables (see Russell & Clout 2004). Models were constructed in order to identify and interpret explanatory variables, not to maximise predictive power (Russell & Clout 2004).

| Parameters | Description | Range | GLMs |
|---|---|---|---|
| *Explanatory variables* | | | |
| **Area** | Island area (ha) | 0.021–364 016 ha | Rats & Seabirds$^{(A, D)}$ |
| **Elevation** | Maximum island elevation (m) | 3–1 445 m | Rats & Seabirds$^{(A, D)}$ |
| **Rat presence** | Ship rat absence or presence on islands | 0/1 | Rats & Seabirds$^{(A, D)}$ |
| **Distance continent** | Minimum distance (m) to continent or land mass (i.e. Sardinia, Corsica, Sicilia) | 5–245 300 m | Rats |
| **Distance source** | Minimum distance (m) to nearest island >5 ha or to continent (whichever is closer) | 2–70,000 m | Rats |
| **Humans** | A: currently uninhabited<br>B: rare/occasional human presence and/or past human presence (in the last 100 years)<br>C: permanent human presence (and presence of tourism) | 0/1 | Rats |
| **Dist. near rats** | Minimum distance (m) to nearest rat-infested island | 2–67 000 m | Seabirds$^{(A, D)}$ |
| **Substrate** | Main island rock substrate: limestone or non-limestone | | Seabirds$^{(A, D)}$ |
| **Geographical region** | E: Eastern Mediterranean islands from Gibraltar Strait to French islands<br>W: Western Mediterranean islands from Sardinia to the Maltese archipelago | | Rat impact$^{(C)}$ |
| **Rat impact** | Y: ship rat presence and no management action<br>C: local ship rat control<br>A: ship rat absence (with or without eradication) | | Rat impact$^{(C, M)}$ |
| **Year of study** | Year when breeding success was monitored | 1979–2007 | Rat impact$^{(C)}$ |
| *Response variables* | | | |
| **Seabird abundance** | Seabird abundance on islands (i.e. number of breeding pairs) | 1–25 000 pairs | Seabirds$^{(A)}$ |
| **Seabird presence** | Seabird absence or presence on islands | | Seabirds$^{(D)}$ |
| **Breeding success** | Shearwater mean breeding success (%) | 0–100% | Rat impact$^{(C, M)}$ |

**Table 1.** Explanatory and response variables with their description and integration in each statistical analysis (Rats = GLM on rat distribution; Seabirds $^{D,A}$ = GLMs on seabird distribution (D) and abundance (A); Rat impact $^{C,M}$ = GLMs on rat impact on the breeding success of *Calonectris diomedea* (C) and Kruskal-Wallis ANOVA for *Puffinus mauretanicus* (M).

## 2.2.3. Results

### 2.2.3.1. Factors affecting the distribution of ship rats on Mediterranean islands

Ship rats were present on 201 (68.8%) out of the 292 Mediterranean islands for which reliable data were found. The smallest rat-infested islet was 0.021 ha. Rats were found on 36% of islands ≤ 0.5 ha and on 99% of islands ≥ 30 ha (Figure 3). Ship rat presence was positively related to island area (Table 2, Figure 3) but negatively related to distance to the nearest potential source of rats (Table 2). Ship rat presence was not related ($P < 0.05$) to elevation, distance to continent or presence and intensity of human activities. There was no evidence of model inadequacy (scaled Pearson $\chi^2 = 219.0$; $df = 250$; $P = 0.08$). In order to clarify the negative relationship between rat presence and distance to the nearest potential source of rats, we performed Mann-Whitney tests to compare, for islands ≤ 5 ha and those > 5 ha, mean distances from the nearest source of rats (i.e., island ≥ 5 ha or continent) between rat-free and rat-infested islets. Small rat-infested islets ≤ 5 ha were significantly closer from the nearest source of rats than small rat-free islets ≤ 5 ha (Mann-Whitney, $Z = 3.5$; $P < 0.001$; $n_{\text{with rats}} = 74$, $n_{\text{without rats}} = 65$), whereas rat-infested islands > 5 ha were not significantly closer than rat-free islands > 5 ha (Mann-Whitney, $Z = 0.77$; $P = 0.44$; $n_{\text{with rats}} = 101$, $n_{\text{without rats}} = 17$). Finally, 141 (55%) out of 257 islands were ≤ 500 m away from either the nearest island ≥ 5 ha or the continent, among which 118 islands (81%) were ≤ 10 ha (500 m is the maximum-recorded distance ship rats can swim; Russell & Clout 2005). For these 257 islands, the mean distance to the nearest source of rats was 3,654 m ($SE = 672$ m).

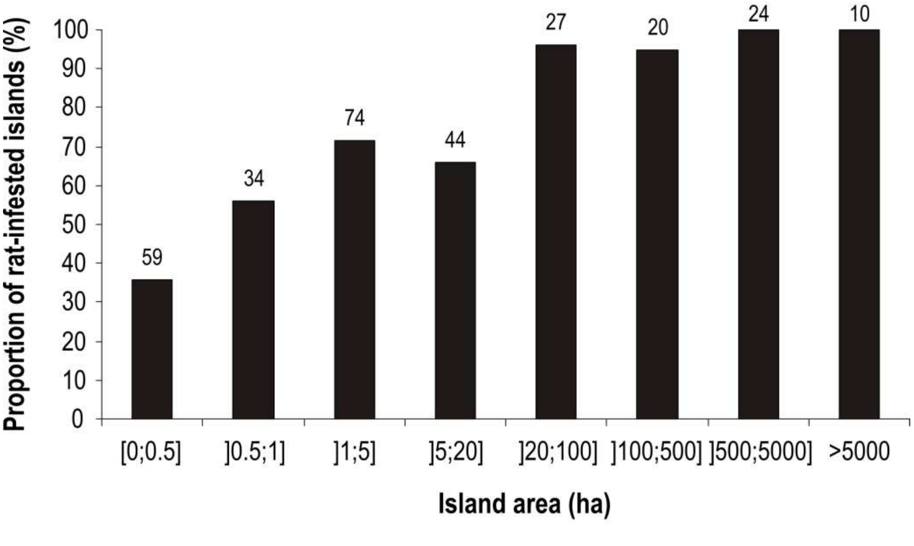

**Figure 3**. Proportions of rat-infested islands in relation to island area. The number of islands used for each area interval is indicated above bars (total $n = 292$).

| Parameters | *ß* | *SE* | Wald statistic | *P*-Value |
|---|---|---|---|---|
| Intercept | 3.57 | 1.07 | 11.14 | *** |
| Humans (C) | 0.58 | 0.74 | 0.61 | ns |
| Humans (A) | 0.18 | 0.50 | 0.13 | ns |
| log10 (area) | 2.07 | 0.36 | 33.03 | *** |
| log10 (distance continent) | -0.17 | 0.16 | 1.07 | ns |
| log10 (distance source) | -1.27 | 0.31 | 16.74 | *** |
| log10 (elevation) | -0.04 | 0.05 | 0.01 | ns |

**Table 2.** Significance of explanatory variables and associated statistic parameters in the rat distribution GLM ($n$ = 257; *ß* = estimate; *SE* = standard error of the estimate). See Table 1 for more thorough information on explanatory variables. Significance levels: *** ($P < 0.001$); ** ($P < 0.01$); * ($P < 0.05$); ns (not significant).

### 2.2.3.2. Factors explaining seabird distribution and abundance on Mediterranean islands

Island area was positively related to Yelkouan and Balearic shearwater presence, Yelkouan and Cory's shearwater abundance ($P < 0.05$) and weakly negatively related to storm petrel presence ($P = 0.06$; Tables 3, 4). Island elevation was positively related to Cory's and Yelkouan shearwater presence and Balearic shearwater and storm petrel abundance. Limestone substrate was positively related to Yelkouan shearwater abundance and storm petrel presence. Rat presence on islands was negatively related to storm petrel abundance, but did not influence either the presence or the abundance of the three shearwaters. Ship rats are present on most islands where the three shearwaters breed (Figure 4). Distance to the nearest source of rats was positively related to storm petrel presence and abundance.

There was no evidence of model inadequacy for Cory's shearwater presence (scaled Pearson $\chi^2$ = 194.3; $df$ = 174; $P$ = 0.86) and abundance ($\chi^2$ = 78.0; $df$ = 72; $P$ = 0.71), Yelkouan shearwater presence ($\chi^2$ = 131.8; $df$ = 129; $P$ = 0.58) and abundance ($\chi^2$ = 30.0; $df$ = 24; $P$ = 0.82), Balearic shearwater presence ($\chi^2$ = 50.6; $df$ = 62; $P$ = 0.15) and abundance (scaled Pearson $\chi^2$ = 13.0; $df$ = 8; $P$ = 0.88) and storm petrel presence ($\chi^2$ = 75.4; $df$ = 94; $P$ = 0.08) and abundance ($\chi^2$ = 23.0; $df$ = 17; $P$ = 0.85).

| | *Calonectris diomedea* | | | | *Puffinus yelkouan* | | | | *Puffinus mauretanicus* | | | | *Hydrobates pelagicus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value |
| Intercept | -4.04 | 0.99 | 16.48 | *** | -8.79 | 2.23 | 15.53 | *** | -3.28 | 92.73 | 0.00 | ns | -6.86 | 2.12 | 10.43 | *** |
| log10 (area) | 0.29 | 0.26 | 1.27 | ns | 1.14 | 0.53 | 4.56 | * | 0.89 | 0.39 | 5.33 | * | -0.85 | 0.45 | 3.49 | 0.06 |
| log10 (elevation) | 2.35 | 0.65 | 12.92 | *** | 4.09 | 1.47 | 7.74 | ** | 0.16 | 0.66 | 0.06 | ns | 1.69 | 1.02 | 2.74 | ns |
| Substrate (limestone) | 0.08 | 1.19 | 0.17 | ns | 0.34 | 0.36 | 0.86 | ns | 1.92 | 92.72 | 0.00 | ns | 1.38 | 0.38 | 14.76 | *** |
| Rats (presence) | 0.19 | 0.25 | 0.58 | ns | 0.14 | 0.63 | 0.05 | ns | 0.35 | 0.27 | 1.68 | ns | 0.31 | 0.39 | 0.60 | ns |
| log10 (Dist. Near Rats) | 0.04 | 0.26 | 0.03 | ns | -0.27 | 0.44 | 0.38 | ns | -0.02 | 0.52 | 0.06 | ns | 1.39 | 0.50 | 7.59 | ** |
| *N* | 179 | | | | 135 | | | | 69 | | | | 101 | | | |

**Table 3.** Statistical significance of explanatory variables in GLMs on seabird presence (*ß* = estimate; *SE* = standard error of the estimate; *W* = Wald Statistic). See Table 1 for more thorough information on explanatory variables. Significance levels: *** (*P* < 0.001); ** (*P* < 0.01); * (*P* < 0.05); ns (not significant).

| | *Calonectris diomedea* | | | | *Puffinus yelkouan* | | | | *Puffinus mauretanicus* | | | | *Hydrobates pelagicus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value | *ß* | *SE* | *W* | *P*-value |
| Intercept | -0.43 | 0.43 | 1.00 | ns | -0.85 | 0.66 | 1.66 | ns | -0.47 | 1.03 | 0.21 | ns | -2.30 | 2.90 | 6.51 | * |
| log10 (area) | 0.43 | 0.08 | 29.93 | *** | 0.36 | 0.14 | 6.62 | * | 0.00 | 0.00 | 0.28 | ns | -0.19 | 0.20 | 0.85 | ns |
| log10 (elevation) | 0.22 | 0.22 | 0.99 | ns | 0.56 | 0.38 | 2.28 | ns | 0.71 | 0.34 | 4.39 | * | 1.25 | 0.49 | 6.42 | * |
| Substrate (limestone) | 0.09 | 0.06 | 0.29 | ns | 0.28 | 0.11 | 6.02 | * | -[a] | -[a] | -[a] | -[a] | 0.31 | 0.19 | 2.53 | ns |
| Rats (presence) | -0.13 | 0.10 | 1.55 | ns | 0.01 | 0.29 | 0.00 | ns | 0.10 | 0.24 | 0.18 | ns | -0.44 | 0.16 | 7.70 | ** |
| log10 (Dist. Near Rats) | -0.05 | 0.10 | 1.55 | ns | 0.17 | 0.15 | 1.34 | ns | 0.32 | 0.39 | 1.24 | ns | 0.62 | 0.25 | 6.35 | * |
| *N* | 79 | | | | 30 | | | | 13 | | | | 23 | | | |

**Table 4.** Statistical significance of explanatory variables in GLMs on seabird abundance (*ß* = estimate; *SE* = standard error of the estimate; *W* = Wald Statistic). See Table 1 for more thorough information on explanatory variables. [a] The substrate parameter was not tested for *P. mauretanicus* abundance since it exclusively breeds on limestone islands.

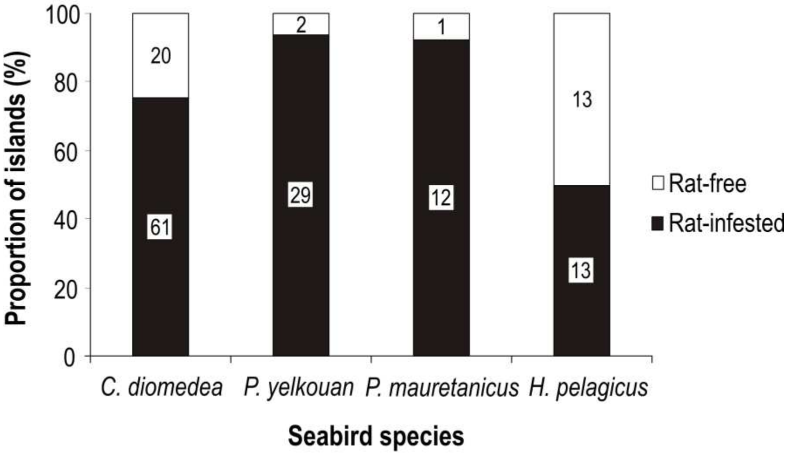

**Figure 4.** Proportion of rat-infested and rat-free islands among the islands where the four Procellariiform species (*Calonectris diomedea*, *Puffinus yelkouan*, *P. mauretanicus*, *Hydrobates pelagicus*) are known to breed in the Western Mediterranean. The number of islands used for each species is indicated.

### 2.2.3.3. Evidence of rat impact on Mediterranean Procellariiformes

The presence of rats had a negative effect on the breeding success of Cory's shearwaters ($ß = – 0.25$; $SE = 0.03$; $W = 55.35$; $P < 0.001$; $n = 219$). The breeding success of Cory's shearwaters was also influenced by the year of study ($ß = – 0.01$; $SE = 0.00$; $W = 7.67$; $P < 0.01$) and the geographical region ($ß = 0.06$; $SE = 0.06$; $W = 7.27$; $P < 0.01$). Breeding success was significantly higher on rat-free islands (rats absent or eradicated) or when rat populations were controlled within shearwater colonies, compared to rat-infested islands where no conservation measure was carried out ($F_{2,\ 216} = 35.2$; $P < 0.001$; Figure 5). The breeding success of Cory's shearwaters was not significantly different between rat-controlled and rat-free islands. Balearic shearwater breeding success was not significantly influenced either by rat control or by rat absence ($H_{2,\ 12} = 1.9$; $P = 0.38$). Chi-squared tests for goodness of fit found no evidence of inadequacy for the Cory's shearwater breeding success model (scaled Pearson $\chi^2 = 219.0$; $df = 214$; $P = 0.61$).

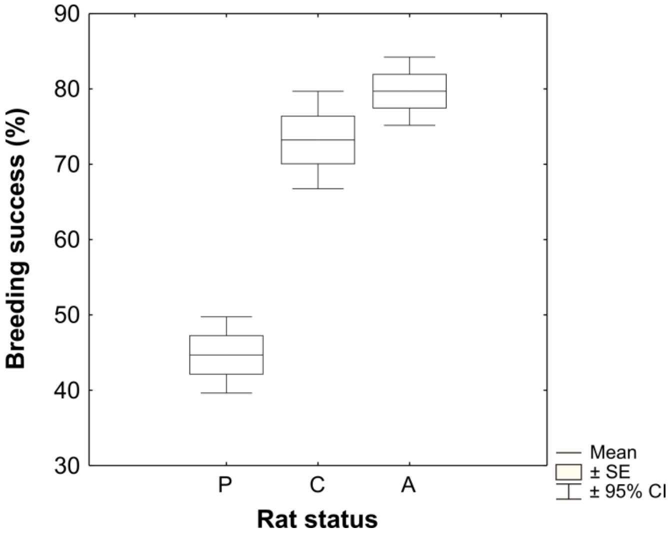

**Figure 5.** Influence of rat presence (noted P), rat control and rat absence (absent or eradicated) (noted C and A respectively) on the breeding success of the Cory's shearwater on Western Mediterranean islands (*n* = 219). Breeding success is defined as the number of fledged chicks divided by the total number of hatched eggs.

### 2.2.4. Discussion

#### 2.2.4.1. Ship rat distribution on Mediterranean islands

Today, few Mediterranean islands remain rat-free. Compared to most oceanic archipelagoes, Mediterranean islands generally exhibit a low degree of geographical isolation and can be considered as a group of continental islands, surrounded by the African and Euro-Asiatic landmasses (Greuter 1995). Moreover, most Mediterranean islands are part of wider island systems (e.g. Sardinia, Sicily, Corsica, Balearic) which decreases their isolation from the continent (Sara & Morand 2002). Thus, many Mediterranean islands (mostly small islands) are close enough to each other or to the continent to be reached by rats by natural dispersal (i.e. ≤ 500 m). However, long-standing and intensive human transport and trade activities within the basin have probably largely facilitated the distribution of this commensal and generalist rodent, which has rapidly become established on most Mediterranean islands (Vigne 1992; Audouin-Rouzeau & Vigne 1994; Masseti 1995; Bover & Alcover 2008). Thus, even though distance to the continent, human presence on islands and intensity of human activities may have played a significant role in rat dispersal in the past, these factors no longer limit rat presence on Mediterranean islands. Island area and isolation from the nearest potential source of rats were the best explanatory factors in ship rat presence on Mediterranean islands. The larger the island, the more likely it is to be rat-infested. This pattern is consistent with island biogeography theories on island species richness (Lomolino 1982, 1984; Adler & Wilson 1985) as well as on the probability of small mammal species occuring on islands (Adler & Wilson 1985; Russell & Clout 2004). Moreover, this area-related pattern may be related to the highest probability of human colonization on large islands due to highest habitat and resource diversity (Lomolino 2000), and thus to the highest probability of accidental rat introduction. However, in the case of the long-invaded Western Mediterranean island system, 74% of islands ranging from 1 to 5 ha support ship rat populations and many very small islets have also been found to be rat-infested, when close enough to continents or other landmasses. On such very small islets close to a potential source, rats are known to maintain only transient populations (Adler & Wilson 1985; Alcover 1993), facing a higher extinction risk due to founder effect, genetic drift and inbreeding depression (Heidrick & Kalinovsky 2000; Frankam 2003). Unfortunately, we could not take into account rat population turnover on the smallest islands in this review due to the lack of available data. Distance from the nearest potential rat population source was a limiting factor for rat presence only for the smallest islets and uninhabited islands, whose isolation may limit natural dispersal and human transport links, thereby preventing the external recruitment required for population persistence (e.g. Cheylan 1999).

#### 2.2.4.2. Ship rat impact on Mediterranean Procellariiformes

Surprisingly, rat presence was not found to be a leading factor explaining the distribution of the four seabird species at the scale of the entire Western Mediterranean Basin. This pattern is particularly clear for the three shearwater species that virtually breed only on rat-infested islands, sometimes with high rat densities (e.g. Zembra Island, Tunisia, M. Pascal, pers. comm.; Molara Island, Sardinia, G. Spano, pers. comm.; records up to 50 individuals/ha were found in Cabrera archipelago, Toro Island in Corsica and Petit Congloué Islet in French Provence, see Alcover 1993 & Cheylan 1999). Only the abundance of the smallest species, the storm petrel, was related to rat presence on islands. Our findings are consistent with those of Jones *et al*. (2008) in their review on rat impact on seabirds, which points out that seabirds of the Hydrobatidae family (i.e. storm petrels) meet all the criteria for susceptibility to rats. Storm petrels are small-sized seabirds, burrow or cavity nesters and have all life stages (i.e., eggs, chicks, adults) likely to be preyed upon. Although rat presence on islands was not a significant component of storm petrel distribution at the scale of the Western Mediterranean, at the archipelago scale storm petrels only breed on rat-free islands (Massa & Sultana 1990-

1991; Martin *et al*. 2000). This is why it is imperative to consider the scale under study when inferences are made (Lomolino 1999, 2000; Wittaker 2000).

Seabird presence and abundance were mainly related to island's physical characteristics, such as elevation, area and substrate. Island cliffs may constitute key intra-island refuges for seabird breeding since they may be less covered by vegetation and less accessible to mammal predators (Igual *et al*. 2006). On New Island, Falklands, Quillfeldt *et al*. (2007) showed that thin-billed prions preferred breeding in areas with little vegetation and seemed to avoid areas covered by native tussoc grass, where ship rat densities were consistently higher. Unlike Cory's shearwaters, which are able to breed in exposed cavities as well as under vegetation without substrate protection (Borg 2000), Yelkouan shearwaters are more selective in their habitat requirements and breeding cavity selection (i.e. selecting deep and winding cavities that may be less accessible to rats; Bourgeois & Vidal 2007, Ruffino *et al*. in press). This may explain why Yelkouan shearwaters only rarely breed on small islands, where the probability of finding suitable and safe breeding sites may be lower than on large islands. Balearic shearwaters breed only on limestone islands, and when breeding on rat-infested islands, breeding sites are generally located in inaccessible sites (i.e. deep limestone caves in high cliffs) where rat densities are low or even nil (Oro *et al*. 2004). In turn, storm petrels preferentially select safe breeding areas on limestone islands. Moreover, they breed almost exclusively on small islands to avoid human activities, and terrestrial and avian predators on large islands (Erwin *et al*. 1995; Borg *et al*. 1992-1994; Oro *et al*. 2005).

However, at a more local scale, most studies dealing with rat impact on Mediterranean Procellariiformes reported benefits of ship rat absence or rat removal on shearwater productivity (Table 5). Moreover, as confirmed by our GLM analyses, the breeding success of the largest burrowing seabird species, the Cory's shearwater, has frequently been shown to be negatively affected by ship rat impact (e.g. Amengual & Aguilar 1998; Thibault 1995; Igual *et al*. 2006, 2007; Pascal *et al*. 2008). From a demographic point of view, population dynamics of Procellariform seabirds have a low sensitivity to changes in fecundity, while changes in adult survival translate into sharp variations of population growth rates (Cuthbert *et al*. 2004; Oro *et al*. 2004; Louzao *et al*. 2006). This low sensitivity, together with some demographic buffer capacities (e.g. age at recruitment, skip breeding, immigration) could explain how shearwater populations have persisted despite centuries of rat impact. Unfortunately, there are not enough reliable data on Yelkouan and Balearic shearwater breeding success and cases of breeding in rat-free islands to allow rigorous inter-species comparison of shearwater sensitivity to rats. This review failed to find an overall significant difference between the effect of rat absence (either naturally absent or eradicated) and local rat control on the breeding success of the Cory's shearwater. This apparent non-significance may be a result of insufficient data available on the long-term monitoring of Cory's shearwater breeding success after rat eradications, since rat eradication has been proven to enhance long-term ecological benefits compared to local control (Pascal *et al*. 2008). This also suggested that both rat control and rat eradication may be efficient methods to recover shearwater breeding success. Unfortunately, rat densities and control efforts were unable to be covered in this review (because of paucity of accurate data), yet these two parameters are expected to determine the magnitude of the increase in shearwater breeding success and thus the success of a rat removal program (Jouventin *et al*. 2003; Igual *et al*. 2006). When rat densities are high, the increase in seabird breeding success after rat removal is expected to be sharper than for colonies where rat densities are low and, similarly, benefits from rat removal should increase with control effort (Igual *et al*. 2006).

Overall, few studies have been published on rat impact on Mediterranean Procellariiformes (Table 5), especially on the storm petrel, although this species seems to be the most vulnerable to rat impact. This lack of data may be due to the difficulty of taking census, monitoring and hence evaluating signs of population changes for this cryptic species. In many cases, unfortunately, reports of rat impact on seabirds were circumstantial and equivocal and sometimes too subjective to allow for clear inferences on the real magnitude of rat impact. Moreover, as predation is a cryptic phenomenon, it is often difficult to make direct observations of predation by rats in the field, especially for burrow-nesting birds (Towns *et al*. 2006) and to distinguish predation events from the consumption of neglected eggs or carrion provided by natural death (Norman 1975; Towns *et al.* 2006; Quillfeldt *et al.* 2007). At present, there is an urgent need to collect more data on the breeding biology of the four Mediterranean burrowing seabirds throughout the Mediterranean Basin, to perform long-term studies and rigorously monitor breeding success of seabirds before and after conservation measures and to routinely quantify rat impact on their productivity with standardized methods.

| Country | Area | Island | Species | Stages affected | Effects on seabird populations | References |
|---|---|---|---|---|---|---|
| Spain | Cabrera, Balearics | Estell Xapat and Estell de s'Esclatasang | C | Eggs & chicks | Major impact: breeding success increased from 0% to 40–42% after rat eradication | Amengual & Aguilar (1998) |
| | | Several islets | H | All stages? | Desertion of colonies after rat colonization in the 1970s | Amengual *et al*. (2000) |
| | Balearics | Cabrera and other islets | M | Chicks? | No apparent impact on breeding success at least under a critical threshold value of rat density | Aguilar (2000), Louzao *et al*. (2006) |
| | | | M | Eggs mainly | Medium overall impact. Locally high | Gallo-Orsi (2003) |
| | | | M | Eggs mainly | Breeding success increased after rat control | Ruiz & Martí (2004) |
| | Chafarinas | | C | Chicks mainly | Breeding success increased from 27 to 70% and chick mortality decreased from 52 to 11% after rat control | Orueta *et al*. (2002), Igual *et al.* (2006) |
| Italy | Olbia, Sardinia | Tavolara and Molara | Y | Eggs mainly | Major breeding failure in certain years | N. Baccetti, personal communication |
| | Lazio, Ponziano | Zannone | C | Eggs & chicks | Major impact: breeding success increased from 0% to 100% after rat control | Corbi *et al*. (2005) |
| | Tuscany | Scola | C | Chicks mainly | Major impact: very low breeding success on rat-infested islands (0%) compared to rat-free islands. Breeding success increased after rat control | Perfetti *et al*. (2001) |

**Table 5. Continued**

| **Country** | **Area** | **Island** | **Species** | **Stages affected** | **Effects on seabird populations** | **References** |
|---|---|---|---|---|---|---|
| | | Montecristo | Y | Chicks mainly | Low breeding success due to rats | Baccetti (1993) |
| Malta | Malta | Malta | Y | Eggs & chicks | Heavy annual losses of eggs and chicks (between 40% and 100%) mainly due to rats | J. Borg, personal communication |
| | | | C | Eggs mainly | Low effect of rat predation compared to egg taking by humans | Borg & Sultana (2000),<br>Borg & Cacha-Zammit (1998) |
| France | Hyères | Port-Cros and Porquerolles | Y | Eggs & chicks | Rat impact fluctuated from year to year | Cheylan (1985), Vidal (1985) |
| | Frioul, Marseilles | Pomègues and Ratonneau | C | ? | Breeding success increased from 25% fledged chicks/ adult to 65% and 75% after rat control | CEEP-Marseille (unpublished report) |
| | Lavezzi, Corsica | Lavezzu | C | Chicks mainly | Rats responsible for nearly 85% of breeding failure in certain years | Thibault (1995) |
| | | Lavezzu | C | ? | Breeding success increased from 44% to 83% after eradication | Lorvelec & Pascal (2005),<br>Pascal *et al*. (2006, 2008) |
| | Northern Corsica | Gargalu and Giraglia | C | ? | Breeding success on Gargalu: 3% (with rats), on Giraglia: 73% (without rats) | Thibault *et al*. (1997) |

**Table 5.** Review of ship rat impact on Mediterranean Procellariiformes (C: *Calonectris diomedea*; Y*: Puffinus yelkouan*; M: *Puffinus mauretanicus*; H: *Hydrobates pelagicus*).

### 2.2.4.3. Conservation implications

Over the past ten years, eradication of invasive species has become a powerful tool to prevent further extinctions and to restore native island ecosystems (Veitch & Clout 2002; Towns *et al*. 2006; Howald *et al*. 2007). In particular, seabird communities have clearly benefitted from the removal of introduced rats from islands worldwide. Indeed, many studies report a significant increase in breeding success of seabirds or new breeder establishment on islands once again suitable for breeding, following rat eradications (Veitch & Clout 2002; Towns *et al*. 2006). In the Mediterranean, few eradication attempts have been carried out on islands in the past 20 years, and most were restricted to islands < 10 ha (L. Ruffino, unpublished data). Today, island managers are provided with a variety of powerful methods to eradicate rats and mitigate non-target effects and secondary poisoning events. Moreover, island area may no longer be a limiting factor for rat eradications. Howald *et al*. (2007) reported 159 successful ship rat eradications worldwide, 14 of them conducted on islands larger than 500 ha. Conservation managers are now able to remove rats from large and biologically complex islands. They also manage to eradicate rodents that have been introduced on islands for hundreds of years (e.g. *Rattus exulans* on New Zealand islands; Howald *et al*. 2007). The main challenges for Mediterranean island managers, then, may be to deal with social, ecological and funding issues. Because most Mediterranean islands are inhabited and closely linked to main islands and continent by human transport and activities, appropriate environmental education and means of preventing reinvasions are required. Furthermore, Mediterranean island systems house non-target vertebrate species with high conservation value which need to be taken into account when planning eradication programmes, but which are expected to benefit from rat removal. As Mediterranean islands are currently under increasing pressure from various human activities, any management operations that would improve seabird population health should be promoted.

### 2.2.5. Conclusion

The Mediterranean context is particularly intriguing, since the survival of the four Mediterranean Procellariiformes after 2,000 years of ship rat presence on islands seems to go against the current global threat to burrowing seabirds from rat impact (Atkinson 1985; Jones *et al*. 2008; IUCN 2008). Thus, the apparent paradox of long-standing coexistence between rats and seabirds raises some new conservation questions, especially on the ability of native island species to persist with introduced rats. Sound understanding of the mechanisms of such persistence is likely to provide important clues to conservation and restoration priorities on other rat-invaded islands worldwide. Here we hypothesize that the long-term persistence of these seabirds at the scale of the Western Mediterranean Basin may have been facilitated by the various biogeographical contexts of Mediterranean islands, providing areas where interactions with introduced rats may be limited. Rat densities on islands and their fluctuations over seasons and years are known to be major factors in seabird vulnerability within breeding sites (e.g. Igual *et al*. 2006), with seabird productivity increasing when rat densities are low (Quillfeldt *et al*. 2007). This intriguing long-term persistence, along with evidence of rat impact on Mediterranean seabirds, also raises new questions on the mechanisms and the intensity by which invasive rats really affect seabirds, and on their ability to drive them to extinction. More work is also needed to clarify the complex relationships linking factors likely to influence rat population densities (i.e. resource abundance, presence of other alien predators or competitors on islands), foraging strategy of rats and rat impact on seabird populations. As claimed by Towns *et al*. (2006), we suggest that the role of rats in seabird population decline should be carefully evaluated relative to that of other factors and caution should be used in attributing any seabird breeding failures, and local or global extinctions to rats. The better we understand both patterns and mechanisms causing decline, the better we can focus our efforts on the most effective measures to mitigate threats.

**Supplementary material.** Location of the 292 islands studied and indication on presence/absence on islands of the four seabird species (C: *Calonectris diomedea*, M: *Puffinus mauretanicus*, Y: *P. yelkouan*, H: *Hydrobates pelagicus*) and *Rattus rattus* (R).

[a] Islands not used in GLMs for rats but in the relationship between rat presence and island area (Figure 3).

A: Algerian coast, B: Balearic islands, C: Corsica, F: French coastal islands, I: Italian coastal islands, M: Moroccan coastal islands, S: Spanish coastal islands, Sa: Sardinia, Si: Sicily, T: Tunisian coastal islands.

| **Area** | **Island/islet** | **Presence** | | | | |
|---|---|---|---|---|---|---|
| | | C | M | Y | H | R |
| A-Bejaia | El Euch=Pigeons | | | 0 | | 0 |
| | Pisans | | | 0 | | 1 |
| | Sahel | | | 0 | | 0 |
| A-Habibas | Ile occidentale=Gharbia | 1 | | | 0 | 1 |
| | Ile orientale=Chergui | 1 | | | 0 | 1 |
| B-Cabrera | Cabrera Gran | 0 | 1 | | 0 | 1 |
| | Ses Bledes | 1 | 0 | | 1 | 1 |
| | L'Imperial | 0 | 0 | | 0 | 1 |
| | Ses Rates | 1 | 0 | | 0 | 1 |
| | Na Redona | 0 | 0 | | 0 | 1 |
| | Estell Xapat | 1 | 0 | | 0 | 0 |
| | Estell de Coll | 1 | 0 | | 0 | 0 |
| | Estell d'en Fora | 1 | 0 | | 0 | 0 |
| | Fonoll | 0 | 0 | | 0 | 1 |
| | Conills=Conejera | 0 | 1 | | 0 | 1 |
| | Esponja | 0 | 0 | | 1 | 0 |
| | S'Alga | | | | | 0[a] |
| | Porcs | | | | | 0[a] |
| B-Ibiza | Ibiza | | | | | 1 |
| | Togomago | | 1 | | | 1 |
| | Caragolé | | 0 | | | 0 |
| | Penjats=Ahorcados | | 0 | | | 0 |
| | Vedra | | 0 | | | 1 |
| | Vedranell | | 0 | | | 1 |
| | S'Espartar=S'Espart | | 0 | | | 0 |
| | S'Espardell de s'Espartar | | | | | 0[a] |
| | Bosc=Bosque | | 1 | | | 1 |
| | Sa Conillera=Conejera | 1 | 1 | | | 1 |
| | Bleda Plana | | | | | 1[a] |
| | Ses Rates | | | | | 1[a] |
| | Escull de Cala d'Hort | | | | | 0[a] |
| | Margalides=Margaritas | | | | | 0[a] |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  | Na Plana | 1 | 0 |  | 1 | 0 |
|  | Na Pobra | 1 | 0 |  | 1 | 0 |
|  | Na Foradada | 1 | 0 |  | 1 | 0 |
|  | Estell de Ss |  |  |  |  | 1[a] |
|  | Estell d'en Terra |  |  |  |  | 0[a] |
| B-Formentera | Formentera |  | 1 |  |  | 1 |
|  | Espalmador |  | 1 |  |  | 1 |
|  | Gastavi |  | 0 |  |  | 1 |
|  | Sa Torre |  |  |  |  | 1[a] |
|  | Pouet |  |  |  |  | 1[a] |
|  | Redona |  |  |  |  | 1[a] |
|  | Na Pelada | 0 | 0 |  |  | 0 |
|  | Na Moltona | 0 | 0 |  |  | 0 |
|  | Na Guardis | 0 | 0 |  |  | 0 |
|  | Pentaleu |  |  |  |  | 1 |
|  | Sa Torre |  |  |  |  | 1[a] |
|  | Alcanada |  |  |  |  | 1[a] |
|  | Sa Porrasa |  |  |  |  | 1[a] |
| B-Menorca | Menorca | 1 | 1 |  |  | 1 |
|  | Colom |  | 0 |  |  | 1 |
|  | Ses Sargantanes |  |  |  |  | 1[a] |
|  | Bledes |  | 0 |  |  | 1 |
|  | L'Aire | 0 | 1 |  |  | 1 |
|  | Porros=Sa Nitja |  | 0 |  |  | 0 |
|  | Grande de Addaia |  | 0 |  |  | 0 |
| C-Ajaccio, Sanguinaires | Binicodrell |  |  |  |  | 0[a] |
| C-Bonifacio Strait | Mezzu Mare |  |  |  |  | 1 |
|  | Petit îlot du Fazzio=Fazzuolo Piccolo | 1 |  | 0 | 0 | 0 |
|  | Santa Eularia |  |  |  |  | 1[a] |
|  | Sal Rossa |  |  |  |  | 1[a] |
|  | Negres |  |  |  |  | 0[a] |
|  | Bleda na Gorra=Pequeña |  |  |  |  | 0[a] |
|  | Bleda na Bose=Mayor |  |  |  |  | 0[a] |
| B-Mallorca | Mallorca |  | 1 |  |  | 1 |
|  | Malgrat | 0 | 1 |  |  | 1 |
|  | Conills=Malgrat Petit | 1 | 1 |  | 1 | 1 |
|  | Toro | 1 | 0 |  |  | 0 |
|  | Sa Dragonera | 1 | 1 |  |  | 1 |
|  | Curt=Caragol | 0 | 0 |  |  | 0 |
| C-Girolata, Scandola | Terra | 0 |  | 0 | 0 | 1 |
|  | Gargalu | 1 |  |  | 0 | 1 |
|  | Garganellu |  |  |  | 0 | 1 |
|  | Palazzu |  |  |  | 0 | 0 |
| C-Lavezzi | Porri | 0 |  |  | 0 | 0 |
|  | Lavezzu | 1 |  | 0 | 0 | 1 |
|  | Ilot A=Luigi Giafferri | 1 |  | 0 | 0 | 1 |
|  | Ilot B=Giacinto Paoli | 1 |  | 0 | 0 | 1 |
|  | Ilot C=Silene |  |  | 0 | 0 | 1 |
|  | Ilot D=Gian Pietro Gaffori |  |  | 0 | 0 | 1 |
|  | Ilot E=Pasquale Paoli |  |  | 0 | 0 | 1 |
|  | Ilot F=Cala della Chiesa |  |  | 0 | 0 | 1 |
|  | Ilot G=Andrea Ceccaldi |  |  | 0 | 0 | 1 |
|  | Ilot H=Cala di Giunco |  |  | 0 | 0 | 1 |
|  | Ilot K=La Sémillante |  |  | 0 | 0 | 1 |
|  | Ilot L |  |  |  |  | 1[a] |
|  | Cavallo | 1 |  | 0 | 0 | 1 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  | Grand îlot du Fazzio=Fazzuolo Grande |  |  | 0 | 1 |
|  | Saint Antoine |  |  | 0 | 0 |
|  | Grain de sable |  |  | 0 | 0 |
|  | Grand îlot Bruzzi | 0 |  | 0 | 1 |
|  | Senetosa=Scoglio Longu |  |  | 0 | 1 |
| C-Calvi | Piana di Portigliolo |  |  | 0 | 1 |
| C-Cap Corse | Spano | 0 | 0 | 0 | 1 |
|  | Giraglia | 1 | 1 | 0 | 1 |
|  | Finocchiarola | 0 | 0 | 0 | 1 |
|  | Mezzana | 0 | 0 | 0 | 1 |
|  | Pietricaggiosa | 1 | 0 | 0 | 1 |
|  | Toro Grande=Grand Toro | 1 | 0 |  | 1 |
|  | Toro Piccolo=Petit Toro | 1 | 0 |  | 0 |
|  | 1er Rocher du Toro Piccolo | 0 | 0 |  | 0 |
|  | 2e Rocher du Toro Piccolo | 0 | 0 |  | 0 |
|  | La Folaca | 0 | 0 | 0 | 1 |
|  | La Folachedda | 0 | 0 | 0 | 1 |
| F-Cannes, Lérins | Rocher NW de la Folachedda | 0 | 0 | 0 | 1 |
|  | Sainte Marguerite | 0 | 0 |  | 1 |
|  | Saint Honorat | 0 | 0 |  | 1 |
|  | La Tradelière | 0 | 0 |  | 1 |
|  | Saint Féréol | 0 | 0 |  | 1 |
| F-Fréjus | Lion de terre | 0 | 0 |  | 1 |
|  | Lion de mer | 0 | 0 |  | 1 |
|  | D'Or | 0 | 0 |  | 1 |
|  | Les Vieilles | 0 | 0 |  | 1 |
| F-Hyères | Grand Ribaud | 0 | 0 | 0 | 1 |
|  | Portugais N | 0 | 0 |  | 1 |
|  | Petit Ribaud | 0 | 0 |  | 0 |
|  | San Bainsu | 1 | 0 | 0 | 1 |
|  | Sperduto | 0 | 0 | 1 | 0 |
|  | Porraggia Grande | 0 | 0 | 0 | 0 |
|  | Porraggia Piccole | 0 | 0 | 0 | 0 |
|  | Ratino | 1 | 0 | 0 | 1 |
| C-Palombaggia | Piana di Cavallo | 0 | 0 | 0 | 1 |
|  | Vacca | 1 | 0 | 1 | 0 |
|  | Forana | 1 | 0 | 0 | 1 |
|  | Maestro Maria | 0 | 0 | 0 | 1 |
|  | Piana | 1 | 0 | 0 | 1 |
|  | Les Cristaux=Christaou | 0 | 0 |  | 0 |
|  | Cap Taillat=Cartaya | 0 | 0 |  | 0 |
|  | Porquerolles | 1 | 1 | 0 | 1 |
|  | Le Levant | 1 | 1 | 0 | 1 |
|  | Port-Cros | 1 | 1 | 0 | 1 |
|  | Bagaud | 1 | 1 | 0 | 1 |
|  | Gabinière | 0 | 0 | 0 | 1 |
|  | Petit Langoustier | 0 | 0 | 0 | 1 |
|  | Gros Sarranier | 0 | 0 | 0 | 1 |
|  | Petit Saranier | 0 | 0 | 0 | 1 |
|  | Rascas | 0 | 0 |  | 0 |
|  | Rousset | 0 | 0 |  | 0 |
|  | Deux Frères des Mèdes N | 0 | 0 |  | 0 |
|  | Deux Frères des Mèdes S | 0 | 0 |  | 0 |
| F-La Ciotat-Sanary | Verte | 0 | 0 |  | 1 |
|  | Bendor | 0 | 0 |  | 1 |
|  | Rousse=Pierreplane | 0 | 0 |  | 1 |
|  | Embiez | 0 | 0 |  | 1 |
|  | Grand Rouveau | 0 | 0 |  | 1 |

| | | | | | |
|---|---|---|---|---|---|
| | Redonne | 0 | 0 | | 0 |
| | Longue | 0 | 0 | | 0 |
| | Ratonnière | 0 | 0 | | 1 |
| | L'Esterel | 0 | 0 | | 0 |
| | Les Fourmigues de l'Escampobariou | 0 | 0 | | 0 |
| | Léoube | 0 | 0 | | 1 |
| | L'Estagnol S | 0 | 0 | | 1 |
| | L'Estagnol N | 0 | 0 | | 1 |
| | Endoume S | 0 | 0 | | 0 |
| F-Marseille, Riou | Maïre | 1 | 1 | 1 | 1 |
| | Les Cristaux=Christaou | 0 | 0 | | 0 |
| | Cap Taillat=Cartaya | 0 | 0 | | 0 |
| | Porquerolles | 1 | 1 | 0 | 1 |
| | Le Levant | 1 | 1 | 0 | 1 |
| | Port-Cros | 1 | 1 | 0 | 1 |
| | Bagaud | 1 | 1 | 0 | 1 |
| | Gabinière | 0 | 0 | 0 | 1 |
| | Petit Langoustier | 0 | 0 | 0 | 1 |
| | Gros Sarranier | 0 | 0 | 0 | 1 |
| | Petit Saranier | 0 | 0 | 0 | 1 |
| | Rascas | 0 | 0 | | 0 |
| | Rousset | 0 | 0 | | 0 |
| | Deux Frères des Mèdes N | 0 | 0 | | 0 |
| | Deux Frères des Mèdes S | 0 | 0 | | 0 |
| F-La Ciotat-Sanary | Verte | 0 | 0 | | 1 |
| | Bendor | 0 | 0 | | 1 |
| | Rousse=Pierreplane | 0 | 0 | | 1 |
| | Embiez | 0 | 0 | | 1 |
| | Grand Rouveau | 0 | 0 | | 1 |
| | Petit Rouveau | 0 | 0 | | 1 |
| | Petit Rouveau | 0 | 0 | | 1 |
| | Croisette | 0 | 0 | | 1 |
| | Deux Frères N | 0 | 0 | | 0 |
| F-Marseille, Frioul | Ratonneau | 1 | 1 | 0 | 1 |
| | Pomègues | 1 | 0 | 0 | 1 |
| | Tiboulen de Ratonneau | 1 | 0 | | 0 |
| | Château d'If | 0 | 0 | | 0 |
| | Endoume N | 0 | 0 | | 0 |
| | Château d'If | 0 | 0 | | 0 |
| | Endoume N | 0 | 0 | | 0 |
| | Endoume S | 0 | 0 | | 0 |
| F-Marseille, Riou | Maïre | 1 | 1 | 1 | 1 |
| | Tiboulen de Maïre | 1 | 0 | 1 | 1 |
| | Pharillons | 0 | 0 | 0 | 0 |
| | Jarron | 0 | 0 | 1 | 1 |
| | Jarre | 1 | 1 | 1 | 1 |
| | Plane=Calseraigne | 1 | 0 | 1 | 1 |
| | Riou | 1 | 1 | 1 | 1 |
| | Grand Congloué | 1 | 0 | 1 | 1 |
| | Petit Congloué | 1 | 0 | 1 | 1 |
| | Empereurs=Impériaux S | 0 | 0 | 1 | 0 |
| | Empereurs=Impériaux N | 0 | 0 | | 0 |
| | Moyade | 0 | 0 | 0 | 1 |
| I-Lazio, Ponziono | Palmarola | 1 | 1 | | 1 |
| | Ventotene | 1 | 1 | | 1 |
| | Santo Stefano | | | | 1[a] |
| | Gavi | | | | 1[a] |
| | Zannone | 1 | 1 | | 1 |
| | Ponza | 1 | 1 | | 1 |
| I-Tremiti | San Domino | 1 | 1 | | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Croisette | 0 | | 0 | | 1 |
| | Deux Frères N | 0 | | 0 | | 0 |
| F-Marseille, Frioul | Ratonneau | 1 | | 1 | 0 | 1 |
| | Pomègues | 1 | | 0 | 0 | 1 |
| | Tiboulen de Ratonneau | 1 | | 0 | | 0 |
| | Montecristo | | | 1 | | 1 |
| | Porto Ercole | | | | | 1[a] |
| | Capraia | | | 1 | | 1 |
| | Pianosa | | | 1 | | 1 |
| | Giglio | | | | | 1 |
| | Palmaiola | 1 | | | | 1 |
| | Elba | | | | | 1 |
| | Peraiola | | | | | 1[a] |
| | Topi | | | | | 1 |
| M-Alboran Sea | Alborán | 0 | 0 | | 0 | 0 |
| M-Chafarinas | Congresso | 1 | | | 0 | 1 |
| | Rey | 0 | | | | 1 |
| | Isabel II | 0 | | | | 1 |
| Ma-Malta | Malta | 1 | | 1 | 0 | 1 |
| | Gozo | 1 | | 1 | 1 | 1 |
| | Fungus | 1 | | | 0 | 1 |
| | Comino | 1 | | 1 | 0 | 1 |
| | Cominoto | 0 | | 1 | 0 | 1 |
| | Filfla | 1 | | | 1 | 0 |
| S-Aguilas | El Fraile | | 0 | | | 0 |
| S-Alicante | Benidorm | 0 | 0 | | 1 | 0 |
| | Mitjana | | 0 | | | 0 |
| | L'Olla | | 0 | | | 0 |
| S-Cabo Nao | Portichol=Portitxol | | 0 | | | 1 |
| | San Nicola | | | 1 | | 1 |
| | Pianosa | | | | | 0 |
| | Capraia=Caprara | 1 | | | | 1 |
| I-Tuscany | Giannutri | 1 | | 0 | 0 | 1 |
| | La Scola | 1 | | 1 | | 1 |
| | Rondella | | 0 | | | 1 |
| | Mayor=del Barón | | 0 | | | 1 |
| | Perdiguera | | 0 | | | 1 |
| S-Cartagena | Las Palomas | 1 | 0 | | 1 | 1 |
| | Escombreras | 0 | 0 | | | 1 |
| S-Castellón, Columbretes | Columbrete Grande=Colibre | 1 | 0 | | 1 | 0 |
| | La Ferrera | 0 | 0 | | | 0 |
| | La Foradada | 1 | 0 | | | 0 |
| | El Bergantin=Carallòt | 0 | 0 | | | 0 |
| S-Girona, Medes | El Medallot | 0 | 0 | | | 0 |
| | La Meda Gran | 0 | 0 | | | 0 |
| | La Meda Petita | 0 | 0 | | | 0 |
| | Les Feranelles | 0 | 0 | | | 0 |
| | Els Tascons grossos | 0 | 0 | | | 0 |
| | El Carall Bernat | 0 | 0 | | | 0 |
| | Els Tascons Petits | 0 | 0 | | | 0 |
| S-Mazarrón | Cueva de Lobos | | 0 | | | 0 |
| | La Isla | | 0 | | | 1 |
| | Plana | | 0 | | | 1 |
| Sa-Alghero | Foradada | 1 | | | 1 | 0 |
| | Piana de Alghero | | | | | 1 |
| Sa-Capo Altano | San Pietro | | | 1 | | 1 |
| Sa-Capo Carbonara | Cavoli | 0 | | 1 | | 1 |
| Sa-Capo del Falcone | Asinara | | | | | 1 |

| | | | | | |
|---|---|---|---|---|---|
| S-Cabo Palos | Hormiga Grande | 0 | 0 | 1 | 0 |
| | Grosa | | 0 | 1 | 1 |
| | El Farallón | | 0 | | 0 |
| | Sujeto | | 0 | | 1 |
| | Nibani E | | | | 1[a] |
| | Nibani W | | | | 1[a] |
| | Mortorio | 1 | | | 1 |
| | Camere E | 1 | | | 1 |
| | Camere W | 1 | | | 1 |
| | Soffi | | | | 1[a] |
| Sa-Golfo di Palmas | La Vacca | 1 | | 0 | 1 |
| | Torro | | | | 0 |
| Sa-La Maddalena | Spargi | 1 | 1 | | 1 |
| | Spargiotto | 1 | 0 | | 0 |
| | Budelli | 1 | 0 | | 1 |
| | Razzoli | 1 | 0 | | 1 |
| | Santa Maria | 1 | 1 | 0 | 1 |
| | Barrettini | 1 | 0 | | 0 |
| | Corcelli | | 0 | | 1 |
| | Piana de Corcelli | 0 | 0 | | 1 |
| | Stramanari W | 0 | 0 | | 1 |
| | Stramanari E | 0 | 0 | | 1 |
| | Carpa | 1 | 0 | | 1 |
| | Caprera | | | | 1 |
| | Maddalena | | | | 1 |
| Sa-Olbia | Figarolo=Figarello | 1 | 1 | 0 | 1 |
| | Molarotto | 0 | 0 | | 0 |
| | Molara | 0 | 1 | | 1 |
| | Porri | 0 | 0 | | 0 |
| | Piana | | | | 1[a] |
| Sa-Capo Mannu | Mal di ventre | 0 | 0 | | 0 |
| Sa-Costa Esmeralda | Nibani S | | | | 1[a] |
| | Nibani N | | | | 1[a] |
| | Tavolara | 0 | 1 | | 1 |
| | Topi | 0 | 0 | | 0 |
| Sa-Teulada | Rossa | | | | 1 |
| Si-Messina, Aeolian | Vulcano | | | | 1 |
| | Lipari | | | | 1 |
| | Salina | | | | 1 |
| | Alicudi | | | | 1 |
| | Filicudi | | | | 1 |
| | Stromboli | | | | 1 |
| | Stromcolicchio | | | | 1 |
| | Panarea | | | | 1 |
| | Baziluzzo | | | | 1 |
| Si-Palermo | Ustica | 1 | | | 1 |
| Si-Trapani, Aegadian | Marretimo | | | 1 | 1 |
| | Levanzo | | | | 1 |
| | Favignana | | | | 1 |
| Si-Trapani, Stagnone | Grande=Lunga | | | | 1[a] |
| Si | Pantellaria | 1 | | | 1 |
| Si-Pelagie | Linosa | 1 | | | 1 |
| | Lampione | 1 | | | 0 |
| | Lampedusa | | 1 | | 1 |
| T-Zembra | Zembra | 1 | 0 | 0 | 1 |
| | Zembretta | 0 | 0 | 0 | 1 |
| | Lantorcho | | | | 0[a] |

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# Chapitre 3.

## RATS ET OISEAUX MARINS : INTERACTIONS AUX CAVITÉS, CAPACITÉS DE PRÉDATION ET ÉVALUATION DE L'IMPACT

(a) cages de repos pour les rats capturés sur l'île de Bagaud avant le début des tests de prédation de la Partie 3.3. ; (b) puffin yelkouan devant son terrier artificiel sur la colonie du Grand Peyre de Port-Cros ; (c) mise en place des dispositifs expérimentaux pour les tests de prédation ; (d) empreintes de puffins dans le sable déposé à l'entrée d'un terrier ; (e) starique minuscule *Aethia pusilla* prédatée par un rat surmulot sur l'île Kiska, Aléoutiennes ; (f) rat noir consommant un œuf endommagé de paille-en-queue à brin rouge (*Phaethon rubricauda*) sur l'île Europa.

# Avant propos

Après un deuxième chapitre portant sur la dimension temporelle des introductions d'espèces et les interactions entre rats noirs et oiseaux marins de Méditerranée à une large échelle géographique, dans le chapitre 3, nous nous sommes intéressés plus finement aux mécanismes d'interactions entre rats et oiseaux marins sur les iles, et aux mécanismes d'impact des rats.

Au cours des **Parties 3.1.** et **3.2.**, nous avons étudié les interactions entre rats noirs et un oiseau marin, le puffin yelkouan *Puffinus yelkouan*, au niveau des sites de reproduction des oiseaux, sur une île de Méditerranée, l'île de Port Cros (Var, France). Le puffin yelkouan est une espèce endémique du bassin méditerranéen dont les effectifs mondiaux seraient estimés à quelques milliers de couples (Bourgeois & Vidal 2008). C'est une espèce de taille moyenne (poids adulte = 350-500g), nocturne, à nidification hypogée (Figures 6a, b), qui se reproduit exclusivement sur les îles, à l'intérieur de cavités ou terriers (Figures 6c, e), situés au niveau de falaises rocheuses, zones d'éboulis et grottes calcaires (Bourgeois & Vidal 2007 ; Figures 6d, f). L'espèce est longévive, les adultes ne pondent qu'un seul œuf par an et le poussin n'atteind la maturité sexuelle que vers l'âge de 3-5 ans (Bourgeois 2006). Ces caractéristiques la rendent particulièrement vulnérable aux prédateurs introduits, notamment les chats harets (Bonnaud *et al.* 2007) et les rats (e.g. Baccetti 1993 ; N. Bacetti, J. Borg, comm.pers.), aux perturbations anthropiques et captures accidentelles par les engins de pêche (Bourgeois & Vidal 2008). L'île de Port Cros revêt un intérêt particulier pour la conservation du puffin yelkouan. En effet, l'archipel des îles d'Hyères dont elle fait partie concentre environ 95% des effectifs français de puffin yelkouan et une part significative de la population mondiale. La présence du rat noir sur Port Cros date probablement d'une époque ancienne. En effet, un grand nombre d'indices de présence humaine sur l'île ont été découverts depuis la période chalcolithique (de -2300 à -1800 av. J.C.) à la période moderne (Pasqualini 1992). L'idée de ces travaux de recherche (**Parties 3.1.** et **3.2.)** a été d'étudier les interactions entre rats et puffins au niveau des cavités de reproduction des oiseaux dans deux contextes différents. Ainsi, les interactions aux cavités ont été étudiées durant la première année de contrôle d'un prédateur apical, le chat haret (2004-2005 ; **Partie 3.1.**), et après l'opération de contrôle des chats (2007-2008 ; **Partie 3.2.**), lorsque les effectifs de la population de chats ont été réduits de manière drastique. L'objectif principal de ces études a été de suivre l'évolution des patrons d'interactions, du comportement des rats aux cavités de puffins et de l'intensité de l'impact du rat entre les deux contextes écologiques.

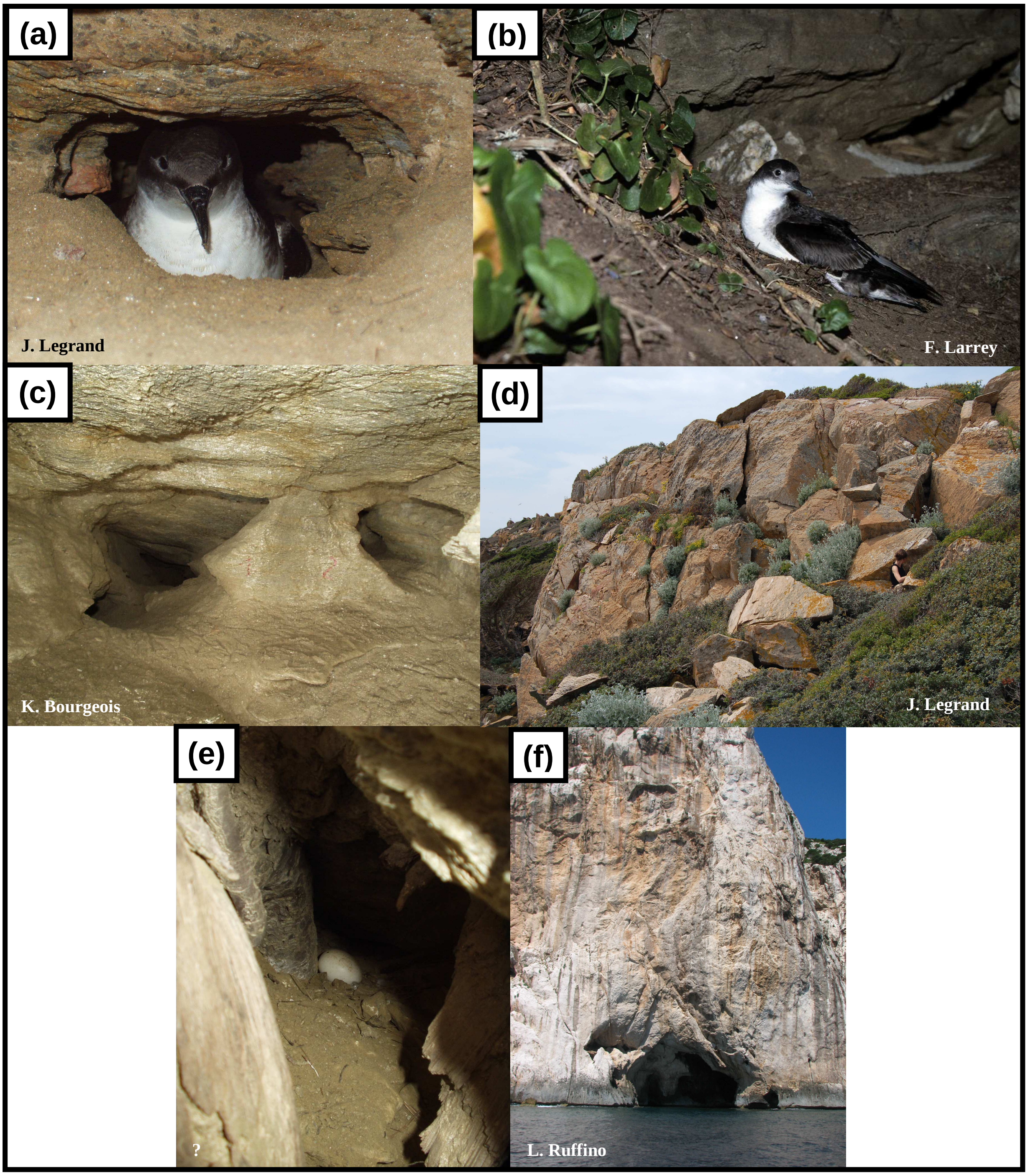

**Figure 6**. Photos de puffin yelkouan dans sa cavité de reproduction (a) et sur la colonie du Grand Peyre de Port-Cros (b), de cavités profondes et sinueuses utilisées par les puffins pour la reproduction (c, e) et de zones marginales de falaises, éboulis ou grottes calcaires sur les îles du Levant, archipel des îles d'Hyères (d) et Tavolara, Sardaigne (f).

Les travaux qui ont été développés dans la **Partie 3.3.** répondent à la nécessité de mieux comprendre les mécanismes d'impact des rats introduits sur les oiseaux, et en particulier à la méconnaissance des déterminismes de prédation des rats sur les œufs. Ainsi, dans cette partie nous nous sommes intéressés aux capacités des rats noirs à casser et consommer des œufs, et aux facteurs susceptibles d'influencer leur succès de prédation. Les tests de capacités de prédation ont été effectués sur des individus sauvages sur l'île de Bagaud, située à 500m de Port Cros, à proximité des sites où les rats ont été capturés afin de limiter le stress lié au transport des individus. Dans le cadre de ces expérimentations comportementales, plusieurs variables ont été testées, à savoir la taille de l'œuf, l'état de l'œuf, la masse corporelle des individus, leur sexe ainsi que leur habitat d'origine.

Enfin, au travers des travaux présentés dans la **Partie 3.4.**, nous nous sommes penchés sur les méthodologies qui ont été employées depuis une trentaine d'années dans le but de mesurer l'impact des rats introduits sur les oiseaux marins. Un grand nombre d'études attestent de l'impact du rat sur les oiseaux marins de part le monde. Comment l'impact est-il évalué ? Quelles méthodologies semblent être les plus adaptées à la compréhension des mécanismes et à la quantification de l'impact ? Quels sont les bais associés à chaque méthodologie, ainsi que les lacunes dans nos recherches ? Nous proposons, dans cette partie, une vue générale des outils et méthodes employées ainsi que des perspectives de recherches pour une meilleure évaluation de l'impact des rats.

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# - Partie 3.1. -

## 3.1. INTRODUCED PREDATORS AND CAVITY-NESTING SEABIRDS: UNEXPECTED LOW LEVEL OF INTERACTION AT BREEDING SITES

3.1. Interactions limitées entre prédateurs introduits et oiseaux marins à nidification hypogée aux sites de reproduction des oiseaux

**Résumé :**

Les mécanismes d’interaction et de coexistence entre prédateurs introduits et oiseaux marins longévifs sont encore peu connus à l’heure actuelle. Dans cette étude, les interactions entre le rat noir (*Rattus rattus*), espèce invasive dont les effets délétères sur les populations d’oiseaux marins sont largement reconnus, et un oiseau marin endémique de Méditerranée à nidification hypogée, le puffin yelkouan (*Puffinus yelkouan*), ont été étudiées sur un lot de 60 cavités favorables à la reproduction du puffin tout au long du cycle de reproduction de l’oiseau. Nos résultats ont montré que les visites de cavités par les rats sont significativement plus fréquentes lorsque les puffins ont quitté les colonies que lors de la reproduction proprement dite. Parmi l’ensemble des cavités favorables à la reproduction, ce sont les cavités les plus profondes et les plus sinueuses qui sont préférentiellement utilisées par les puffins. Très peu de visites de rats ont été enregistrées dans les cavités occupées par les puffins et aucun phénomène de prédation n’a été observé. De manière inattendue, ces résultats semblent témoigner d’un faible degré d’interaction entre les rats noirs et les puffins yelkouan, ce qui pourrait avoir facilité la longue coexistence de ces deux espèces sur certaines îles de Méditerranée.

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**Ruffino L., Bourgeois K., Vidal E., Icard J., Torre F. & Legrand J. (2008) Introduced predators and cavity-nesting seabirds: unexpected low level of interaction at breeding sites. *Canadian Journal of Zoology* 86: 1068-1073.**

### 3.1.1. Introduction

Mammalian predators introduced on islands are known to have severely depleted populations of native species, leading some, especially birds, to extinction or local extirpation (e.g. Owens & Bennet 2000; Courchamp *et al*. 2003). Rats *Rattus sp*. are among the most successful predators introduced on islands worldwide, making them one of the largest plagues for island avifauna, especially for small and medium-sized petrels (Moors & Atkinson 1984; Atkinson 1985; Jones *et al*. 2008). As a consequence, numerous cases of breeding failures, sharp decreases in breeding population and local extirpations have been reported after rat introduction on islands (Atkinson 1985; Towns *et al*. 2006). Even if the effects of introduced rats on seabird populations are generally considered to be well-known, the mechanisms by which they interact are still under debate (Courchamp *et al*. 2003; Towns *et al*. 2006). Indeed, as predation is a cryptic phenomenon, direct observations of predation by rats are extremely difficult in the field, especially for cavity and burrow-nesting birds (Norman 1975; Johnston *et al*. 2003; Towns *et al*. 2006). However, according to their predatory-foraging behaviour, we can hypothesise that rats may visit petrel burrows significantly more during the breeding period of birds, especially when birds are the most vulnerable (i.e. egg-incubating and chick-rearing periods), compared to the bird interbreeding exodus period.

From an evolutionary point of view, recent theories (i.e. evolutionary and ecological trap concepts) suggest that indigenous species that have long evolved without predators may fail to rapidly evolve or learn mechanisms to cope with invaders, and predict that they could become “trapped” by their life history traits (i.e. philopatry or longevity), experiencing therefore reduced reproductive success and survival (Schlaepfer *et al*. 2002; Battin 2004). In the Mediterranean, ship rats (*Rattus rattus*, Linnaeus 1758) have been widely introduced on islands for a very long time (up to the Roman period; i.e. 2000 years ago) (Audouin-Rouzeau & Vigne 1994; Vigne & Valladas 1996; Ruffino *et al*. 2009). In this context, the survival of petrels and shearwaters on some of these islands despite hundreds or thousands of years of ship rat presence constitutes an amazing conservation paradox. Moreover, most Western Mediterranean islands where these species breed are rat-invaded (Ruffino *et al*. 2009). Even if the mechanisms by which this coexistence is maintained are not known, we can hypothesise that this may have been facilitated on some islands by a low level of interaction between rats and birds at the bird breeding sites.

In this study, we investigated the interactions between ship rats and a long-lived cavity-nesting seabird, the yelkouan shearwater (*Puffinus yelkouan*, Acerbi 1827) throughout the annual breeding cycle of this seabird, on an island where rat presence has been uninterrupted for centuries. The yelkouan shearwater is strictly endemic to the Mediterranean Basin. Its global distribution is sparse and the world population may be limited to only thousands of breeding pairs (Bourgeois & Vidal 2008). Breeding sites extend from Marseille islands (France) to Bulgarian islands (Black Sea), most of them invaded by rats (Bourgeois & Vidal 2008; Ruffino *et al*. 2009).

Patterns of both shearwater and rat visits to shearwater breeding-cavities were analysed in order to (i) estimate the level of temporal interaction between the two species during the different periods of egg, chick and adult seabird vulnerability, (ii) investigate breeding cavity selection by shearwaters in relation to cavity characteristics and rat visits, and (iii) correlate the breeding success of yelkouan shearwaters with rat visits.

## 3.1.2. Materials and methods

### 3.1.2.1. Study site and data collection

This study was conducted on Port-Cros Island (Hyères archipelago, South-East coast of France), benefiting from National Park status since 1963. Ninety five percent of the French yelkouan shearwater population (1,100-1,600 pairs, IMEP unpublished data) nest along the coast of this archipelago, generally in rock cavities among fallen boulders. At these breeding sites, bird densities are quite low (i.e. 0.027 occupied cavities.m$^{-2}$ (*SD* = 0.002); Bourgeois and Vidal 2007) compared to most Procellariiformes. Moreover, yelkouan shearwaters do not use the overall available set of suitable breeding cavities (i.e. 33% (*SD* = 3.7); Bourgeois & Vidal 2007).

Patterns of rat and shearwater visits, along with shearwater breeding success were recorded during the 2004-2005 breeding season (November 2004 to August 2005) in the largest yelkouan shearwater colony of Port-Cros Island (Figure 6). Rat capture success recorded throughout the year on the island supported moderate rat densities (i.e. 0.022 rat trapped per trap night (*SD* = 0.010); IMEP unpublished data). This colony covers 0.23 ha and we monitored the 60 most accessible cavities. Because our study colony covers a small area and home range sizes of rats are expected to be at least as large as the study area (e.g. Hooker & Innes 1995; Whisson *et al*. 2007), all the cavities monitored for this study were considered to be accessible to rats and thus likely to be visited by rats. The studied cavities (i.e., natural cavities, crevices and burrows) were considered suitable for shearwater nesting when cavity depth and entrance height were sufficient to entirely house and allow passage of shearwaters (Bourgeois & Vidal 2007). Each cavity was tagged and monitored throughout one year, covering the whole yelkouan shearwater breeding cycle and the subsequent interbreeding exodus (Figure 6). Each cavity was checked for rat and shearwater visits 24 times (6 breeding cycle periods and 4 consecutive nights by breeding cycle period; Figure 6) throughout the year (i.e. 1440 observations for the set of 60 cavities). Rat and shearwater visits to each cavity entrance were recorded through tracks printed in fine sand. Feathers, droppings and hairs found inside cavities were also considered as evidence of rat and/or shearwater visits (Russell 2003; Steinkamp *et al*. 2003). Evidence of rat and/or shearwater visits was removed after each record. Results were analysed as frequencies of rat ($f_r$) and shearwater ($f_s$) visits as follows:

$f_r = n_r/(n_c * n_n * n_p)$

$f_s = n_s/(n_c * n_n * n_p)$

$n_r$, $n_s$=number of rat or shearwater visits into cavities

$n_c$=number of cavities monitored

$n_n$=number of nights monitored

$n_p$=number of periods monitored

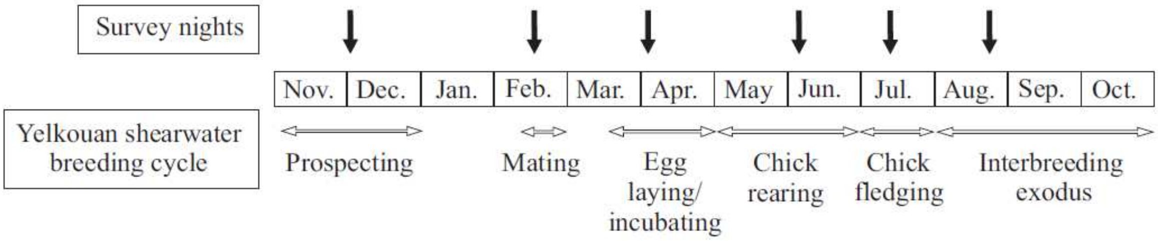

**Figure 7.** Survey nights of shearwater and rat visits to cavities throughout the breeding cycle of the yelkouan shearwater on Port-Cros Island.

Because many cavities were deep and winding, and incubation chambers generally impossible to observe directly, breeding status of cavities (occupied or not by shearwaters) and breeding success were determined using an infra-red mini camera device (Markwell 1997). Finally, the physical characteristics of studied cavities were measured in order to correlate them to rat visits and shearwater breeding success. The physical characteristics of cavities described were (i) cavity depth (in cm, from the entrance to the incubation chamber), (ii) presence/absence of a tunnel leading to the incubation chamber, and (iii) tunnel shape (straight or winding).

#### 3.1.2.2. Data analysis

To test the difference in frequencies of rat and shearwater visits to cavities between the different periods of egg, chick and adult shearwater vulnerability to rats, we used the nonparametric Cochran *Q* test for related samples. Indeed, the different series could not be considered as independent because of the small area of the breeding colony (see the description of the studied area). Frequencies of rat and shearwater visits between two particular periods were also compared through McNemar chi-squared tests in 2x2 contingency tables for these temporally correlated data. For these two binary tests, we applied 1 when at least one rat or shearwater visit was recorded during the four survey nights of each breeding period, and 0 when no visit was recorded. Bonferroni correction for multiple comparisons was applied when needed. A Pearson chi-squared test for independent samples was performed to test the difference between frequencies of rat visits to breeding and non-breeding cavities. To characterise patterns of breeding-cavity selection by yelkouan shearwaters, mean tunnel depths between breeding and non-breeding cavities were compared by performing *t*-test. The proportions of cavities with a winding tunnel and without any tunnel were tested between the set of breeding and non-breeding cavities with the use of Pearson chi-squared tests for independent samples. For Pearson chi-squared tests, Yates correction for continuity was used when $df = 1$ (Quinn & Keough 2002).

### 3.1.3. Results

#### 3.1.3.1. Temporal interaction patterns between shearwaters and rats in cavities

Forty one (68%) monitored cavities were visited by rats at least once, 46 (77%) by yelkouan shearwaters, and 29 (48%) were visited both by rats and shearwaters at least once during the overall 24 survey nights. Overall, frequencies of rat visits to cavities were significantly different between the six periods of the breeding cycle of shearwaters (Cochran *Q* test = 63.0, *df* = 5, $P < 0.001$). Fifty four percent of rat visits (41 rat visits and 31 cavities visited) were recorded during the interbreeding exodus (August). The mean frequency of rat visits.cavity$^{-1}$.night$^{-1}$ was significantly higher when shearwaters had completed their breeding cycle and left the colonies ($f_{r\text{ (interbreeding)}} = 0.173$; McNemar chi-squared tests, significant at the $P = 0.05$ level in all cases, except interbreeding *vs* prospecting ($P = 0.057$); Figure 7). Shearwater visits to breeding and non-breeding cavities were mostly recorded during egg incubating, chick rearing and chick fledging periods (from early March to late June; Figure 72).

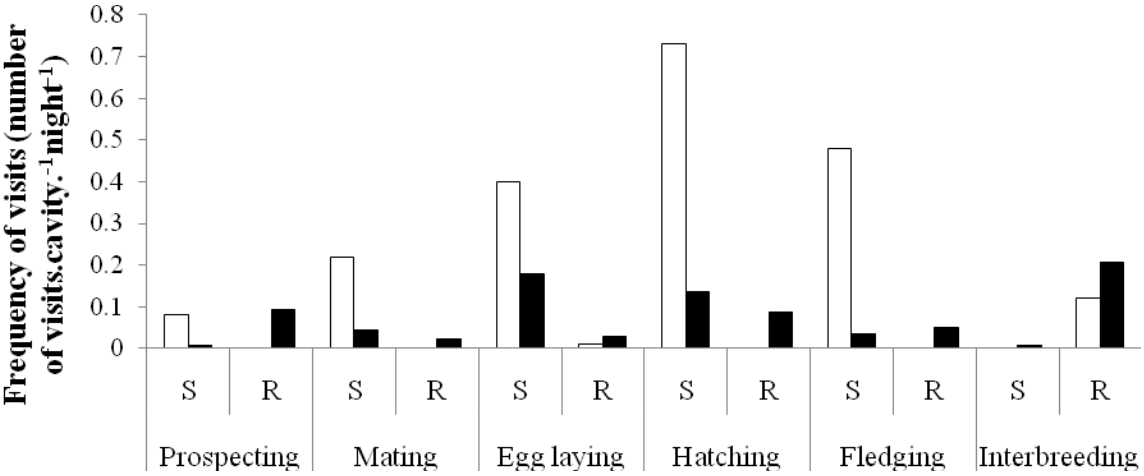

**Figure 8.** Frequency of yelkouan shearwater (*Puffinus yelkouan*; S) and rat (*Rattus rattus*; R) visits to breeding (*n* = 25 cavities) and non-breeding cavities (*n* = 35 cavities) throughout the breeding cycle of yelkouan shearwaters. Open bars are yelkouan shearwater or rat visits to breeding cavities, while solid bars are yelkouan shearwater or rat visits to non-breeding cavities.

### 3.1.3.2. Cavity selection by shearwaters in relation to rat visits

Among the set of 60 studied cavities, 15 (25%) were visited by rats during the shearwater prospecting and mating periods (November-February). Then, all but one of these previously rat-visited cavities were not selected by shearwaters for breeding this year. That is to say that only one of the 25 cavities used by shearwaters for breeding was recorded to have been visited by rats before the breeding period of birds.

### 3.1.3.3. Cavity selection by shearwaters and rat visits in relation to cavity occupation by shearwaters

Yelkouan shearwaters occupied 42% (25 out of 60) of the set of suitable cavities for breeding. The physical characteristics of cavities selected by shearwaters were significantly different from the unoccupied cavities. Yelkouan shearwaters selected the deepest and the most winding cavities, generally exhibiting a tunnel entrance leading to the incubation chamber (Table 6). Cavities selected for breeding were significantly less visited by rats than non-occupied cavities ($f_{r\ \text{(breeding cavities)}} = 0.022$; $f_{r\ \text{(non-breeding cavities)}} = 0.081$; $\chi^2 = 19.9$, $P < 0.001$). Ninety two percent of rat visits to breeding cavities occurred after shearwater departure from the breeding site, whereas rat visits to non-breeding cavities were recorded throughout the entire breeding cycle, with 43% of rat visits observed during the interbreeding exodus (Figure 7).

### 3.1.3.4. Breeding success of shearwaters in relation to rat visits

Nineteen out of 25 (76%) cavities selected by shearwaters for breeding exhibited breeding success (chick fledging). Only 8% ($n = 1$) of rat visits to breeding cavities were recorded during the periods of egg and chick vulnerability (egg incubating, chick rearing and chick fledging). During the five periods when shearwaters were present at colonies (from prospecting to chick fledging), cavities where breeding failed were not more visited by rats than cavities where breeding was a success ($n_{\text{(failure)}} = 0$ rat visit, $n_{\text{(success)}} = 1$ rat visit). When breeding failed, neither evidence of rat predation nor rat tracks were recorded during the periods of egg and chick vulnerability. Rat visits to these cavities were only recorded after shearwaters had left the colony for the interbreeding period.

| | Cavity status | | Statistical results | | |
|---|---|---|---|---|---|
| | Non-breeding cavities | Breeding cavities | *t* | $\chi^2$ | *P*-value |
| *N* | 35 | 25 | | | |
| Mean depth ± SE (m) | 85.1 ± 6.4 | 111.0 ± 8.0 | -2.5 | | < 0.05 |
| Winding tunnel | 6% | 36% | | 9.4 | < 0.01 |
| No tunnel | 34% | 4% | | 3.4 | 0.067 |

**Table 6.** Physical characteristics of cavities in relation to cavity breeding status (breeding or non-breeding).

### 3.1.4. Discussion

This study confirms that ship rats dwell within shearwater colonies and visit their cavities, but surprisingly, our results also showed that rats and shearwaters rarely interact at the colony during the breeding season. Furthermore, no predation incident was detected throughout the entire breeding cycle despite intensive burrow monitoring, and only one rat visit was detected when eggs and chicks were the most vulnerable (egg-laying and chick-rearing periods). Consequently, in this colony, yelkouan shearwaters seem unaffected by rat predation during the breeding cycle. This interesting pattern of limited interactions between introduced rats and shearwaters may be related to the moderate rat densities. On Port-Cros Island, a feral cat population (around 30 individuals) has been established for at least two centuries and, by preying mostly upon rats, cats may have contributed to control rat populations (Bonnaud *et al*. 2007). Moreover, yelkouan shearwaters are restricted to island coastal cliffs for breeding, which are low vegetated compared to inland forest. Vegetation cover has been shown to constrain rat densities since vegetation provides shelter and food for rats (Igual *et al*. 2006; Quillfeldt *et al*. 2008). Thus, by breeding in such marginal habitats, less favoured by rats, shearwaters may be less vulnerable to rat impact.

Unexpectedly, rat visits to cavities were significantly more frequent during the interbreeding exodus (summer), when shearwaters had left the breeding sites. In turn, non-occupied cavities by shearwaters for breeding appeared to be significantly more visited by rats than occupied cavities, even after shearwaters had left the colony. Higher frequencies of rat visits during the interbreeding seabird exodus may not be related to higher rat abundances in summer, as supported our data on rat capture success within shearwater colony (IMEP, unpublished data). Indeed, high rat abundances are not expected during summer on Mediterranean islands since the dry and harsh climate during this season reduces available resources for rats (Cheylan 1988; Thibault 1995). However, during this period of resource scarcity, rats are more likely to search for alternative resources (e.g. Imber *et al*. 2000), and hence may increase their foraging movements into shearwater cavities during summer. This intriguing spatio-temporal segregation pattern, along with lack of predation events, is not consistent with a predatory-foraging behaviour, but more with a bird-avoidance behaviour. Indeed, even if burrowing seabirds have long been known as one of the groups most vulnerable to alien predators (Atkinson 1985; Burger &Gochfeld 1994; Jones *et al*. 2008), medium-sized adult shearwaters (yelkouan shearwater mean body size = 416g; Zotier *et al*..

1999) may be aggressive and may dissuade rats from entering breeding cavities by defending their cavities (Towns *et al*. 2006), and thus may reduce the foraging movements of rats within the colony when shearwaters are breeding. However, numerous cases of sharp breeding failures due to rat impact have been reported for yelkouan shearwaters, and even for the larger Cory’s shearwater (*Calonectris diomedea* Scopoli 1979) on other Mediterranean islands (e.g. Igual *et al*. 2006, 2007; Ruffino *et al.* in press), but rat densities were supposed to be higher than on Port-Cros Island. This study also suggests that the selection of the deepest and most winding cavities by shearwaters for breeding may have helped shearwaters coping with introduced mammal predators, such as cats and rats in this colony, by increasing concealment, reducing accessibility and detectability to predators and thus leading to a higher breeding success (Penloup *et al*. 1997; Regher *et al*. 1998; Bourgeois & Vidal 2007).

Our results suggest that selection patterns of breeding cavities by shearwaters may also be influenced by rat visits when shearwaters are prospecting for suitable breeding cavities at the beginning of the breeding cycle. We hypothesise that olfactory cues (e.g., urine and faeces) left by introduced predators inside cavities when visiting may induce a signal or a stress for these birds, since petrels and shearwaters show a well-developed olfactory system (Bonadonna *et al*. 2004; Nevitt & Bonadonna 2005) to avoid predator-dwelling areas, as already proven for native mammals (e.g. Dickman & Doncaster 1984; Kats & Dill 1998).

Anyway, this unusual spatio-temporal segregation between ship rats and endemic shearwaters still has to be tested in other colonies and other ecological contexts before inferring any conclusions on how this native seabird could have co-existed with introduced predators for hundreds or thousands of years on Mediterranean islands without being driven to extinction. As rat densities may highly constrain rat impact on seabird populations (Igual *et al*. 2006; Quillfeldt *et al*. 2008), it would be highly valuable to set out comparative experimental studies, manipulate rat densities (i.e. rat local control) and measure behavioural response of seabirds. More data is also needed on the local survival and fidelity of adult yelkouan shearwaters breeding in the less accessible cavities within this colony, and on the breeding cavity selection behaviour of newly established breeders.

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# - Partie 3.2. -

## 3.2. EFFECT OF TOP PREDATOR CONTROL ON THE BEHAVIOUR AND IMPACT OF AN INTRODUCED MESOPREDATOR

3.2. Effets du contrôle d'un prédateur apical sur le comportement et l'impact d'un mésoprédateur introduit

**Cette partie est tirée de l'article en révision suivant :**

**Bonnaud E., Zarzoso-Lacoste D., Bourgeois K., Ruffino L., Legrand J. & Vidal E. Top predator control boost endemic prey but not mesopredator. Sous presse dans *Animal Conservation*. (voir Annexe 1**)

### 3.2.1. Contexte général de l'étude

Au cours des dernières décennies, de nombreuses opérations d'éradication et de contrôle de prédateurs apicaux comme les chats harets ont été menées sur les îles de la Planète dans le but de supprimer ou réduire la menace exercée sur les populations d'oiseaux marins (Twyford *et al.* 2000 ; Veitch 2001 ; Nogales *et al*. 2004 ; Rodriguez *et al*. 2006 ; Rauzon *et al*. 2008 ; Hugues *et al*. 2008). Cependant, des études ont pointé du doigt le risque indirect associé à la suppression de tels prédateurs apicaux sur les populations indigènes (oiseaux marins) lorsque celles-ci constituaient une proie partagée par plusieurs prédateurs, comme les chats et les rats (Courchamp *et al.* 1999 ; Rayner *et al.* 2007 ; Dumont *et al*. soumis). En effet, la réduction ou suppression complète des effectifs de prédateurs apicaux (chats) par opération de gestion peut conduire à un phénomène de relâche du mésoprédateur (rats), dans un système où les populations de rats sont majoritairement contrôlées par le prédateur apical (système de contrôle dit « top-down »). Cette relâche de mésoprédateur implique un impact plus fort sur la proie native, et peut se manifester soit par une augmentation des abondances du mésoprédateur (Zavaleta *et al*. 2001), soit par un changement de son comportement (Hugues *et al*. 2008).

L’île de Port-Cros a hébergé durant probablement environ 200 ans (Pasqualini 1995) une population de chats harets (*Felis catus*), dont l’impact de la prédation sur les populations de puffins yelkouan *Puffinus yelkouan* de l’île a été estimé comme alarmant (Bonnaud *et al*. 2007). Dans un but de conservation des populations de puffins de l’île, une opération de contrôle par piégeage non léthal de la population de chats harets a débuté dès Janvier 2004, sur Port Cros (voir Annexe 1). L’opération s’est prolongée jusqu’en Août 2005 et a conduit à l’élimination de 28 chats harets. A cette date, il a été considéré que la quasi-totalité des chats harets avait été éliminée, du fait de l’arrêt du succès de piégeage et de la raréfaction nette des fécès de chats harets récoltés sur les chemins de l’île (voir Annexe 1). En parallèle, un suivi fin des paramètres reproducteurs des puffins yelkouan (taux d’occupation des cavités, succès à l’éclosion, succès à l’envol, succès reproducteur total) ainsi qu’un suivi des abondances de rats noirs sur l’île ont été effectués de Décembre 2004 à Août 2008, afin de suivre l’évolution des dynamiques de populations de deux proies principales du chat : les puffins et les rats noirs (les rats noirs sont présents dans 79% des fécès de chats récoltés entre Février 2000 et Août 2004 ; Bonnaud *et al*. 2007). Par ailleurs, un suivi des visites de rats aux cavités de puffins a été entrepris durant la première année de contrôle des chats (2004-2005) et réitéré après l’opération de contrôle des chats (2007-2008) dans le but de mettre en évidence un changement éventuel de comportement des rats suite au contrôle des chats.

L’étude des patrons d’interactions aux cavités entre rats noirs et puffins yelkouan qui a été réalisée durant l’année 2004-2005, a révélé un faible degré d’interaction entre rats et puffins selon des patrons de visites de rats aux cavités plutôt inattendus (**Partie 3.1.**). D’une part, alors que les cavités non occupées par les puffins ont été régulirèrement visitées par les rats durant les principales phases du cycle reproducteur de l’oiseau, celles occupées par les puffins pendant leur reproduction n’ont été que très rarement visitées. D’autre part, les fréquences de visites moyennes des rats aux cavités se sont révélées être significativement plus importantes durant la période internuptiale, lorsque les oiseaux étaient absents de la colonie. Ainsi, la mise en place d’une opération de contrôle intensif des chats sur Port Cros de Janvier 2004 à Août 2005 a représenté une opportunité intéressante pour réitérer cette étude de suivi des patrons de visites des cavités de reproduction des puffins par les rats, 28 mois après la fin de l’opération de contrôle des chats (soit de Décembre 2007 à Août 2008). Notre question est donc la suivante : le contrôle intensif des chats harets de Port Cros s’est-il traduit par un changement dans le comportement de visites de rats aux cavités de puffins et par un impact plus fort des rats sur les puffins?

### 3.2.2. Méthodes

Au cours du cycle annuel 2007-2008 de reproduction des puffins yelkouan de Port Cros, les patrons de visites de cavités par les rats ont été suivis au niveau de 61 cavités présentant des caractéristiques favorables à la reproduction des oiseaux. Parmi ces 61 cavités, 23 ont été utilisées pour la reproduction des oiseaux et ont fait l'objet d'un suivi régulier du succès reproducteur. Le suivi des visites de rats à l'entrée de chacune des 61 cavités s'est effectué 24 fois dans l'année, soit durant quatre nuits successives (1 observation par nuit) au cours des six phases principales du cycle de reproduction du puffin (Décembre 2007 = prospection des cavités ; Février 2008 = accouplement ; Avril 2008 = incubation ; Mai 2008 = éclosion ; Juin 2008 = envol des jeunes ; Août 2008 = internuptial ; Figure 8), pour un total de 1461 observations pour l'ensemble des cavités durant le cycle annuel des oiseaux. Les visites de cavités par les rats ont été observées grâce aux empreintes laissées après leur passage dans un sable fin posé à l'entrée de chaque cavité. Les crottes et poils laissés dans l'entrée des cavités ont également été considérés comme des indices de visite de rats. L'utilisation complémentaire de dispositifs photographiques à infrarouge mis en place devant l'entrée d'un lot réduit de cavités nous a permis d'identifier les animaux visitant les cavités et de confirmer les visites de rats (Figure 9). Les indices de visite de rats ont été retirés après chaque visite, et les empreintes dans le sable effacées. Les résultats ont été analysés en tant que fréquences de visites de rats ($f_r$) suivant la formule suivante : $f_r = n_r/(n_p n_c n_n)$, où $n_r$ représente le nombre de visites de rats, $n_p$ le nombre de périodes suivies ($n_p = 6$), $\mathrm{n}_c$ le nombre de cavités ($n_c = 38$ ou 23) et $n_n$ le nombre de nuits de suivi ($n_n = 4$). Des tests $\chi^2$ de Cochran et de McNemar pour échantillons appariés ont été appliqués pour comparer les distributions de fréquences de visites de rats entre plusieurs périodes du cycle et entre deux périodes, respectivement. Des tests $\chi^2$ de Pearson pour échantillons indépendants ont été appliqués pour tester la difference entre les fréquences de visites de rats entre les deux années de suivi.

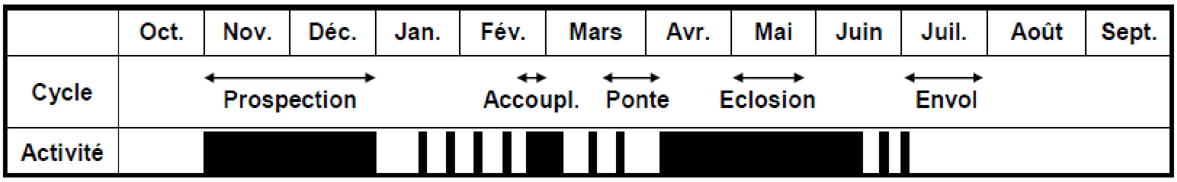

**Figure 9.** Phases principales du cycle de reproduction et d'activité vocale du puffin yelkouan (d'après Vidal 1985 et Zotier 1997).

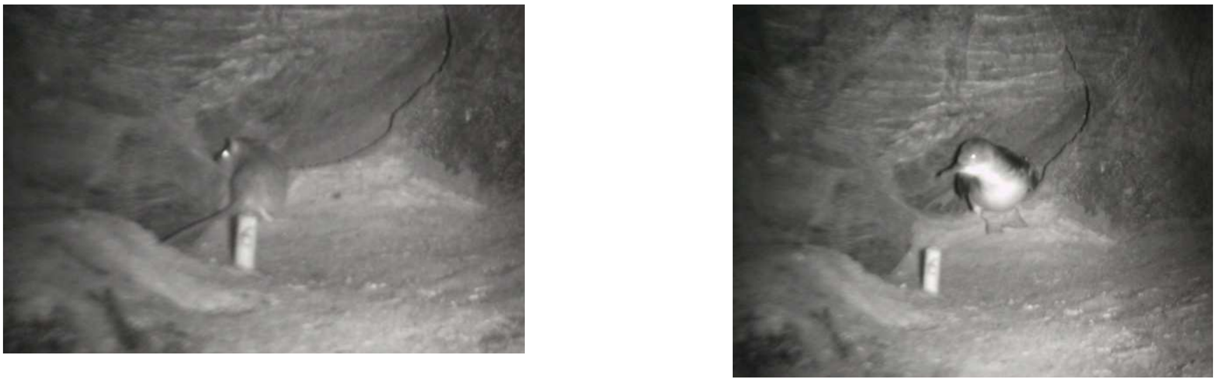

**Figure 10.** Photos prises grâce aux dispositifs d'appareil photo infrarouge, disposés devant l'entrée d'une cavité naturelle utilisée par les puffins pour la reproduction. La photo (a) montre un rat noir entrant dans la cavité n°26 le 4 Avril 2008 à 23h40, et la photo (b) montre un puffin sortant de cette même cavité la même nuit à 02h10.

## 3.2.3. Résultats

### 3.2.3.1. Patrons temporels de visites des cavités par les rats

La totalité des 61 cavités suivies en 2007-2008 a été visitée au moins une fois par les rats durant les 24 nuits d'observations le long du cycle reproducteur des puffins. Au total, 364 visites de rats ont été enregistrées, soit une moyenne de 0,242 visite.cavité$^{-1}$.nuit$^{-1}$, alors qu'en 2004-2005, la fréquence moyenne de visites de rats était de 0,054 visite.cavité$^{-1}$.nuit$^{-1}$, soit 4,5 fois moins élevée. Pour l'année 2007-2008, les patrons de visites de cavités par les rats ont été significativement différents entre les six périodes de suivi (Cochran $Q = 77.4$, $P < 0,001$ ; Figure 10). En particulier, les fréquences de visites de rats ont été significativement plus importantes durant la période de prospection des oiseaux ($f_r = 0,561$) que durant les cinq autres périodes (McNemar $\chi^2$, toutes les valeurs de $P > P_{\text{corr. Bonferroni}}$). Les périodes d'envol des poussins ($f_r = 0,066$) et internuptiale ($f_r = 0,113$) ont enregistré les fréquences de visites de cavités par les rats les deux plus faibles, comparé aux quatre autres périodes du cycle (Figure 10).

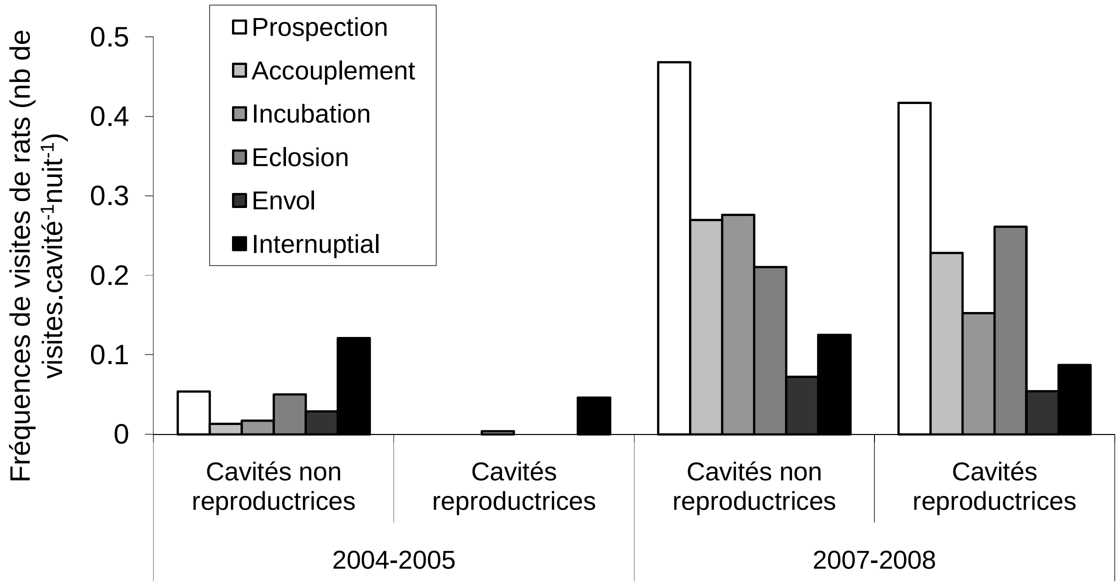

**Figure 11.** Fréquences de visites par les rats des cavités utlisées ou non pour la reproduction par les puffins au cours de la première année de contrôle des chats harets sur Port Cros (2004-2005) et 28 mois après la fin du contrôle (2008-2009).

### 3.2.3.2. Patrons de visites des rats aux cavités utilisées par les puffins pour la reproduction

En 2004-2005, durant la première année de contrôle des chats, les fréquences de visites de cavités par les rats ont été significativement différentes entre les cavités utilisées par les puffins pour la reproduction ($f_{\mathrm{r}}$ = 0,008) et celles non utilisées ($f_{\mathrm{r}}$ = 0,048) (voir **Partie 3.1.**), alors qu'en 2007-2008, après contrôle des chats, aucune différence significative n'a été enregistrée entre les deux types de cavités ($f_{\mathrm{r\ (reproduction)}}$ = 0,217; $f_{\mathrm{r\ (non\ reproduction)}}$ = 0,257 ; Pearson $\chi^2$ = 1.77 $P > 0.05$). La fréquence moyenne de visites de rats aux cavités utilisées par les puffins pour la reproduction a significativement augmenté entre 2004-2005 et 2007-2008 (Pearson $\chi^2$ = 70, $P < 0.001$). En 2004-2005, seule une cavité de reproduction a été visitée par les rats (4%, $n$ = 25 cavités suivies) durant les trois périodes de vulnérabilité des œufs et poussins (incubation, éclosion, envol de poussins), alors que 87% des cavités de reproduction ($n$ = 23) ont été visitées par les rats au moins une fois en 2007-2008 durant ces mêmes périodes. Durant ces périodes de vulnérabilité des œufs et poussins, la fréquence moyenne de visites des cavités de reproduction par les rats a été significativement plus élevée en 2007-2008 ($f_{\mathrm{r}}$ = 0,156) qu'en 2004-2005 ($f_{\mathrm{r}}$ = 0,003 ; Yates cor. Pearson $\chi^2$ = 30.1, $P < 0.001$). En

2007-2008, six cavités (25% sur les 61 cavités suivies) ont rencontrées un échec reproducteur et quatre (17%) en 2004-2005. Durant les deux années de suivis, aucun cas d'échec reproducteur n'a pu être attribué à la prédation du rat, et les cavités ayant subi un échec reproducteur n'ont pas montré un taux de visites de rats plus important que les cavités où la reproduction a réussi, que ce soit durant l'ensemble du cycle reproducteur (2004-2005 : $f_{r\ (succès)} = 0{,}002$, $f_{r\ (échec)} = 0$ ; 2007-2008 : $f_{r\ (succès)} = 0{,}219$, $f_{r\ (échec)} = 0{,}208$), ou durant les trois périodes de vulnérabilité des œufs et poussins (2004-2005 : $f_{r\ (succès)} = 0{,}004$, $f_{r\ (échec)} = 0$ ; 2007-2008 : $f_{r\ (succès)} = 0{,}487$, $f_{r(échec)} = 0{,}375$).

### 3.2.4. Eléments de discussion

L'étude des interactions entre rats noirs et puffins yelkouan au niveau des sites de reproduction des oiseaux, 28 mois après l'opération de contrôle des chats harets de l'île de Port Cros, a révélé des patrons de visites de rats aux cavités significativement différents de ceux précédemment observés durant la première année de contrôle des chats. D'une part, les fréquences de visites de rats aux cavités ont significativement augmenté après le contrôle des chats, notamment au niveau des cavités utilisées par les puffins pour la reproduction. D'autre part, le schéma temporel des visites de rats plutôt inattendu observé en 2004-2005, montrant des fréquences de visites nettement plus importantes en période internuptiale, n'a pas été observé durant l'année 2007-2008. Ces changements de patrons de visites des cavités par les rats pourraient s'expliquer par deux phénomènes distincts ou synergiques : (1) une augmentation des abondances de rats sur l'île suite au contrôle du prédateur apical (Zavaleta *et al.* 2001 ; Russell *et al.* 2009), ou (2) un changement de comportement des rats dans l'exploitation de l'habitat suite au contrôle du prédateur apical (Huges *et al.* 2008). Le suivi des abondances moyennes de rats qui a été effectué sur Port Cros de 2004 à 2008 (Figure 11) ne montre pas d'augmentation nette des abondances de rats sur l'île après contrôle des chats ($r^2 = 0{,}196$). Au contraire, les fluctuations du succès de piégeage des rats enregistrées pendant et après le contrôle des chats s'inscrivent parmi les fluctuations saisonnières et annuelles fréquentes enregistrées au cours de ces 20 dernières années (Granjon & Cheylan 1993). Durant la période de suivi des visites de rats aux cavités après contrôle des chats, de Décembre 2007 à Août 2008, le succès de piégeage des rats reste modéré, mais apparait cependant plus élevé que durant l'année 2004-2005. Cependant, les données disponibles ne nous permettent pas de trancher entre l'hypothèse d'une augmentation d'abondance et celle d’un changement de comportement des rats pour expliquer l’augmentation des fréquences de visites de terriers après contrôle des chats. Par ailleurs, durant l’année 2007-2008, la décroissance des fréquences de visites de rats depuis la période de prospection des puffins jusqu’aux périodes d’envol des poussins et internupiale suivantes pourrait être liée à une diminution des abondances de rats à ces périodes, comme le suggère la diminution conséquente du succès de piégeage des rats entre Octobre 2007 et Août 2008 (Figure 11). Enfin, malgré des patrons temporels de visites différents, voire inverses, entre les deux années de suivi, les fréquences de visites moyennes de rats en période internuptiale, lorsque les puffins sont absents des colonies, restent dans le même ordre de grandeur entre les deux années.

De manière intéressante, malgré une augmentation significative des interactions entre les rats et les puffins entre les deux années de suivi, aucun indice ne nous a permis d’attribuer les échecs reproducteurs des puffins à la prédation par les rats en 2007-2008. Par ailleurs, le suivi des paramètres reproducteurs de 100 couples de puffins de la colonie d’étude entre 2003 et 2008 révèle un succès reproducteur globalement élevé avec peu de variations inter-annuelles (succès moyen à l’éclosion = 0,849 ± 0,043 ; succès moyen à l’envol = 0,901 ± 0,021 ; succès reproducteur moyen = 0,763 ± 0034) ; particulièrement pour l’année 2007-2008 où il atteind son maximum (0,853 ; voir Annexe 1.). Ces valeurs de succès reproducteur sont relativement élevées si l’on se réfère aux autres îles de Méditerranée, pour le puffin yelkouan (Montecristo, Italie, Baccetti 1993-1994 ; Tavolara et Molara, Sardaigne, N. Baccetti comm.pers. ; Malte, J. Borg comm.pers.) ou pour le puffin cendré (Cabrera, Baléares, Amengual & Aguilar 1998 ; îles Chafarines, Igual *et al.* 2006 ; Zannone, Italie, Corbi *et al.* 2005) et démontrent donc un impact insignifiant des rats noirs sur les populations de puffins yelkouan de l’île de Port Cros. Même si les patrons d’interactions entre rats et puffins semblent avoir changé au niveau des cavités de reproduction, le contrôle des chats harets sur l’île de Port Cros ne s’est pas traduit par une relâche du mésoprédateur, le rat noir, dont l’impact sur la productivité des puffins reste globalement faible depuis cinq ans.

Cette étude confirme que le contrôle d’un prédateur apical comme le chat haret sur les îles ne se traduit pas systématiquement par une augmentation de l’impact du prédateur secondaire, comme les rats sur les populations indigènes d’oiseaux marins (Cooper *et al.* 1995; Girardet *et al.* 2001). Grâce à la modélisation des dynamiques de populations d’une espèce d’oiseau marin et de deux prédateurs introduits (chats et rats), Russell *et al.* (2009) ont montré que le phénomène de relâche de mésoprédateur après contrôle des populations de chats ne se produisait qu'en situations où les chats exerçaient un fort contrôle sur les populations de rats (contrôle de type « top-down »). En effet, les populations de rats introduits sur les îles sont reconnues pour fluctuer largement entre les saisons et années, selon l'abondance et la disponibilité des ressources (Clark 1980 ; Moller & Craig 1987 ; Miller & Miller 1995). Ainsi, dans le cas de l'île de Port Cros, avant le contrôle des chats harets, il est probable que les populations de rats étaient plus fortement contrôlées par l'abondance et la disponibilité des ressources (contrôle de type « bottom-up ») que par la prédation par les chats (contrôle de type « top-down »). De manière générale, les résultats de ces expérimentations conduites sur l'île de Port Cros rejoignent les récentes interrogations au sujet de la nature réelle de l'impact des rats introduits sur les oiseaux marins, l'intensité de cet impact et des facteurs intrinsèques et extrinsèques favorisant cet impact (e.g. Towns *et al*. 2006 ; voir aussi **Partie 3.4.**).

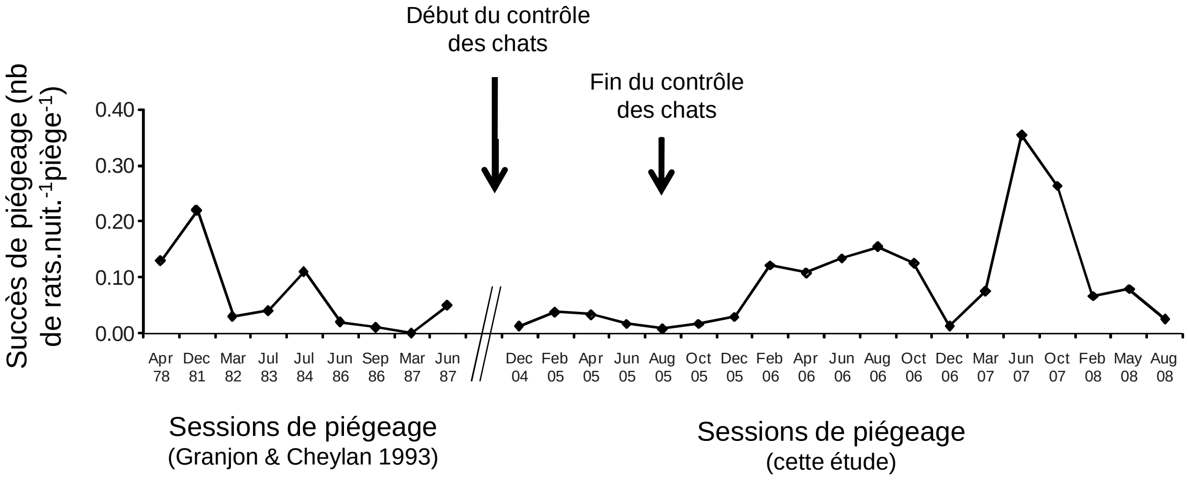

**Figure 12.** Succès de piégeage de rats noirs sur l'île de Port Cros, avant le contrôle des chats harets (1978-1987; Granjon & Cheylan 1993), durant et après le contrôle des chats (2005-2008; cette étude).

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# - Partie 3.3. -

## 3.3. LIMITED PREDATION CAPACITIES ON BIRD EGGS BY INVASIVE RATS: AN EXPERIMENTAL APPROACH

3.3. Capacités de predation limitées des rats introduits sur les oeufs d'oiseaux marins: une approche expérimentale.

**Résumé:**

Les prédateurs introduits sur les îles sont connus pour affecter négativement la productivité des oiseaux insulaires et leurs dynamiques de populations. Récemment, certains questionnements ont émergé concernant les mécanismes d'impact des rats introduits *Rattus* spp. et la sévérité de l'impact causé par la prédation sur les oiseaux. Dans cette étude, il a été question d'évaluer les capacités de prédation du rat noir *R. rattus* sur des œufs d'oiseaux, grâce à l'utilisation de tests comportementaux de capacités de prédation réalisés sur des individus prélevés sur une île de Méditerranée (Bagaud, S-E France). Cinq variables suceptibles d'affecter le succès de prédation des rats sur les œufs ont été testées : la taille de l'œuf, l'état de l'œuf, la masse corporelle des rats, leur sexe ainsi que leur habitat d'origine. Les résultats montrent que les rats identifient les œufs comme une source de nourriture potentielle, mais de manière surprenante, il s'avère que les rats sont globalement incapables de consommer des oeufs intacts de taille moyenne (oeufs de caille) et de large taille (œuf de poule), alors que les œufs intacts de petite taille (œufs de canari) sont très largement consommés. Par contre, le taux de réussite à la consommation d'œufs augmente significativement lorsque les œufs sont au préalable endommagés. Ces résultats sont en accord avec l'hypothèse que les capacités de prédation des rats sur les œufs d'oiseaux puissent avoir été quelque peu sur-estimées et donnent également de l'importance au comportement de charognard des rats visant la consomamtion d'œufs endommagés. Nos résultats suggèrent que les capacités de prédation des rats sur les œufs pourraient être liées à des facteurs mécaniques ou physiques et soulèvent l'hypothèse de l'existence de techniques complexes de prédation dans le but de casser et consommer des œufs intacts d'oiseaux. Une compréhension plus fine des mécanismes d'impact des rongeurs introduits sur l'avifaune insulaire est susceptible d'apporter de précieux éléments pour une gestion plus adaptée des rongeurs introduits et une meilleure conservation des populations d'oiseaux insulaires.

**Cette partie correspond à l'article en préparation suivant:**

**Zazoso-Lacoste D., Ruffino L. & Vidal E. Limited predation capacities on bird eggs by invasive rats: an experimental approach. En préparation pour *Conservation Biology* (rubrique *Research Note < 3000 mots*).**

### 3.3.1. Introduction

The impacts of alien predators on island native species have been studied extensively and invasive rats (*Rattus* spp.) are considered as major contributors to documented extirpations and extinctions of island avifauna (Atkinson 1985; Burger & Gochfeld 1994; Courchamp *et al.* 2003; Blackburn *et al.* 2004). The global-scale and strong impact of invasive rats on island bird populations are mainly related to their potential to prey on birds at different life stages (eggs, chicks and adults), and to affect, for the most vulnerable species, both breeding parameters and adult survival, leading to sharp bird population declines (Atkinson 1985; Booth *et al.* 1996; Penloup *et al.* 1997; Robinet *et al.* 1998; Traveset *et al.* 2009).

Understanding the mechanisms of rat impact and quantifying the effects of rat predation on bird populations are often challenging. Indeed, most predation is cryptic, occurs by night and sometimes underground, and leaves few signs, especially for burrowing seabirds (Jones et al. 2008). As a consequence, rat impact is often assessed through indirect methods, such as the monitoring of bird breeding parameter change before and after the experimental removal of rats (Igual *et al*. 2006; Jouventin *et al*. 2003; Pascal *et al*. 2008). However, even with this widely-used approach, the mechanisms by which rats really affect birds still remain unclear. In the light of these questionings, identifying ways for a more reliable estimation of rat impacts and their real predatory capacities on eggs appears necessary (Prieto *et al*. 2003; Towns *et al*. 2006). Experimental tests with artificial nests in the wild, conducted by Prieto *et al*. (2003), showed that ship rats only managed to prey upon seagull eggs when eggs were experimentally damaged, suggesting thus that the intensity of rat predation on eggs may have sometimes been overestimated. Experimental approaches using behavioral tests or feeding trials conducted on wild populations under controlled conditions offer an alternative way to study predation processes and to test for possible drivers of predation capacity and success (DeGraff & Maier 1996; Whelan *et al.* 1994; Bramley *et al.* 2000), yet these methods remain too poorly used.

In this paper, we tested the predation capacities on bird eggs of one of the most damaging invasive rat species, the ship rat *R. rattus.* Wild-trapped rats were subjected to several predation trials in captivity. We particularly aimed at testing the effects of five factors likely to influence rat predation success, namely egg size, egg state, rat body mass, rat sex, and rat's habitat of origin. Better understanding the mechanisms of impact of so cryptic predators like rats is necessary to evaluate and thus mitigate their threats to island avifauna and help designing appropriate conservation strategies.

### 3.3.2. Material and methods

#### 3.3.2.1. Study area

This study was conducted on Bagaud Island (43°00’42 N; 6°21’45 E; total area = 58 Ha), a natural reserve within the Port-Cros National Park (Hyères Islands, France), 7.5 km of the French Mediterranean coast. This island culminates at 59 m and is covered by a dense native scrubland mainly composed of *Pistacia Lentiscus*, *Myrtus communis*, *Phillyrea angustifolia* and *Erica arborea.* A colony of ca. 460 pairs of yellow-legged gulls (*Larus michahellis*) nest on the island from February to August.

Ship rats were wild-trapped on a 4.25-ha trapping grid of 117 permanent trap stations covering the southern part of Bagaud Island. Trapping was conducted from February to August 2009 and was part of a 24-month capture-mark-recapture survey of ship rat population dynamics and movements, in which rats were individually marked using subcutaneous PIT tags (type FDX-B, IER Paris, France) (L. Ruffino in prep). Traps were baited with peanut butter, set before dusk and checked early in the morning.

#### 3.3.2.2. Feeding trials

Wild-trapped rats were weighed, sexed and individually kept in captivity during 24h in wire-mesh cages (29 x 10 x 10 cm) containing cotton bedding for acclimatization. Feeding trials were performed within a building (small fort) present on Bagaud Island, reducing thus the stress induced by animal translocation from the trapping area to the testing zone. Each rat was individually subjected to a series of four feeding trials which were performed on days 1, 2, 3 and 4 from 8:00 to 12:00. Feeding trials were separated by periods of rest (with water and sunflower seeds *ad libitum*) followed by periods of fasting (at the end of the meal, food and water were removed until the next morning) (Massei *et al.* 2002; Meyer & Shiels 2009).

Five variables were tested for their influence on the capacity of rats to prey on eggs: egg size, egg state, rat body mass, rat sex and rats’ habitat of origin. First, to assess the capacity of rats to depredate different egg sizes, three types of eggs were proposed to rats: hen eggs (56.18 ± 1.63 × 43.49 ± 1.17 mm), quail eggs (35.33 ± 1.85 × 27.17 ± 0.77 mm) and canary eggs (18.40 ± 1.03 × 14.16 ± 0.42 mm). Second, the effect of the egg state on the frequency of egg depredation was tested by offering rats perforated or intact (not damaged) hen and quail eggs. Perforated eggs were punctured with a 2-mm-diameter circular hole at the apex (Massei *et al.* 2002). In addition, the effect of the puncture position was investigated by comparing the frequency of egg depredation between eggs punctured at the apex and eggs punctured on the side. Tests were also realized on cracked (damaged but not perforated) eggs, and on intact eggs coated with yolk and albumen, to check whether egg depredation frequencies differed from those of punctured eggs and non-coated eggs, respectively. Third, the effect of rat body mass was tested by comparing egg depredation frequency for two classes of rat weight : (1) 110-170 g ± 5g (i.e. immature and sub-adult individuals), and (2) > 220 g (adults). Finally, the effect of the habitat of origin of the tested rats was investigated by comparing egg depredation frequencies between rats captured in two different habitats: (1) a seabird habitat comprising a yellow-legged gull colony during the breeding period, where the egg resource (intact or damaged) was usually available to rats, and (2) a non-seabird habitat (native scrubland), 150 to 500 m away from the gull colony, where the egg resource was absent. A long-term capture-recapture of rats conducted during the 24 previous months on Bagaud Island provided the history of captures for each rat and revealed very low probabilities of movements between habitats (L. Ruffino soumis), which make us confident when assigning the origin of rats to one or another habitat (see **Chapter 4.**).

Feeding trials were performed in rodent cages (50 × 36 × 28 cm) with floor covered by fine sand. During each feeding trial, rats were offered one egg. Eggs were proposed to rats in decreasing order of predation difficulty to limit the effects of learning from one test to another (Trial 1: intact hen egg, Trial 2: intact quail egg, Trial 3: perforated hen egg, Trial 4: perforated quail egg). Eggs were protected under plastic covers which were simultaneously removed five minutes after rats were placed in experimental cages to synchronize the beginning of the experiments. Masking devices were placed between cages to prevent any visual contact among rats during trials. Eggs and cages were always manipulated with latex gloves to reduce human scent (Whelan 1994). After each feeding trial, sand was removed and cages were cleaned with alcohol and then ventilated. Each feeding trial lasted four hours and the egg fate (consumed, cracked, moved, intact) was recorded at the end of each trial. Intact eggs were considered depredated when left open or cracked. Perforated eggs were considered depredated when their existing hole was significantly expanded by the rat (Massei *et al.* 2002;

Prieto *et al.* 2003). After each feeding trial, evidence of predation attempts was recorded on the shell of intact eggs (licking, tooth marks or claw marks).

### 3.3.2.3. Data analysis

Chi-square tests for independent samples were used to compare frequencies of egg predation attempts between rats trapped in both habitats. Non-parametric Cochran Q tests for temporally correlated data were performed to compare the frequencies of depredated eggs among the four successive feeding trials (Trials 1 to 4). McNemar $\chi^2$ tests for related samples were performed to test for differences in frequencies of depredated eggs between two factors (egg size, egg state, rat body mass, rat sex, habitat of origin), in 2 x 2 contingency tables. Bonferroni adjustments for multiple comparisons were applied when necessary (Quinn & Keough 2002).

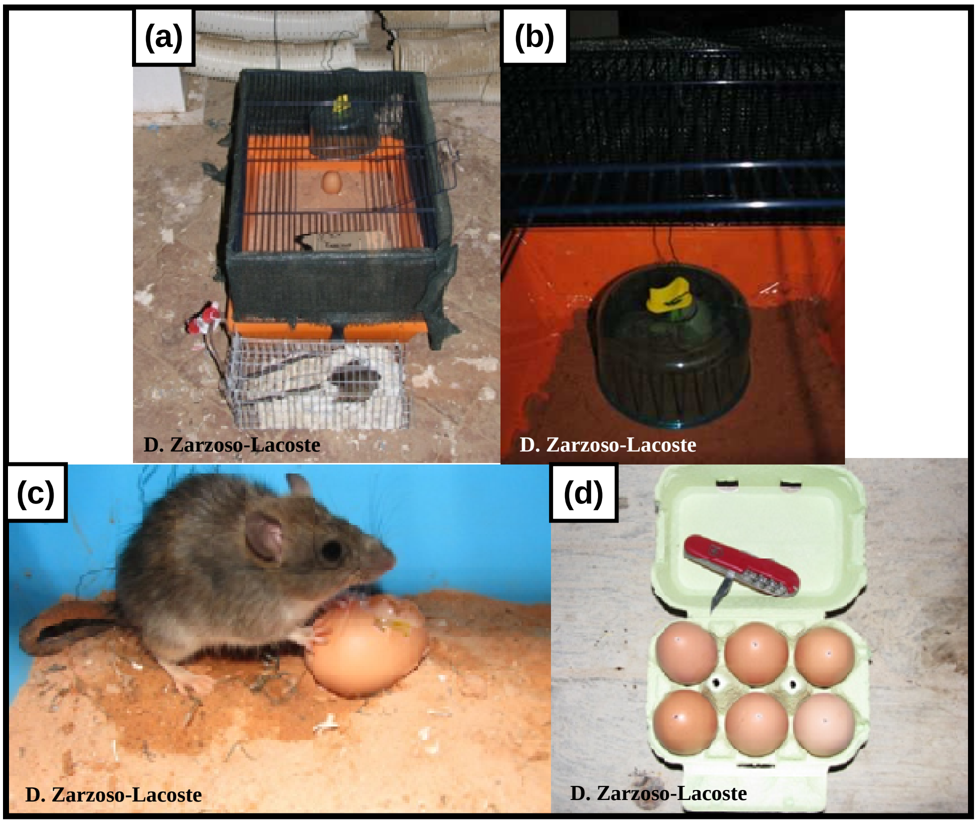

**Figure 13.** Photos du dispositif experimental mis en place pour les tests comportementaux de capacities de predation des rats noirs sur les oeufs. Les photos (a) et (b) montrent les cages de repos et expérimentale ainsi que le système de cloche qui protège l'œuf avant le début de l'expérimentation. La photo (c) montre un rat noir consommant un œuf préalablement endommagé, et la photo (d) montre 6 œufs de poule de taille moyenne perforés à leur apex d'un trou de 2mm de diamètre.

### 3.3.3. Results

At least 60% of the intact eggs showed evidence of predation attempts whatever the egg size (hen eggs: 63%, *n* = 65; quail eggs: 67%, *n* = 102; canary eggs: 90%, *n* = 19; Figure 12). Frequencies of predation attempts were not significantly different between rats captured in the gull colony (62%; *n* = 78) and rats captured in the non-seabird scrubland (50%; *n* = 108) ($\chi^2$ = 1.3, *P* > 0.05).

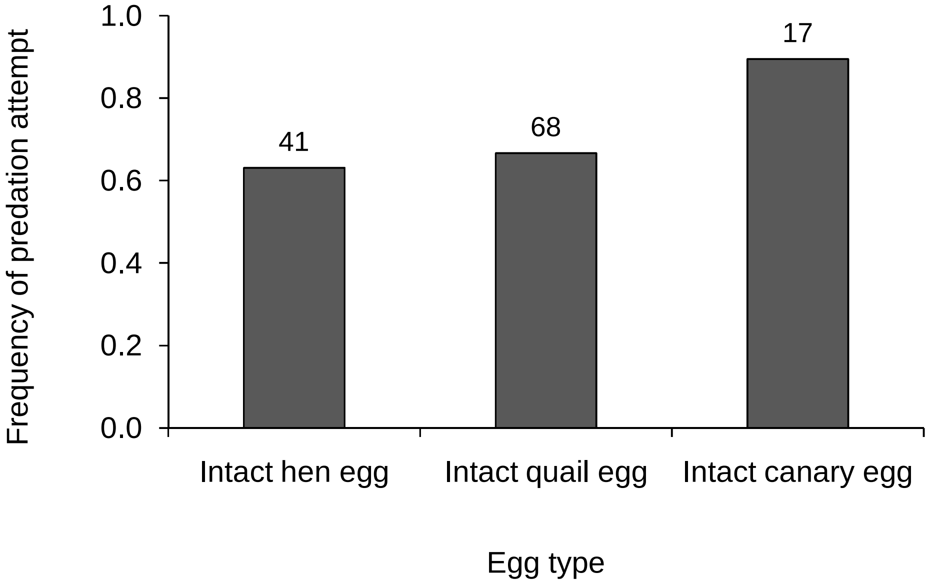

**Figure 14.** Frequencies of predation attempts by *Rattus rattus* on intact hen (*n* total = 65), quail (*n* total = 102) and canary eggs (*n* total = 19). Numbers of depredated eggs are indicated above each bar.

For all the 104 tested rats, the frequencies of depredation on intact eggs were 0% for hen eggs (*n* = 102), 3% for quail eggs (*n* = 89) and 90% for canary eggs (*n* = 19). The frequency of depredation on intact eggs was not enhanced when eggs were coated with yolk and albumen and remained null (*n* = 21) (Figure 12). However, the frequencies of depredation on perforated eggs were higher than 90% for both hen (*n* = 84) and quail eggs (*n* = 95).

The frequency distributions of depredated eggs were significantly different among the four feeding trials (Trials 1 to 4), whatever rat body mass class, sex and habitat (Cochran *Q* tests; all *P* values < 0.001). In particular, the frequencies of egg depredation were significantly lower for intact eggs (Trials 1 and 2) than perforated eggs (Trials 3 and 4), whatever rat body mass, sex or habitat (McNemar $\chi^2$ tests; all *P* values < 0.001). The frequencies of egg depredation did not differ significantly between hen or quail egg, whatever rat body mass, sex or habitat (McNemar $\chi^2$ tests; all $P$ values > $P_{\text{Bonferroni}}$). In turn, neither sex, rat body mass nor habitat significantly affected the frequencies of egg depredation (males: 53%, $n$ = 55; females: 47%, $n$ = 49; rats from the lowest body mass class: 46%, $n$ = 48; rats from the highest body mass class: 39%, $n$ = 41; rats from the seabird colony: 49%, $n$ = 51; rats from the scrubland: 51%, $n$ = 53; McNemar $\chi^2$ tests; all $P$ values > $P_{\text{Bonferroni}}$). Finally, the puncture position on eggs (top- or side-perforated) had no significant effect on the frequencies of egg depredation ($n_{\text{top-perforated}}$ = 18 [91%]; $n_{\text{side-perforated}}$ = 84 [100%]; Figure 15). The frequencies of egg depredation did not differ between cracked and perforated eggs, whatever the egg size (88% for hen eggs, $n$ = 16; 100% for quail eggs, $n$ = 6; $\chi^2$ = 0.6, $P$ > 0.05).

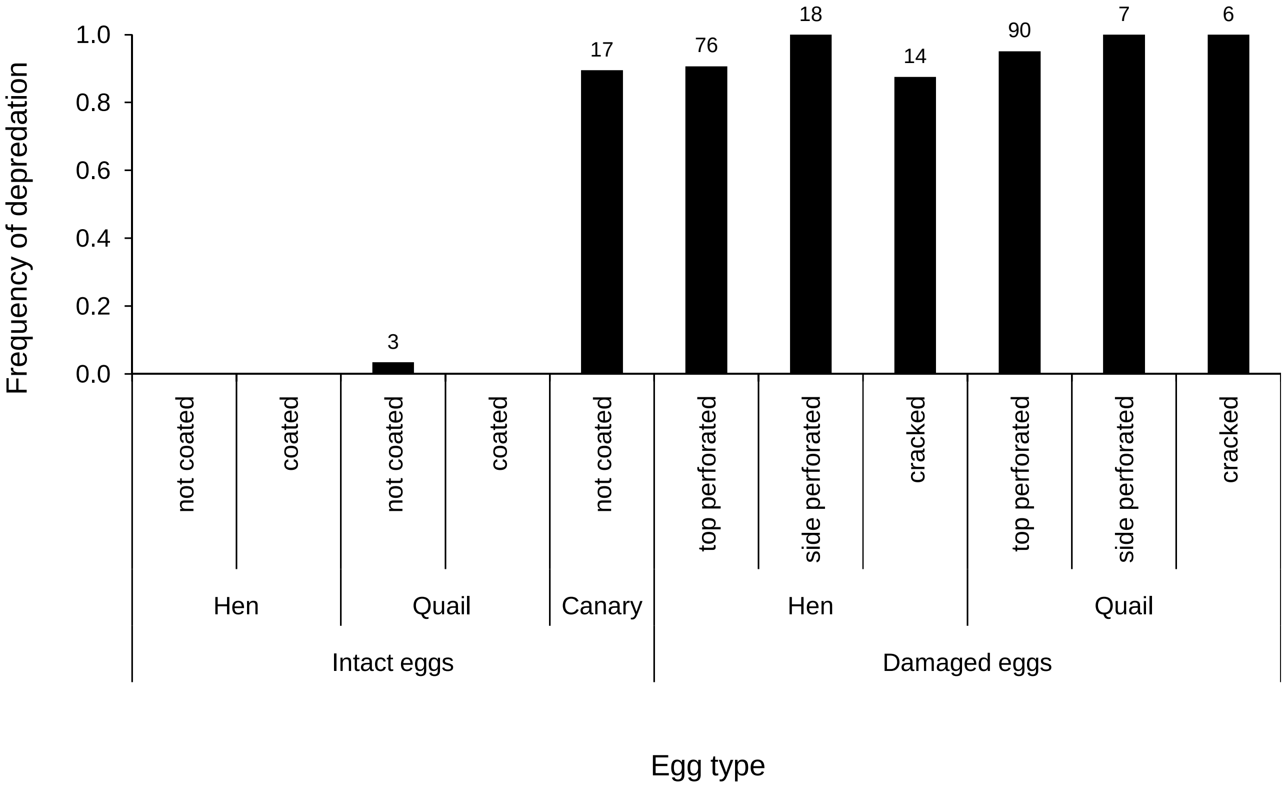

**Figure 15.** Frequencies of egg depredation by *R. rattus* on eggs of varying sizes (hen, quail or canary eggs) and states (intact, perforated or cracked), on eggs coated or not by yolk and albumen, and on eggs perforated at the top or on the side.

### 3.3.4. Discussion

Several aspects of interactions between introduced predators and native insular species remain poorly understood. In particular, the mechanisms of invasive rodent predation on native species would be worthy of more investigation, especially for birds with cryptic nesting behavior such as burrowing seabirds. This study confirms the potential of experimental approaches with behavioral tests on wild individuals to offer interesting possibilities for studying rat predation. However, results from captive trials should always be interpreted with caution, since experimental biases could restrict the relevance of extrapolated results to *in natura* conditions. In this study, the potential methodological biases were limited by (i) testing wild-trapped rats instead of laboratory rats (Meyer & Shiels 2009), (ii) conducting feeding trials on the same island where rats were captured in order to reduce the stress induced by animal translocation, and (iii) using standardized protocols for experiments in captivity (DeGraff & Maier 1996; Massei *et al.* 2002).

Our results showed that, whatever egg size and egg state (intact or damaged), rats identified eggs as a potential food resource. This pattern was consistent between habitats and independent from the fact that rats could have encountered bird eggs in their habitat of origin before. Indeed, rats coming from the non-seabird habitat did not show significantly lower frequencies of predation attempts on eggs than rats coming from the seabird colony, where eggs were abundant during the breeding season. Moreover, although olfaction plays an important role in the foraging behaviour of rats (Galef & Heiber 1976; Galef 1994; Bramley *et al.* 2000), here, olfactory cues (odors released by yolk and albumen of coated eggs) did not seem to be necessarily required for the identification of eggs as a food resource or to trigger egg predation.

Almost all the canary eggs were successfully predated by rats. This confirms the strong vulnerability of small birds (e.g. passerines) to rat predation (Atkinson 1985; Steadman 2006). Conversely, rats showed strong difficulties to break and prey on intact eggs of both large-size (hen eggs) but also, surprisingly, medium-size (quail eggs) eggs. This pattern may be related to mechanical limiting factors such as rat jaw gap (DeGraaf & Maier 1996; Prieto *et al.* 2003) or bite force (Anderson *et al.* 2008), or to a lack of predation skills, as suggested by Prieto *et al.* (2003). Social learning is important in rodents (Galef & Whiskin 2001) and has been shown to be determinant to learn complex feeding-skills, such as pine cone stripping behavior in a pine forest habitat in Israel (Terkel 1994), or egg removal and eating in Bonin petrel

(Grant *et al.* 1981) and little shearwater colonies (Booth *et al.* 1996) on Midway island and in New Zealand, respectively. Moreover, no significant effect of the habitat of rats' origin was identified on egg predation success. This could suggest that on Bagaud Island, no apparent learning behaviour was developed by the rats dwelling in the seagull habitat to prey upon eggs. However, it is plausible that the aggressive behaviour of gulls defending their nests, along with the large size of gull eggs, may have reduced the access of intact eggs to rats and decreased the possibility that they may have already managed to consume intact eggs in the wild.

Egg predation success substantially increased once the egg presented a tiny notch on the shell (cracked or perforated on the apex or on the side), allowing rats to get caught in the egg shell and break it. These results reinforce and extend to small-sized birds the idea raised by Prieto *et al.* (2003) that the egg state (intact *vs* damaged) is a key driver in determining the success of egg predation by rats, and suggest that a part of predated eggs by rats in the wild could have been cracked or failed eggs i.e. eggs that would have not hatched. Another implication of this result would be that hatching eggs are particularly sensitive to rat impact, especially when eggs are left unattended by the parents. Our findings also support the propensity of rats to scavenge food, particularly failed eggs, and raise the hypothesis that the food acquired by feeding on dead avian materials could represent an under-estimated part of the diet of invasive rats. Unfortunately, scavenging has too poorly been mentioned as an alternative hypothesis of predation (but see Norman 1975 and Harper 2007), rarely observed (but see Witmer *et al.* 2006 and Quillfeldt *et al.* 2008) and quantified in the field. However, evaluating how much of the food ingested by rats may be acquired by scavenging should be highly valuable to provide complementary data for the interpretation, often difficult, of results of conventional diet studies and signs of mortality lefts in the field (Harper 2007), and hence should contribute to avoid over-estimation of predation and alarmist conclusions (Norman 1975).

In the other hand, our results did not exclude any other mechanisms of rat impact on bird eggs. For example, a rat rolling an incubating egg outside the nesting chamber would have the same impact on the bird breeding success than a real egg predation event (Estrada *et al.* 2002) since the rolling egg, even when not consumed, would be neglected by the parents and would not hatch (Seto & Conant 1996; Whtiworth *et al.* 2005). To elucidate whether rats could prey on intact eggs using learned skills such as egg rolling, experimental approaches with artificial nests coupled with video surveillance could be developed (e.g. Booth *et al.* 1996; Thompson & Burhans 2004).

The existence of a threshold in the rat body mass/egg size ratio beyond which egg predation success may be enhanced have been hypothesiszed (Prieto *et al*. 2003). In our study, the non-significant effect of rat body mass on egg predation success could indicate that this threshold was not reached, and that the predation success on intact eggs of the size of those of small petrels by adult black rats of 200-300 g may be far from being obvious. This is why, it could be interesting to perform these feeding trials on the three other invasive rodent species, the Norway rat *Rattus norvegicus*, the Pacific rat *Rattus exulans* and the house mouse *Mus musculus*, also known as egg predators, but with different body sizes, ecologies and behaviors, and therefore different predation capacities (e.g. Booth *et al.* 1996; Imber *et al.* 2000; Major *et al.* 2006; Angel *et al.* 2009). Results of these experiments could help to prioritize bird conservation actions on island depending on rat species and bird species in presence (Jones *et al.* 2008).

This study leads us to question on the real mechanisms and the intensity by which invasive rats affect bird population dynamics. The mechanisms and magnitude of the direct and indirect impacts of invasive rats on birds are strongly likely to vary among island contexts. Furthermore, bird sensitivity to rats is related to complex confounding factors, such as rat population densities (Igual *et al.* 2006; Quillfeldt *et al.* 2008), rat learning behaviour (Grant *et al.* 1981), and the presence of other introduced species (e.g. Imber *et al.* 2000; Igual *et al*. 2009). Combining appropriate methods and using multiple sources of corroborating evidence should promote a better overview of the processes involving bird population declines and design relevant conservation strategies.

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# - Partie 3.4. -

## 3.4. RAT IMPACT ON SEABIRDS: DO WE NEED BETTER DATA?

3.4. Impact des rats sur les oiseaux marins: avons-nous besoin de meilleures données?

**Résumé :**

Les espèces introduites sont impliquées de façon majeure dans la crise d'extinction et de raréfaction d'espèces, en particulier au niveau des écosystèmes insulaires. Les rats *Rattus* spp., introduits sont considérés comme une menace majeure pour les oiseaux marins sur l'ensemble des îles de la Planète. Dans ce contexte, il apparait indispensable d'évaluer la pertinence des méthodologies mises en œuvre pour évaluer l'impact de ces rongeurs introduits sur les populations d'oiseaux marins. Ici, nous avons conduit une synthèse puis une analyse de l'ensemble des articles scientifiques publiés depuis 1980 ayant étudié l'impact des rats sur les oiseaux marins afin de faire le point sur les méthodologies employées pour évaluer cet impact, pointer du doigt les biais liés à chaque méthodologie, afin de proposer de nouvelles perspectives de recherche. Toutes les méthodologies employées ne permettent pas d'affirmer l'existence d'un impact, et d'évaluer les mécanismes et l'intensité de l'impact. Le couplage de sources d'information variées semble vivement à recommander afin de limiter les erreurs d'interprétation de résultats issus de certaines méthodologies. Certains outils ou expérimentations restent encore peu usités, comme l'utilisation de la vidéo ou de tests comportementaux en situation contrôlée, pourtant susceptibles de fournir de précieuses informations. Enfin, la prise en compte et l'étude des situations de coexistence entre rats et oiseaux marins pourraient contribuer à une meilleure évaluation des critères de vulnérabilité des oiseaux face aux rats à une échelle globale.

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### 3.4.1. Introduction

On islands, introduced predators are identified as a key driver of species endangerment, extirpations and extinctions, especially for birds (Blackburn *et al*. 2004; Ricketts *et al*. 2005; Steadman 2006). The conservation status of seabirds, in particular, has become alarming in the last 20 years (Butchard *et al*. 2004) and nearly one third (30%) of the 334 seabird species are currently recognized as globally threatened, IUCN 2008). For decades, a growing literature has pointed to pervasive effects of invasive rats (*Rattus* spp.) on many seabird taxa in most archipelagos of the world (e.g. Jones *et al*. 2008) and rats are often identified as a leading cause of seabird extinction risk (e.g. in 70 % of petrel and shearwater species, IUCN 2008). Most of the impact of rats on seabirds has been reported through rat predation on eggs and chicks, the two most sensitive early life stages to small introduced predators (Jones *et al*. 2008).

Despite the apparent well-recognized major impact of rats on seabirds, recent questionings have emerged on the deficiencies in our knowledge regarding the mechanisms and the magnitude of the impact of so cryptic predators like rats (e.g. Towns *et al*. 2006). Some recent papers have highlighted the long-term persistence of seabird populations to persist despite the presence of invasive rats on islands (Catry *et al*. 2007; Quillfeldt *et al*. 2008; Ruffino *et al*. 2008, 2009). Some others have moderated the ability of invasive rats to prey on bird eggs, and have given much importance on the contribution of scavenging in the food habits of rats (Prieto *et al*. 2003; Zarzoso-Lacoste *et al*. in prep; see also **Part 3.3.**). Moreover, modeling of long-lived seabird population dynamics suggested that the effects of egg and chick predation by rats on seabird population decline should be of lowest concern compared to factors specifically affecting adult survival, such as large introduced predators (Le Corre 2008) or long-line fisheries (Igual *et al*. 2009).

Concern over the island biodiversity crisis has prompted scientists to quantitatively model species extinction probability and pinpoint species at higher imminent risk for management prioritization. Reliable predictions should be achieved by obtaining robust data and a detailed understanding of the processes of species endangerment by introduced predators. The global critical status of seabirds and the growing interest on the impacts of invasive rats have prompted us to investigate how the effects of rats on seabirds has been assessed for the last 30 years (Which methods were most commonly used?), to pinpoint gaps in our research and biases related to each method, in order to draw future research perspectives for a better understanding of the mechanistic causes of seabird population decline and extinction risk.

### 3.4.2. Literature review

We reviewed published papers describing either significant or non-significant impacts of any introduced rat species (*R. rattus, R. norvegicus, R. exulans*) on any species of the seabird group, from 1980 to 2009. We searched electronic engines (Web of Knowledge, Science Direct, Google Scholar) using combinations of the following keywords: *Rattus, rats, seabirds, impact*, *effect*, *eradication*, *island nesting*, *breeding success*, *predation*, *extinction*. We also searched for relevant sources in the reference list of each paper found. Grey literature and unpublished reports were excluded and we only restricted our search to peer-reviewed papers. The methods used by authors to investigate rat impact on seabirds were assigned to ten categories: (1) experimental manipulation of rat densities (monitoring of changes in seabird breeding parameters before and after rat control or removal), (2) monitoring of causes of seabird breeding failure though the record of possible signs of mortality left in the field (disappearance of eggs, chicks, birds from nests or remains of eggs, chicks, adult birds found inside or around the nest), (3) rats' diet studies (stomacal or faecal content analyses, stable isotope analyses), (4) direct observations of predation (photo- or video-monitoring, personal observations), (5) seabird distribution patterns on islands (rat-free *vs* rat-invaded islands), (6) subfossil records and zooarcheological data (7) artificial nest techniques, (8) feeding trials or behavioral tests, (9) population dynamic modeling, (10) meta-analysis.

A total of 48 papers fit the criteria for review (Table 7, and see also Supplementary material). 54% of the reviewed studies were based on a monitoring of the causes of seabird breeding failure and the extrapolation of their causes, as a unique way (*n* = 4) or combined with other methods (*n* = 22), to evaluate the impact of rats. 35% of studies experimentally manipulated rat densities. 23% of studies used rats' diet analyses and 10% compared seabird distribution patterns on rat-free and rat-invaded islands. Only a few studies cited direct observations of rat predation or used artificial nests or behavioral tests (Table 7). Eleven studies used a multi-source approach to investigate rat impact, by combining for example the monitoring of seabird breeding failure with either diet studies or direct observations or the experimental removal of rats or the comparison of distribution patterns on islands with or without rats.

### 3.4.3. Pinpointing some methodological biases

Rat predation is generally elusive, because it often occurs by night, sometimes below ground for burrow-nesting seabirds, and left few signs in the field. One of the most straightforward methods to quantify rat impact on seabirds remains the monitoring of a relative index of seabird breeding parameter change before and after the experimental manipulation of rat densities or the complete removal of rats from an island. Even if the reduction or complete removal of the rat threat can reveal positive effects on seabird populations, neither the mechanisms nor the cause-and-effect relationships are clearly demonstrated. Long-term monitoring (≥ 10 years; *n* = 6 studies reviewed) of the population dynamics of long-lived seabirds is therefore strongly recommended to overcome intrinsic and extrinsic confounding effects on seabird population demography, such as those of food shortage, mortality at sea and predation by or competition with other introduced mammals (Imber *et al*. 2000; Jouventin *et al.* 2003).

Diet studies are common ways to investigate the impacts of rats on seabirds. From our review, of the 33 studies that concluded to major negative effects of rats on seabird populations, five studies (15%) only used gut content or stable isotope analyses without any other sources of corroborating evidence that predation has occurred. Although diet approaches allow the identification of ingested or assimilated food, they are in any way surrogates of direct observations of predation. Rats could acquire their consumed food from scavenging (e.g. Quillfeldt *et al*. 2008), especially on large seabird colonies where dead birds or abandoned eggs are abundantly available to scavengers (Witmer *et al*. 2006). One major issue in diet analyses stands in the inability to reliably quantify the relative parts of the food scavenged and prey on in the diet of consumers, since predation and scavenging yield similar gut contents and stable isotope ratios (Stapp 2002; Harper 2007). Faulty evidence and speculation at this most important stage of investigation could have important implications in the evaluation of the severity of rat impact. The combination of multiple techniques (e.g., direct observations, rat removal, breeding success monitoring, feeding trials) should provide more conclusive results on the propensity of ship rats to scavenge seabird remains left in the field (e.g. Harper 2007).

Estimating the implication of introduced rats in seabird extirpations or extinctions by comparing the timing of rat arrival with that of the disappearance of seabirds is likely to generate misleading conclusions since the apparent circumstantial relationship between species disappearance and rat incursion is often complicated by additive or synergetic confounding factors such as human hunting, mortality at sea, food shortage, climate change or the presence of other introduced species (Steadman 2006). Such cumulative factors should also be carefully taken into account when comparing distribution patterns of seabirds between rat-free and rat-invaded islands, especially for islands with different biogeographical contexts, species compositions and disturbance regimes (Wittaker 2000).

### 3.4.4. Future research directions

The several potential biases associated with each method reviewed should prompt us to question on the adequacy of the methods used to answer a particular question (How do rats affect seabirds? What is the magnitude of the effects?), on the relevance of the parameters measured to answer this question and of the conclusions inferred from the parameters analyzed, in terms of rat predation rate, the relative contribution of rats in seabird population decline and extinction risks. Moreover, bearing in mind that the impact of rats may vary among island contexts (Martin *et al*. 2000) or species (Jones *et al*. 2008) and that invasive rats do not systematically lead to significant negative impacts on seabird populations and species, future research should dwell on the mechanisms facilitating the persistence of seabirds in the presence of rats, which is likely to provide a better overview of the global vulnerability of seabirds to invasive rats. Studies on rat impact are often motivated by conservation goals and island managers and researchers focus their efforts on the situations where they expect or know that rats negatively affect seabirds. Our feeling is that published papers are generally biased towards some types of interactions or some species (e.g., predation upon chicks or the most susceptible species may have a greater reporting rate than others; Jones *et al*. 2008) and towards studies showing a negative effect of rats, which at a global scale unfairly vilifies rats. Cause-and-effect relationships between the perceived threat on seabirds and the real implication of rats in the decline of seabird populations are often complex and equivocal because of other additive or synergetic factors. Even when effects are demonstrated, their mechanisms are usually unknown. In conclusion, approaches with multi-sources of corroborating evidence are strongly recommended to avoid faulty estimations of extinction risks. Over-estimation of the effects of rats may influence endangerment status by IUCN criteria, management directives and prioritizations, and hence fail to invest funding and efforts on the most critical conservation contexts, while under-estimation of seabird vulnerability may precipitate the decline of seabird populations if management efforts are not expended to overcome the real risks.

Some methods are still underused. For example, the use of automatic video and photographic equipments remains the only way to observe interactions between species, distinguish between predation and scavenging, detect the timing and mechanisms of predation and identify signs left by predators, especially for cryptic predators (Sanders & Maloney 2002; Johnston *et al*. 2003; Thompson & Burhans 2004). The lack of experimental studies in controlled situations in the field or at lab (artificial nests, feeding trials, behavioral tests) is a significant gap in our current research. They should provide, however, useful means to look at the propensity of rats to use scavenged food, quantify this behavior and test for the factors likely to affect predation rate and capacity (e.g. egg size, egg type, rat body size; Prieto *et al*. 2003; Zarzoso-Lacoste *et al*. in prep.; see also **Part 3.3.**). Finally, other types of interactions such as competition for habitat or the consequence of physiological stress induced by the presence of introduced predators are rarely mentioned in the literature as alternative mechanisms of rat impact on seabirds, yet their importance have probably been under-estimated.

| **Methods** | ***N* reviewed studies (%)** | **Information** | | |
|---|---|---|---|---|
| | | **Mechanisms** | | **Quantification of the impact at the population level** |
| | | **Consumption** | **Predation *vs* scavenging** | |
| • **Monitoring of the causes of seabird breeding failure** | 26 (54%) | Requires a thorough interpretation of the signs left in the field and a precise identification of the consumers involved | Difficulty to distinguish predation from scavenging without direct observations or reliable evidence | - Difficulty to quantify without other sources of corroborating evidence<br>- Intrinsic and extrinsic synergetic factors should be overcome<br>- Often difficult to distinguish the effects of multiple native or introduced predators (cats, mongooses, stoats often co-occur on islands). |
| • **Rat control/removal** | 17 (35%) | **NO** | **NO** | **YES** - Long-term studies are recommended |
| • **Gut content analyses** | 9 (19%) | **YES** | **NO** | **NO** |
| • **Stable isotope Analyses** | 6 (13%) | **NO** | **NO** | **NO** |
| • **Direct observations** | 6 (13%) | **YES** | **YES** | Requires a large enough sample size |
| • **Distribution patterns** | 5 (10%) | **NO** | **NO** | Requires a small study scale and similar island contexts for a thorough comparison of the level of rat impact among islands |
| • **Zooarcheology** | 2 (4%) | **NO** | **NO** | **NO** |
| • **Modeling** | 2 (4%) | **NO** | **NO** | **YES** - Needs to be applied to field data |
| • **Meta-analysis** | 1 (2%) | **NO** | **NO** | **NO** |
| • **Artificial nests** | 1 (2%) | **YES** - Only if coupled with direct observations | **YES** | Precautions needs to be taken when extrapolating results to *in natura* conditions |
| • **Feeding trials Behavioral tests** | 1 (2%) | **YES** | **YES** | **NO** - Precautions needs to be taken when extrapolating results to *in natura* conditions |

**Table 7.** Description of the methods used in the 48 reviewed studies on invasive rat impact on seabirds and their potential to reveal the consumption by rats of eggs or birds, distinguish predation from scavenging, and quantify the impact of rats at the seabird population level.

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# Chapitre 4.

## INFLUENCE DE L’ HÉTEROGÉNÉITÉ DE L’HABITAT, DES RESSOURCES ET DE LA DISPONIBILITE HYDRIQUE SUR L’ÉCOLOGIE TROPHIQUE, LA STRUCTURATION ET LA DYNAMIQUE DE POPULATIONS INSULAIRES DE RATS NOIRS

(a) autopsies dans le fort de l’île de Bagaud ; (b) analyse de régime alimentaire de rats à la binoculaire ; (c) plume d’oiseau et (d) épiderme de fruit de salsepareille observés au microscope ; (e) radiotélémétrie ; (f) rat noir équipé d’un collier émetteur ; (g) lecture du transpondeur sous-cutané ; (h) prise de note sur le terrain ; (i) fruit de *Carpobrotus* spp. consommé par les rats noirs sur Bagaud ; (j) rat noir consommant un fruit de *Carpobrotus* spp. sur Bagaud ; (k) tri de contenus stomacaux ; (l) rat noir ; (m) fort de Bagaud.

# Avant propos

Dans le cadre du chapitre 4 suivant, nous nous sommes intéressés au fonctionnement des populations insulaires de rats noirs, à partir d'un suivi de leur écologie (utilisation des ressources et de l'espace) et leur dynamique spatio-temporelle de populations sur le long terme (trois années de suivi). Les rats noirs sont reconnus pour avoir une écologie très généraliste (e.g. Harper *et al.* 2005), capables d'exploiter un grand nombre d'habitats et environnements (Jones *et al.* 2008), et un large spectre de ressources (Clark 1980 ; Campbell *et al.* 1984 ; Miller & Miller 1995 ; Quillfeldt *et al.* 2008). C'est également une espèce que l'on rencontre sur des îles aux conditions environnementales parfois drastiques (absence permanente d'eau douce sur l'île, faible abondance de ressources ; e.g. Clark 1980 ; Cheylan 1988 ; Caut *et al.* 2008). Peu d'études sur les dynamiques de populations insulaires des rats introduits ont été conduites sur plusieurs saisons et années. Or, les dynamiques de populations de rongeurs, notamment celles de rats, sont reconnues pour subir des fluctuations très fréquentes au cours de leurs cycles annuels et inter-annuels, en fonction des conditions climatiques et de la disponibilité des ressources (Clark 1980 ; Moller & Craig 1987 ; Miller & Miller 1995). Dans le but de mieux comprendre le fonctionnement des populations de rats introduits et de développer des opérations adaptées et efficaces à leur gestion, il apparait nécessaire de suivre l'évolution de leurs populations sur plusieurs générations, identifier les facteurs influençant leur dynamique de population, et comprendre leurs mécanismes d'action.

Depuis quelques décennies, les îles de Méditerranée ont subi des changements importants dans leurs conditions trophiques. Ces changements se manifestent par l'apport de ressources d'origine allochtone (i.e. provenant de l'extérieur du système insulaire), par l'intermédiaire notamment (1) des colonies d'oiseaux marins à expansion démographique d'origine anthropique, comme les goélands leucophées, qui, en nichant sur les îles, apportent des nutriments enrichis en azote, phosphore et carbone (via les dépôts de guano et les déchets ; Vidal *et al.* 1998 ; Ellis 2005 ; Wait *et al.* 2005), ainsi que des ressources riches en protéines (via les carcasses, œufs abandonnés et rejets d'alimentation ; Stapp & Polis 2003), et (2) des plantes succulentes envahissantes, comme *Agave* spp., *Carpobrotus* spp. ou *Opuntia* spp. (Hulme 2004), représentant des ressources alimentaires potentielles pour les rats introduits. Les ressources enrichies d'origine allochtone sont connues pour fertiliser les chaines trophiques des îles de faible productivité et favoriser les dynamiques de populations de leurs consommateurs (Polis & Hurd 1996; Sanchez-Pinero & Polis 2000 ; Anderson *et al.* 2008). Si un grand nombre d’études ont montré les bénéfices de ces apports d’origine allochtone sur les chaines trophiques indigènes des îles, aucune ne s’est jusqu’à présent attardée sur l’influence que ces ressources enrichies pouvaient avoir sur la dynamique de populations envahissantes de rongeurs. Or, l’identification des mécanismes susceptibles d’influencer le maintien d’espèces aussi dévastatrices que les rats noirs sur les îles revêt un intérêt majeur en matière de conservation de la biodiversité insulaire. Par ailleurs, dans le contexte particulier des îles méditerranéennes où le rat noir a été introduit de longue date, il se pourrait que l’apparent équilibre que l’on observe aujourd’hui entre les populations d’oiseaux marins et les rats noirs soit menacé par certains facteurs exogènes, comme les apports de ressouces d’origine allochtone, qui, indirectement, pourraient favoriser l’impact des rats sur les oiseaux.

Ainsi, dans le cadre des trois parties suivantes, nous nous sommes intéressés à analyser (1) la plasticité alimentaire d’une population insulaire de rats noirs ainsi que celle des individus, sur une petite île oligotrophe de Méditerranée, où la disponibilité et la qualité des ressources varient entre habitats adjacents et en fonction des saisons (**Partie 4.1.**), (2) les effets des ressources d’origine allochtone ainsi que ceux des conditions climatiques sur la dynamique de populations du rat noir, en particluier sur les taux de croissance des individus, leur masse corporelle, les paramètres reproducteurs et les densités (**Partie 4.2.**), ainsi que (3) sur la suvie des individus (**Partie 4.3.**).

## ❖ Présentation du site d’étude, l’île de Bagaud

### *Géographie, caractéristiques physiques et climatiques*

L’île de Bagaud (43°00’42 N ; 6°21’45 E) est située à l’Ouest de l’île de Port-Cros, au sein des eaux du Parc National de Port Cros (Var, France ; Figure 16). Cette île de 58 ha présente un relief peu escarpé, culminant à 57 m. Ses falaises maritimes ne dépassent pas 30 m et quelques pointes rocheuses se dressent le long de sa ligne de crête, plus prononcées au nord qu’au sud. Le substrat est formé de quartzites à ovoïdes, de phyllades gréseux à chloritoïdes et de micaschistes (Médail 1998).

L’archipel des îles d’Hyères est soumis à un climat méditerranéen subhumide tempéré. L’île de Bagaud se situe à la limite entre les étages thermo et méso-méditerranéens. La période sèche couvre les trois mois d’été, et les pluies, qui peuvent être très abondantes au printemps et à l’automne, n’excédent cependant pas une hauteur totale annuelle de 602.5 mm en moyenne pour la période 1998-2008 (station météorologique du Levant). L’insularité et la situation méridionale confèrent à l’archipel un hiver tempéré et une forte humidité relative de l’air, même en été. La température moyenne annuelle est de16.5°C pour la période 1998-2008. Les températures moyennes annuelles atteignent 9.5 et 24.7 °C pour les mois les plus froids et les plus chauds, respectivement. Les maxima quotidiens estivaux dépassent fréquemment les 30°C. Sur l’archipel, le vent d’est et le Mistral (nord-ouest) sont les vents qui soufflent le plus fréquemment (Parc National de Port-Cros 2002).

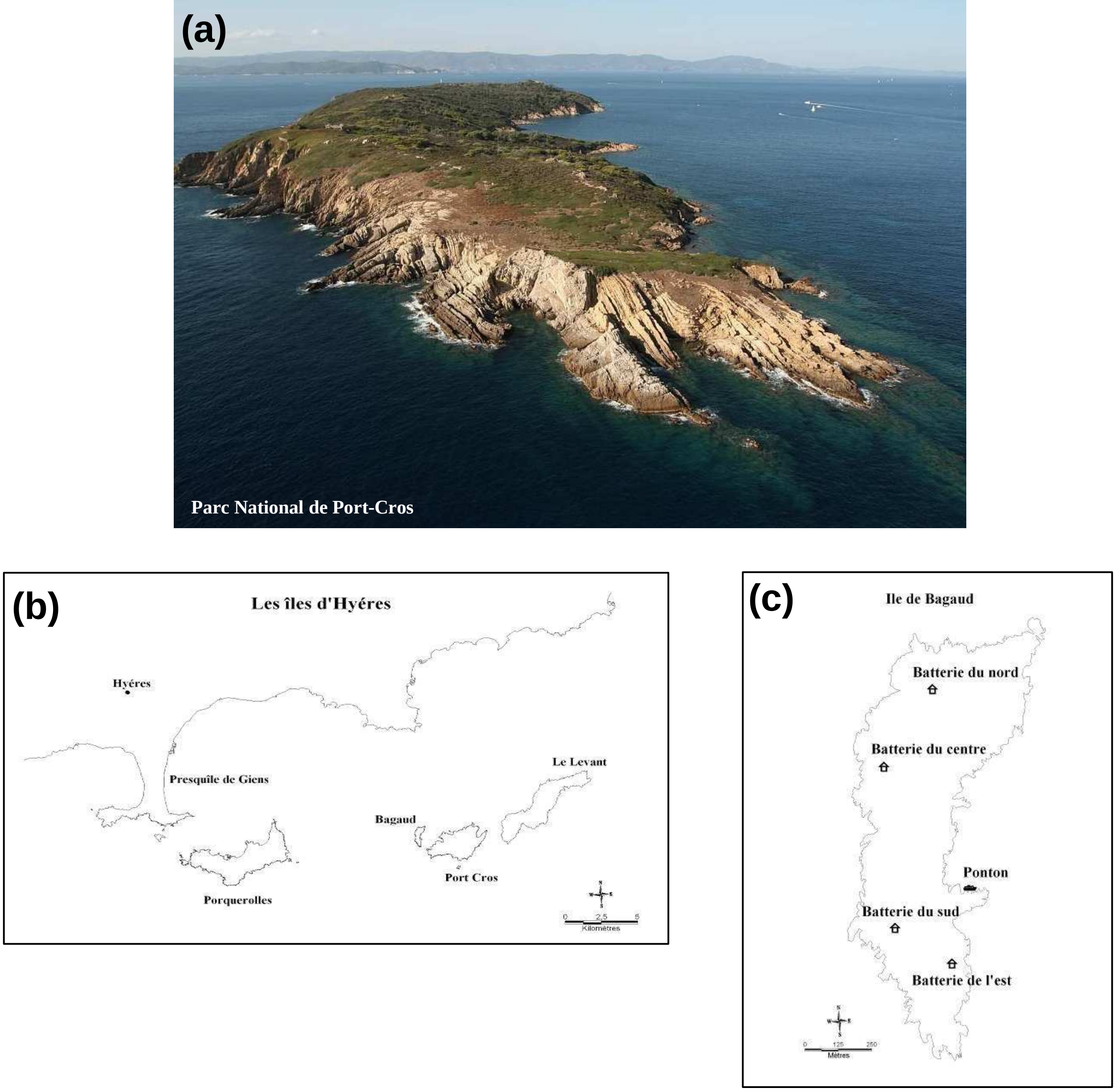

**Figure 16.** Photographie de l’île de Bagaud depuis Port Cros (a) et cartographies représentant la situation géographique de l’archipel des îles d’Hyères (b) et l’île de Bagaud (c).

### *Satut juridique et occupation humaine*

Le Parc National de Port-Cros couvre 700 ha de terres émergées et 1288 ha de surfaces marines. Crée le 14 décembre 1963, c'est l'un des deux plus anciens parcs nationaux de France et le premier parc marin européen. L'île de Bagaud, après avoir été propriété du Ministère de la Défense, appartient aujourd'hui au Conservatoire du Littoral. Sa gestion est assurée par le Parc National de Port-Cros, et l'île a récemment été classée en réserve intégrale d'après le décrêt du 9 mai 2007. Le débarquement, l'amarrage à la côte, la pénétration et la circulation des personnes y sont interdits, sauf dans le cadre d'études scientifiques et opérations de gestion.

La période précise de première colonisation de l'île de Bagaud par l'Homme reste inconnue. Cependant, de nombreux indices de présence humaine sur l'île de Port-Cros, voisine de 500 m, sont datés des époques chalcolithique (de -2300 à -1800 av. J.C.) et romaine (surtout durant les I$^{er}$ et II$^{ème}$ siècles ap. J.C. ; Pasqualini 1992). Plus tard, en 1707, lors de la succession d'Espagne, cet îlot vu le débarquement de la flotte anglo-hollandaise et de ces102 bâtiments (Bernard 1989). Par la suite, quatre petits forts y ont été construits entre 1794 et 1813. En effet, à l'époque de Napoléon (début XIX$^{ème}$ siècle), l'île de Bagaud, comme l'ensemble des îles d'Hyères, a représenté un site stratégique pour défendre la rade d'Hyères face à l'invasion des troupes anglaises. L'une des batteries fut restaurée en 1860 pour accueillir les soldats mis en quarantaine par crainte des maladies contagieuse à leur retour du Tonkin. Durant les 200 dernières années, la propriété de l'île a fréquemment changé, passant propriété de l'état, à celle de particuliers ou encore du ministère de la défense (Bernard 1989).

### *Flore et faune*

La végétation de l'île est majoritairement représentée par un maquis méditerranéen élevé et dense, composé notamment de *Pinus halepensis*, *Phyllyrea* spp., *Arbutus unedo*, *Erica arborea*, *Myrtus communis* (Médail 1998 ; Figure 17a, b). Les zones littorales, en particulier la côte occidentale soumise aux vents forts, sont couvertes de buissons bas de *Pistachia lentiscus* et *Juniperus phornicea*. Les plantes succulentes envahissantes du genre *Carpobrotus* spp. ont recouvert une large partie du littoral de l'île (Passetti *et al*. 2009). Une large tâche (environ 1500 m²) formée par *Carpobrotus acinaciformis*, *C. edulis* et des hybrides se trouve sur le secteur sud-est de l'île, en contre-bas de la Batterie Sud (Figure 15c, d). Sur le secteur extrême sud de l'île se trouve une colonie de goélands leucophées, composée d'environ 120 couples (recensement 2006 ; C. Duhem inedit), qui par piétinement, déjections de guano et apports de nutriments enrichis, contribuent à modifier la composition spécifique des plantes et arthropodes de ce secteur, formant ainsi un milieu ouvert dominé par des plantes ornitho-coprophiles rudérales (Médail 1998) et insectes polyphages et nécrophages (Orgeas *et al.* 2003) (Figure 15e, f).

L'île de Bagaud héberge une population de rats noirs, seule espèce de mammifères non volants de l'île. La période d'introduction du rat noir sur l'île n'est pas connue, mais la présence ancienne de l'Homme sur l'île voisine de Port Cros durant l'époque romaine ainsi que l'occupation fréquente de l'île de Bagaud par l'Homme au cours des derniers centenaires laissent penser que la présence du rat noir sur cette île est relativement ancienne. Enfin, la présence sur Bagaud des deux espèces de puffins nichant sur les îles voisines de l'archipel, les puffins yelkouan et cendrés, est relictuelle, et leurs effectifs seraient en déclin depuis les dernières décennies (Pascal 2006).

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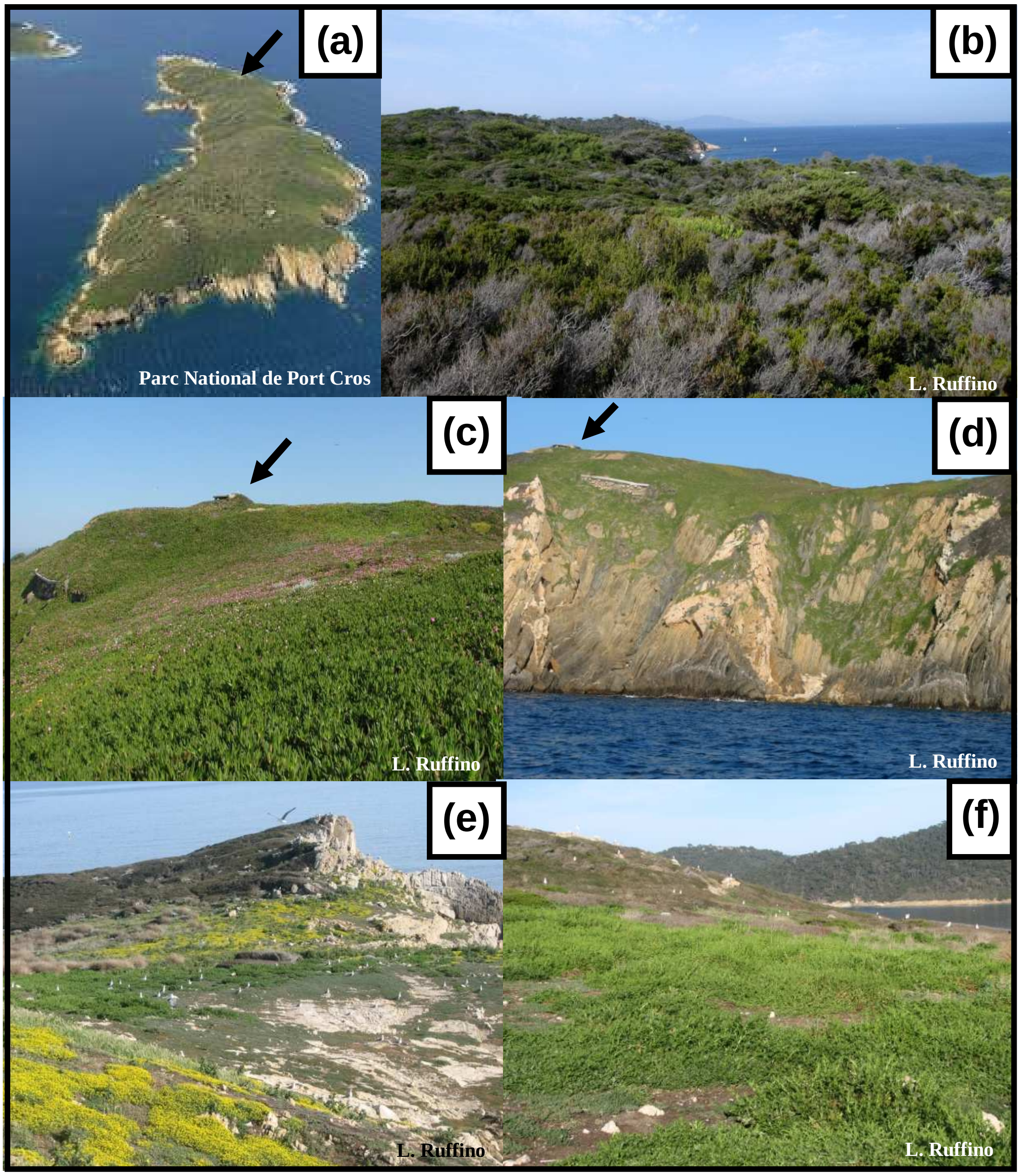


**Figure 17.** Vues des trois types d'habitats principaux de l'île de Bagaud : l'habitat de maquis élevé et dense (a, b), l'habitat colonisé par *Carpobrotus* spp. sur le secteur sud-est de l'île en contre-bas de la Batterie Sud, dont l'emplacement est marqué par une flèche (c, d), et l'habitat colonisé par les goélands leucophées sur la pointe sud de l'île (e, f).

# - Partie 4.1. -

## 4.1. LOW INDIVIDUAL DIET PLASTICITY IN A GENERALIST INVASIVE FORAGER

4.1. Plasticité alimentaire resteinte chez des individus d’une espèce généraliste invasive

**Résumé:**

Les capacités des espèces introduites à ajuster leurs patrons d’exploitation des ressources en réponse aux changements des conditions trophiques sont souvent mises en avant pour expliquer leurs succès d’invasion, notamment sur les îles où la disponibilité des ressources fluctue fortement dans le temps et l’espace. Dans le cadre de ce travail, nous avons examiné la plasticité alimentaire d’une espèce au régime alimentaire généraliste, le rat noir *Rattus rattus*, sur une petite île de Méditerranée, Bagaud (S-E France), où les ressources fluctuent en abondance et en qualité au cours des saisons et au sein d’habitats différents, mais spatialement très proches. La plasticité alimentaire du rat noir a été testée à deux échelles, celle de l’individu et celle de la population, en couplant plusieurs méthodologies complémentaires : des analyses de régime alimentaire de fécès et en isotopes stables à des échelles de temps variées, et une étude de capture-marquage-recapture sur 24 mois pour évaluer les déplacements des individus entre habitats adjacents au cours de l’année. Les résultats d’analyse de régime alimentaire et des déplacements illustrent la capacité du rat noir, en tant qu’espèce, à exploiter un large spectre de ressources et d’habitats. Cependant, à l’échelle de l’individu, la plasticité dans l’utilisation des ressources et des habitats apparait beaucoup plus restreinte. Les rats n’utilisent quasi-exclusivement que les ressources qu’ils trouvent dans leur habitat d’origine. Très peu d’individus se déplacent entre les habitats dans le but d’exploiter les ressources de meilleure qualité, alors que ces ressources sont abondantes et disponibles dans leur environnement proche. Ces résultats contre-intuitifs suggèrent que les interactions intra-spécifiques pourraient restreindre la mobilité des rats. Ils suggèrent également que même sur des îles de petite taille, l’accessibilité des ressources de haute qualité, mais à distribution ponctuelle n’est pas systématique pour tous les individus d’une même population. Ce résultat a d’importantes implications pour la quantification de l’impact des rats sur des espèces à distribution restreinte, plus particulièrement lorsque des méthodes indirectes sont utilisées, comme les analyses de régime alimentaire, en tant que substituts aux observations directes de prédation.

**Cette partie correspond à l’article soumis suivant :**

**Ruffino L., Russell J., Pisanu B., Caut S. & Vidal E. Low diet plasticity in an invasive generalist forager. Soumis à *Population Ecology*.**

### 4.1.1. Introduction

In a constantly changing world, species must continually adapt their behavior, at both the individual and population level, in order to succeed in their environment. Intrinsic attributes that may predispose a species to be successful are generally related to niche breadth (Ehrlich 1989; Williamson 1996; Vasquez 2005) and may include behavioral flexibility (Sol & Lefebvre 2000; Sol *et al*. 2002) and dietary or habitat breadth (Ehrlich 1989; Brousseau *et al*. 1996; Vasquez 2005; Jeschke & Trayer 2006; Blackburn *et al*. 2009). According to the optimal foraging theory, generalist foragers should exploit the food that maximize the net rate of energy intake by focusing on high-quality and abundant resources (MacArthur & Pianka 1966; Pyke *et al*. 1977). A non-specialized forager can opportunistically switch to alternative resources, as a result, for example, of seasonal resource fluctuations or of drastic environmental changes (Ben-David *et al*. 1997; Begg *et al*. 2003; Stapp & Polis 2003; Dell-Arte *et al.* 2007; Popa-Lisseanu *et al*. 2007). This is particularly true when the different resources are becoming available to species in their immediate environment (Pyke *et al*. 1977; Boutin 1990; Lin & Batzli 2001).

Invasive mammals have established on islands of various environmental conditions and their impacts on native communities are often devastating (e.g. Courchamp *et al*. 2003). Island systems often undergo marked spatio-temporal variations in resource availability, often driven by the seasonal pulses of enriched resources, for example the seasonal patterns of seabird or sea turtle island nesting (Polis *et al*. 1997a; Caut *et al.* 2008a), or the seasonal flush of plant productivity such as fruit and seed ripening (e.g. Polis *et al.* 1997b; Gregory & MacDonald 2009). Therefore, identifying specific foraging and habitat use strategies in invasive species that help them maintaining on islands and coping with sometimes extreme temporal variation in trophic conditions is crucial to better understand their impacts on native communities.

The three species of invasive rats *Rattus rattus*, *R. norvegicus*, *R. exulans* are among the most successful vertebrate invaders on islands (Courchamp *et al*. 2003). Rats have been introduced on more than 80% of the world's archipelagos (Atkinson 1985) and are identified as a leading cause of decline, extirpation and extinction of island species (Towns *et al*. 2006; Jones *et al.* 2008). Dietary flexibility and ecological plasticity have been suggested to explain their wide introduced range, from wet tropical to subarctic toundra (Courchamp *et al*. 2003; Caut *et al*. 2008a; Jones *et al.* 2008). Rats feed on various parts of plants (leaves, stems, fruits, roots; Daniel 1973; Clark 1981; Grant-Hoffman & Barboza, in press), macro-invertebrates (Palmer & Pons 1996; Ruffaut & Gibbs 2003; Towns *et al*. 2009), reptiles (Towns *et al.* 2003; Towns *et al.* 2007), birds (Imber 1975; Blackburn *et al*. 2004; Jones *et al*. 2008), and probably some mammals (Harris 2009). Rats are also known to preferentially select food items with high energy and nutrient value, such as fruits and seeds (Clark 1981; Grant-Hoffman & Barboza in press), and also animals such as eggs, birds and sea-turtle hatchlings (Imber 1975; Jones *et al*. 2008; Caut *et al*. 2008a). Moreover, the spatio-temporal variability of such high-quality resources has recently been hypothesized to affect rat movements, implying individual dietary shifts towards the highest profitable resources (Caut *et al*. 2008a).

Because of their widespread distribution and opportunistic feeding habits, black rats are excellent models for testing adjustments in their foraging behavior to the spatio-temporal variability of resource availability and quality. Comparative analyses of naturally occurring stable isotope ratios of carbon ($^{13}C/^{14}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) between consumers' tissues of different turnover rates (e.g. liver *vs* muscle) are a powerful tool to determine seasonal diet shifts of the same individuals (Phillips & Eldridge 2006; Crawford *et al*. 2008), especially when resources differ in their carbon origin (e.g. marine *vs* terrestrial or $C_3$ plants *vs* $C_4$ plants) and trophic levels (e.g. N-enriched habitats within seabird colonies on shore *vs* oligotrophic inland; Caut *et al*. 2008a). The ability to track seasonal dietary or habitat shift in individuals should be improved by combining analyses of resource use and individual-based movements over several periods of resource availability (Crawford *et al*. 2008), yet this approach of combined methods has never been used for invasive rodents.

In this study we investigated diet breadth and plasticity for a generalist forager, the island-invasive black rat *R. rattus*, on a small Mediterranean island where resources were differentially available in quality and time within adjacent habitat patches. We selected three small habitat patches in very close proximity to ensure that resources would be successively available to rats in their immediate environment. More specifically, we tested for the level at which plasticity (i.e. the capacity to opportunistically switch diet when higher quality resources are available) became apparent by analyzing resource use by individuals at various time scales (i.e. individual-level plasticity) and comparing diet among individuals (i.e. population-level plasticity) from different habitats and during different seasons, over three years. To investigate patterns of resource and habitat use by rats, complementary methods were used. Diet and trophic analyses were used as dietary tracers and spatial markers at successively increasing time scales: traditional diet analysis (reflecting the daily diet) and stable isotope analysis of liver (reflecting the diet of the previous week; Kurle 2009) and muscle (reflecting the diet of the previous month; Kurle 2009). These resource use analyses were combined with a two year capture-mark-recapture survey and one month radio-tracking study of rat movements within and among adjacent habitats. As opportunistic generalist foragers, we hypothesized that rats would successively use different resources, according to their availability and quality, to maximize energy intake, especially during drastic seasons. We expected diet breadth and plasticity would vary at the individual level and rats would move among adjacent habitats through seasons.

### 4.1.2. Materials and methods

#### 4.1.2.1. Study site

This study was conducted on Bagaud Island (58 ha, 1.48 km long, 0.59 km wide), a natural reserve in the Mediterranean Sea, lying 7.5 km from the southeast coast of France, within the Port-Cros National Park (Figure 18). The island is mainly composed of acid rock substrate and lies 57 m above sea level at its highest point. Mean monthly temperatures range from 9.5°C to 24.7°C. Total monthly precipitations vary from 1 mm to 151.6 mm (Levant Island Meteorological Office 1998-2008). The black rat was probably introduced during the Roman times (Ruffino *et al*. 2009) but persists as the only non-volant mammal on the island, despite no permanent fresh water.

For this study, we identified three contrasted habitats in close proximity and without any geographical barrier among them (Figure 18), varying seasonally in the availability and quality of their resources: (1) the gull habitat (hereafter *GU*) comprises a yellow-legged gull (*Larus michahellis*) colony with a ruderal grassland mainly composed of Fabaceae, Poaceae and Juncaceae. In this habitat, plant and arthropod communities were expected to be substantially enriched in nitrogen (especially $^{15}N$) due to high guano deposition (Vidal *et al*. 1998; Orgeas *et al*. 2003). March through May is the gull breeding period and, thus, are the three months of the year when gull influence is maximal (e.g. high input of marine-derived nutrients, adults feeding chicks, egg/chick carcasses); (2) the iceplant habitat (hereafter *IC*) was identified as a 1 500 m² patch of the mat-forming *Carpobrotus* spp. (Aizoaceae). This invasive plant abundantly produces large fleshy figs, enriched in $^{13}C$, energy (310 kJ/100g dry mass$^{-1}$) and water (80% water; Vila & D'Antonio 1998) that mature during the dry Mediterranean summer; (3) the scrubland habitat (hereafter *SC*), a native dry Mediterranean mattoral, was identified as a lower-quality habitat compared to *GU* and *IC*. This habitat is composed of a dense high-elevated mattoral dominated by *Pinus halepensis*, *Erica arborea*, *Myrtus communis*, *Arbutus unedo* and *Phyllirea* spp. (Médail 1998) and a much less dense low-elevated scrubland, dominated by *Pistacia lentiscus* and *Juniperus phoenicea* (Figure 16). In each habitat, resources were seasonal, unavailable at the same time and differentially enriched in nutrients (e.g. marine-derived nutrients in *GU*; fresh water and energy in *IC*). On Bagaud Island, the black rat population dynamics (i.e. density, reproductive output, individual growth rates) have been shown to be substantially enhanced by the enriched resources found in *GU* and *IC* (L. Ruffino unpublished). This is why those resources were considered of high-quality for rats.

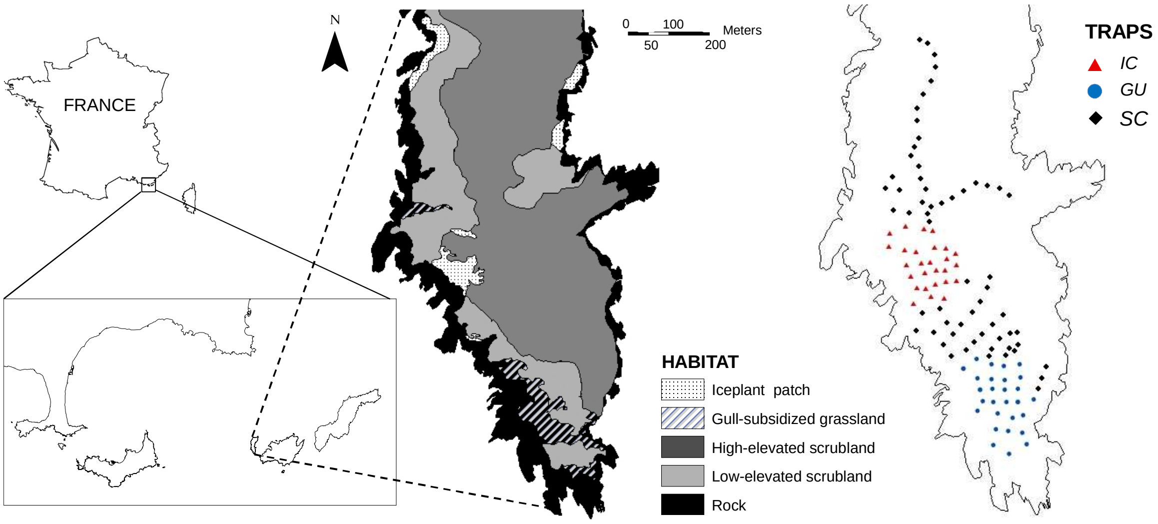


**Figure 18.** Map of Bagaud Island (43°00'42 N; 6°21'45 E), Port-Cros National Park, south-east France, showing the main habitats and trap location (*IC* = iceplant habitat, *GU* = gull habitat, *SC* = scrubland habitat).

#### 4.1.2.2. Diet analyses

##### 4.1.2.2.1. Rat trapping

In 2006-2007, three kill-trapping sessions were conducted to assess resource use by rats. Rat trapping was conducted within the three study habitats (*GU*, *IC*, *SC*) during three seasons (spring: early May 2006, hereafter MAY; summer: early September 2006, hereafter SEP; winter: early February 2007, hereafter FEB). 25 cage traps (BTS-Mécanique, Manufrance, Saint-Etienne, France) were set in each habitat during two or three consecutive nights. Traps were baited with peanut butter before dusk, checked twice a night to avoid rapid digestion of gut contents, and closed each morning. Rats were euthanized to collect faecal contents and tissue samples for diet and stable isotope analyses respectively. Classic biometric measures for rodents were recorded: body length, body mass, sex and maturity.

##### 4.1.2.2.2. Faecal content analysis

Rats are nocturnal and discrete small rodents which preclude the use of direct observations for diet determination, and traditional analyses use stomach and/or faecal contents analysis (Hansson 1970; Jordan 2005). Rat faecal contents were extensively analyzed under microscope lenses for the three habitats during the three sampling seasons in 2006-07. The three terminal faeces of each rat were removed from the gut and thoroughly rinsed with water through a 250 µm mesh sieve to remove the smallest fragments. For each rat, three microscope slides were extensively analyzed (mean number of items analyzed per rat = 259 ± 96 SD) and plant items were identified to the lowest systematic level possible with the use of a reference collection of the epidermal parts of most plants found on the island. A relative abundance index for each consumed item was calculated as the mean individual abundance of each item for each habitat-season combination.

##### 4.1.2.2.3. Stable isotope analysis

Effort was made in the field to extensively sample all available potential food items for rats during each season and for each habitat. Samples of rat liver and muscle were preserved in 70% alcohol before being processed. All samples were dried and ground to fine powder. Specific parts of plants identified to be consumed by rats were treated separately. Isotopic analyses were performed by a spectrometer Delta V Plus (Service Central d'Analyses, CNRS Solaize, France). Stable carbon (C) and nitrogen (N) isotope ratios were expressed as:

$\delta^{13}C$ or $\delta^{15}N = [(R_{\text{sample}}/R_{\text{standart}}) - 1] \times 1000$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ for $\delta^{13}C$ or $\delta^{15}N$ respectively.

The standard for C is the IAEA-NBS 21 (graphite: –28·13‰) and for N the IAEA-N1 (+0·4‰) and IAEA-N2 (+20·3‰). Ten replicate assays of internal laboratory standards indicated measurement maximum errors (*SD*) of ± 0·15‰ and ± 0·2‰ for stable carbon and nitrogen isotope measurements, respectively.

Since iceplant figs have a well-distinct isotopic signature compared to $C_3$ plants and other resources on Bagaud Island, we used the SIAR package of R to assess the relative contributions of figs in the diet of rats from *IC* and *SC* across seasons. By quantifying the assimilated proportion of figs in the consumer's diet, this method overcomes the possible biases related to faecal content analysis which can only quantify excreted proportions of seeds or pulpe in the diet. No attempt was made to run isotopic models for rats trapped in *GU* since no evidence of fig consumption was recorded in this habitat with traditional diet analysis (see results). SIAR package uses Bayesian inference and allows all sources of variation and uncertainty (i.e. standard deviations in consumer and source signatures) to be propagated through the model to return a true probability distribution of estimated dietary proportions (Jackson et *al*. 2009). Liver tissue was used to reconstruct resource use by rats because the turnover rates of stable isotopes are high in liver and reflect recent diet (Kurle 2009). As discrimination factors depend on several sources of variation (e.g. taxon, environment and tissue; Caut *et al*. 2008b), discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) for rat liver were calculated by using specific regression equations between rat liver $\Delta^{13}C$ and $\Delta^{15}N$ and their corresponding diet isotopic ratios (Caut *et al*. 2008b).

#### 4.1.2.3. Movement analyses

##### 4.1.2.3.1. Capture-mark-recapture

In 2007-2009, we investigated whether rats would move among adjacent habitats according to the seasonal resource availability. From April 2007 to April 2009, 19 capture-mark-recapture sessions were conducted, each separated by 1-3 months. During the two years of study, 117 trap stations (BTS-Mécanique, Manufrance, Saint-Etienne, France) were set permanently to cover the three study habitats (*SC*, *GU*, *IC*; 4.25 ha) and record movements. Geolocalized traps were set every 20-25 m, depending on the vegetation cover. Traps were baited with peanut butter before dusk, set between 3 and 8 consecutive nights depending on weather conditions, and all checked before 9am to avoid releasing rats too late in the day. During cold and humid seasons, bedding material was provided inside traps. Rats were individually marked using subcutaneous PIT tags (type FDX-B, IER Paris, France), sexed, weighted to the nearest 2.5 g, checked for sexual maturity and released after capture. Software Ranges7 (Kenward, South & Walls 2006) was used to calculate distances moved between subsequent captures.

#### 4.1.2.3.2. Radio-tracking

In August 2008, a radio-tracking survey was conducted in combination of diet analyses and capture-recapture to precise the foraging behavior and habitat use of rats at a finer scale (night, week). The nightly movements of a subset of pit-tagged individuals were monitored around *IC* during the period of maximum availability and attractiveness of fleshy figs (i.e. summer). Over the 11 radio-tracked individuals, seven were collared within the 100 - 200 m boundary strip around *IC*. Cable tie radio-collars (Biotrack Ltd, Dorset, UK) weighting less than 5% of the animals' body weight (Kenward 2007) were fitted to individuals. Animals were tracked on foot during 21 nights ([2-5] fixes per night, mean number of fixes per rat = 40 [20-54]) using hand-held TR4 receivers and a flexible three-element Yagi antenna (Telonics Inc., AZ, USA). The 50 % home-range Fixed Kernels (FK) were estimated to locate the core areas of each animal and check whether they would overlap *IC*. Maximum home range widths were obtained from 100 % minimum convex polygons (MCP). Both 50 % FK and 100 % MCP were estimated with Ranges7.

### 4.1.2.4. Statistical analysis

The consumed food by rats identified by faecal analysis were assigned to the following groups: $C_3$ Plants (i.e. use enzyme Rubisco to fix $CO_2$), $C_4$ Plants (i.e. fix $CO_2$ with phosphoebolpyruvate carboxylate; only formed by *Carpobrotus* spp. on Bagaud), Arthropods 1 (low-order consumers), Arthropods 2 (high-order consumers) and Gulls. For each season, the effect of habitat on $\delta^{13}C$ and $\delta^{15}N$ of consumed food (all groups combined per season), and on both rat liver and muscle, were tested with ANOVAs. Dependent variables were tested for normality of their distribution before conducting parametric tests. To detect significant interactions between habitats and seasons, post-hoc Scheffe tests were performed.

To identify whether a seasonal diet shift occurred in rats towards gull and iceplant resources during the periods of maximum availability and attractiveness (i.e. spring: peak of gull resources and summer: peak of fig ripening), we performed several statistical analyses. First, centroid hierarchical cluster analyses (Euclidian distances) were performed on both rat liver and muscle isotopic ratios for each habitat-season combination to (1) identify groups of individuals that could be clustered in three isotopic 'niches', related to the three study habitats, then (2) identify marginal individuals which may have switched habitats in one week or one month time scales. Before clustering, response variables were standardized to a mean of 0 and a standard deviation of 1. Second, we compared the magnitude of variation of both isotopic ratios of the same rats over one month scale among habitat and seasons to pinpoint any shift of isotopic signatures. The depletion or enrichment of isotopic ratios between tissues were calculated as follows: $D\delta^{x}Y = \delta^{x}Y_{(foie)} - \delta^{x}Y_{(muscle)}$ and $D\delta^{15}N$ and $D\delta^{13}C$ mean values were compared among habitats and seasons with non-parametric bootstrap estimates of confidence intervals. 1000 values were randomly sampled with replacement for each habitat–season combination from our data and 95% confidence intervals were calculated from these bootstrap distributions. Finally, Spearman rank correlations between empty body mass (i.e. digestive tract removed) of individuals and both $D\delta^{15}N$ and $D\delta^{13}C$ were applied to test for a relationship between isotopic ratio variation and body weight (relative age). Non-parametric Mann-Whitney tests were also performed to test whether $D\delta^{13}C$ or $D\delta^{15}N$ may differ by sex.

Mann-Whitney tests were performed to test differences in (1) mean distances moved by animals between subsequent captures between sexes and (2) mean distances moved by animals between subsequent captures within the same trapping session and between different sessions. Spearman rank correlations were used to test for a relationship between distances moved between different sessions and time between subsequent captures (we expect large distances indicate range shifts by animals). Individual movement probabilities ($\psi$) between habitats were estimated by calculating a state-transition matrix based upon records of rat captures by habitat. This matrix is only partially observed (the habitat of an uncaptured rat during a session is unknown), and so we imputed missing values using a Bayesian approach with a Dirichlet (1,1,1) prior on our state-transition matrix $\psi_{gh}$ for probabilities of movement between sessions from habitat $g$ to $h$ (where $\sum_{h=1}^{3}\psi_{gh} = 1$ for $g$ = 1, 2, 3) (see Schofield, Barker and MacKenzie 2009). We estimated $\psi_{gh}$ in WinBUGS 1.4 with the first 1 000 iterations discarded as burn-in, and a further 5 000 iterations for statistical summary of the stationary posterior distribution. This method assumes survival is consistent across habitats, which appeared to be true (JCR Russell unpublished).

### 4.1.3. Results

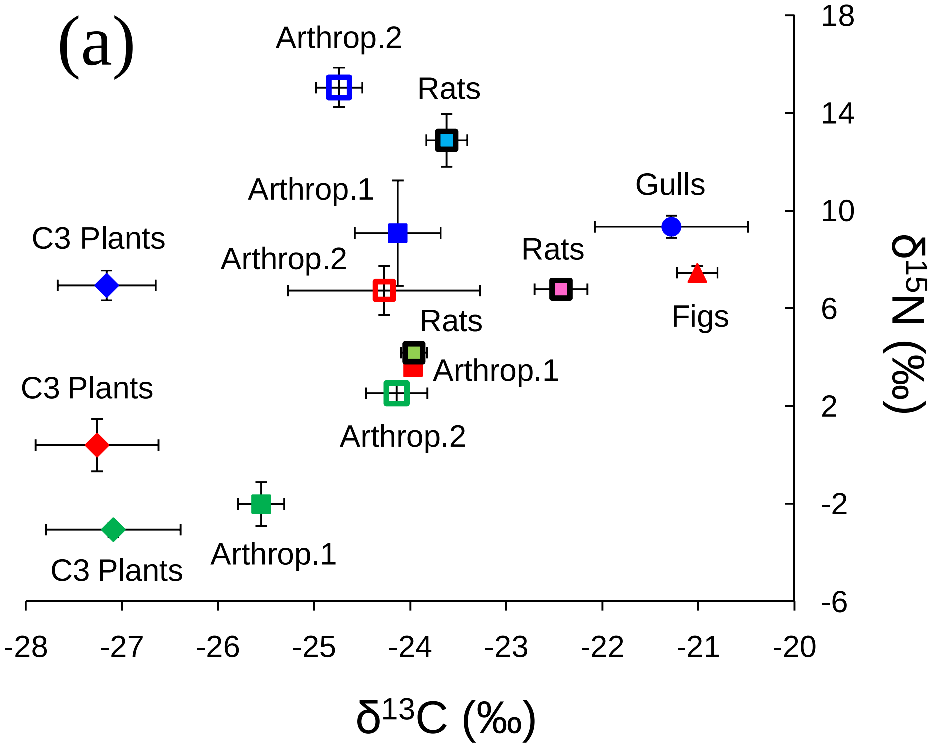
#### 4.1.3.1. Resource use

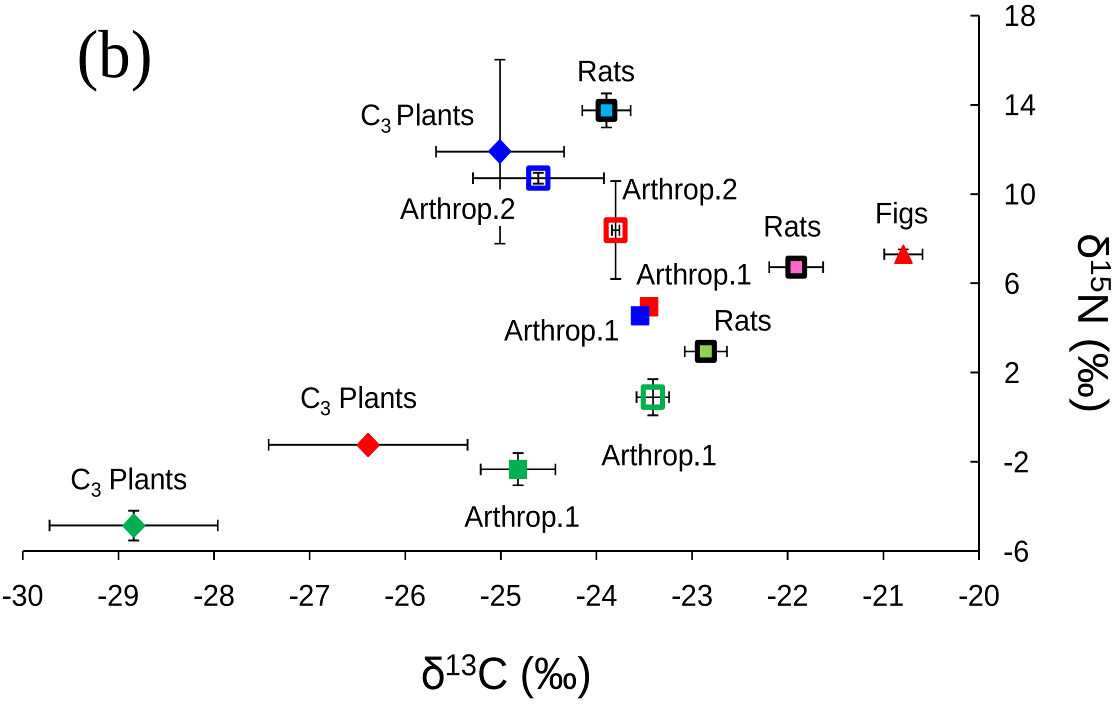
In total, 163 rats were captured for diet analysis in 2006-2007 (51 rats in May 2006, 76 in September 2006, 36 in February 2007). The analyses of faecal contents of a subset of 87 rats revealed that, across the population, rats consumed a wide range of food throughout habitats and seasons (Table 8). The animal part in the diet was low, mostly represented by terrestrial arthropod remains; their relative abundance ranges from 3 - 6 % to 17 - 20 % according to season and habitat. In May 2006, bird feathers were only recorded in *GU*. Plant material dominated in the diet with an overall mean number of different plant taxa consumed ranging from 7 (*SD* = 3) to 9 (*SD* = 4). The main eaten species varied with seasons and were characteristic of the habitat where rats were trapped, mainly formed by Fabaceae, Poaceae and Juncaceae in *GU*, Cyperaceae, Rubiaceae and Smilaceae in *SC*, and Aizoaceae in *IC*.

For each season, isotopic ratios of consumed food by rats significantly differed among habitats for both $\delta^{13}$C ($F_{2,82} = 4.06$, $P < 0.05$) and $\delta^{15}$N ($F_{2,82} = 31.83$, $P < 0.001$; Figure 19). Results of ANOVAs on isotopic ratios of rat liver and muscle for each season all revealed a significant effect of habitat on both $\delta^{13}$C and $\delta^{15}$N (all *P* values < 0.001; Figures 19, 20). Overall, Scheffe tests showed significant interactions between habitats for both ratios and all seasons, except the difference in $\delta^{13}$C *SC-GU* for liver in MAY, for muscle in FEB and in MAY. For each season, both rat tissues were significantly enriched in $\delta^{15}$N in the gull-influenced habitat (*GU*) compared to *IC* and *SC* (Figures 19, 20). In SEP, during the maximum availability of fleshy figs, both rat tissues were significantly enriched in $\delta^{13}$C in *IC* compared to *SC* and *GU* (Figures 19, 20).

| Site | | | | *GU* | | *SC* | | *IC* | |
|---|---|---|---|---|---|---|---|---|---|
| Diet | | | | *FO* | *IA* ± SE | *FO* | *IA* ± SE | *FO* | *IA* ± SE |
| **MAY 2006** | | | | (*N* = 7) | | (*N* = 11) | | (*N* = 12) | |
| Arthropoda | | | exoskeleton | *86* | 2.9 ± 0·1 | *100* | 17.0 ± 4.0 | *100* | 11.1 ± 2.3 |
| Chordata | Aves | | feathers | *57* | 4.9 ± 3·4 | *0* | - | *8* | 0.02 ± 0.02 |
| Coniferopsida | *Pinus halepensis* | | cones | *0* | - | *27* | 1.0 ± 0.9 | *0* | - |
| Aizoaceae | *Carpobrotus* sp. | | seeds | *0* | - | *27* | 0.4 ± 0.4 | *58* | 28.5 ± 9.3 |
| Asteraceae | *Senecio leucanthemifolius* | | leaves | *29* | 1.5 ± 1.3 | *9* | 0.1 ± 0.1 | *25* | 0.3 ± 0.1 |
| Cyperaceae | *Carex haleriana* | | seeds | *29* | 0.7 ± 0.6 | *45* | 18.9 ± 8.9 | *8* | 1.0 ± 1.0 |
| Euphorbiaceae | *Euphorbia pithyusa* | | floral part | *43* | 0.3 ± 0.2 | *27* | 4.6 ± 2.8 | *58* | 1.6 ± 0.6 |
| Fabaceae | *Lotus cytisoides* | | leaves | | | | | | |
| | *Vicia bengalensis* | | leaves | *43* | 3.5 ± 1.3 | *36* | 17.5 ± 8.2 | *66* | 21.5 ± 7.4 |
| | *Trifolium* sp. | | leaves | | | | | | |
| Liliaceae | *Asparagus acutifolius* | | leaves | *0* | - | *18* | 0.6 ± 0.5 | *16* | 0.3 ± 0.2 |
| Oleaceae | *Olea europaea* | | leaves | *0* | - | *0* | - | *8* | 0.03 ± 0.03 |
| Orobanchaceae | *Orobanche sanguinea* | | leaves | *0* | - | *0* | - | *17* | 0.4 ± 0.3 |
| Poaceae | - | | inflorescences | *100* | 75.7 ± 6.4 | *91* | 16.9 ± 6.5 | *100* | 15.4 ± 3.7 |
| Rubiaceae | *Rubia peregrina* | | leaves | *0* | - | *55* | 5.9 ± 3.0 | *33* | 0.7 ± 0.4 |
| Ruscaceae | *Ruscus aculeatus* | | leaves | *0* | - | *91* | 2.7 ± 0.7 | *67* | 4.0 ± 1.8 |
| Smilaceae | *Smilax aspera* | | leaves | *0* | - | *0* | - | *17* | 0.1 ± 0.9 |
| Undefined items (animals + plants) | | | | *100* | 10.5 ± 4.3 | *82* | 14.4 ± 4.5 | *92* | 15.1 ± 5.7 |
| **SEPTEMBER 2006** | | | | (*N* = 10) | | (*N* = 10) | | (*N* = 9) | |
| Arthropoda | | | exoskeleton | *100* | 19·6 ± 7·8 | *100* | 13·4 ± 3.4 | *100* | 5.8 ± 1.6 |
| Coniferopsida | *Pinus halepensis* | | cones | *30* | 6·2 ± 5·4 | *50* | 0.3 ± 0.2 | *0* | - |
| Aizoaceae | *Carpobrotus* sp. | | seeds | *0* | - | *10* | 0.1 ± 0.1 | *78* | 52.8 ± 13.6 |
| Fabaceae | *Lotus cytisoides* | | vegetative part | *70* | 6.7 ± 3·0 | *0* | - | *0* | - |
| Frankeniaceae | *Frankenia laevis* | | leaves | *50* | 0.9 ± 0.6 | *0* | - | *0* | - |
| Juncaceae | *Juncus acutus* | | stems-seeds | *80* | 16.4 ± 5.9 | *0* | - | *0* | - |
| Liliaceae | *Asparagus acutifolius* | | vegetative part | *0* | - | *10* | 0.2 ± 0.2 | *0* | - |
| Oleaceae | *Phyllyrea* sp. | | fruits | *20* | 0·8 ± 0.6 | *90* | 5.9 ± 2.0 | *11* | 0.06 ± 0.06 |
| Poaceae | - | | vegetative part | *100* | 24·7 ± 6.3 | *30* | 0.2 ± 0.2 | *56* | - |
| Rubiacea | *Rubia peregrina* | | vegetative part | *20* | 0.6 ± 0.6 | *100* | 0.9 ± 0.5 | *0* | - |
| Ruscacea | *Ruscus acleatus* | | leaves+seeds | *0* | - | *100* | 0.2 ± 0.1 | *30* | 0.3 ± 0.2 |
| Smilaceae | *Smilax aspera* | | leaves-fruits | *40* | 2.3 ± 1.6 | *100* | 57.9 ± 10.0 | *100* | 31.9 ± 11.6 |
| Solanaceae | *Solanum nigrum* | | leaves-seeds | *20* | 3.8 ± 3.8 | *0* | - | *0* | - |
| Undefined items (animals + plants) | | | | *90* | 18.0 ± 5.1 | *100* | 20.9 ± 7.3 | *56* | 9.1 ± 5.6 |
| **FEBRUARY 2007** | | | | (*N* = 8) | | (*N* = 10) | | (*N* = 10) | |
| Arthropoda | | | exoskeleton | *38* | 2.5 ± 1.3 | *100* | 5.1 ± 2.5 | *80* | 1.2 ± 0.4 |
| Chordata | Aves | | feathers | *0* | - | *0* | - | *60* | 7.6 ± 7.0 |
| Coniferopsida | *Pinus halepensis* | | cones | *0* | - | *70* | 9.3 ± 6.9 | *10* | 0.1 ± 0.1 |
| Aizoaceae | *Carpobrotus* sp | | seeds | *0* | - | *30* | 8.6 ± 7.7 | *100* | 57.7 ± 7·8 |
| Araceae | *Arisarum vulgare* | | vegetative part | *0* | - | *0* | - | *30* | 1.7 ± 0.9 |
| Capryollaceae | *Lonicera implexa* | | fruits | *0* | - | *0* | - | *20* | 0.2 ± 0.2 |
| Cistaceae | *Cistus* sp. | | stems | *0* | - | *0* | - | *20* | 0.3 ± 0.2 |
| Cyperaceae | *Carex haleriana* | | stems | *0* | - | *50* | 2.8 ± 1.7 | *50* | 1.8 ± 1.0 |
| Ericaceae | *Arbutus unedo* | | fruits | *0* | - | *30* | 0.9 ± 0.6 | *10* | 0.2 ± 0.2 |
| Fabaceae | *Lotus cytisoides* | | vegetative part | *88* | 47.6 ± 12.3 | *10* | 5.0 ± 5.0 | *40* | 0·3 ± 0·2 |
| Frankeniaceae | *Frankenia laevis* | | vegetative part | *13* | 2.5 ± 2.5 | *0* | - | *0* | - |
| Juncaceae | *Juncus acutus* | | seeds | *88* | 12·0 ± 8.0 | *0* | | *40* | 0·3 ± 0·2 |
| Liliaceae | *Asparagus acutifolius* | | vegetative part | *0* | - | *0* | - | *50* | 1.3 ± 0.8 |
| Myrtaceae | *Myrtus communis* | | fruits-seeds | *0* | - | *50* | 2.0 ± 1.0 | *20* | 0.4 ± 0.2 |
| Oleacea | *Phyllyrea* sp. | | leaves-fruits | *0* | - | *50* | 3.5 ± 2.7 | *20* | 0.4 ± 0.2 |
| Poaceae | - | | vegetative part | *75* | 15.4 ± 7.6 | *30* | 1.7 ± 1.1 | *60* | 8.1 ± 4.1 |
| Rubiaceae | *Rubia peregrina* | | vegetative part | *0* | - | *100* | 43.3 ± 9.3 | *60* | 0.8 ± 0.5 |
| Ruscaceae | *Ruscus aculeatus* | | vegetative part | *0* | - | *50* | 0.9 ± 0.5 | *30* | 1.4 ± 1.2 |
| Smilaceae | *Smilax aspera* | | fruits | *0* | - | *30* | 13.4 ± 9.1 | *80* | 10.7 ± 6.9 |
| Solanaceae | *Solanum nigrum* | | seeds | *38* | 6.6 ± 4.0 | *50* | 1.8 ± 1.0 | *0* | - |
| Undefined items (animals + plants) | | | | *75* | 13.4 ± 11.5 | *80* | 3.6 ± 2.0 | *90* | 6.8 ± 2.5 |

**Table 8.** Diet micro-histological analyses of faeces of black rats in the three habitats (*GU* = gull, *SC* = scrubland, *IC* = iceplant) during the three seasons (May 2006, September 2006, February 2007) on Bagaud Island; *FO* is for percentage of occurrence and *IA* for mean relative abundance (± SE), both in %.


(a)
Arthrop.2
Rats
Arthrop.1
Gulls
C3 Plants
Arthrop.2
Rats
Figs
Rats
Arthrop.1
C3 Plants
Arthrop.2
C3 Plants
Arthrop.1
18
14
10
6
2
-2
-6
-28
-27
-26
-25
-24
-23
-22
-21
-20
δ15N (‰)
δ13C (‰)


(b)
Rats
C3 Plants
Arthrop.2
Arthrop.2
Figs
Rats
Arthrop.1
Rats
Arthrop.1
C3 Plants
Arthrop.1
C3 Plants
Arthrop.1
18
14
10
6
2
-2
-6
-30
-29
-28
-27
-26
-25
-24
-23
-22
-21
-20
δ15N (‰)
δ13C (‰)

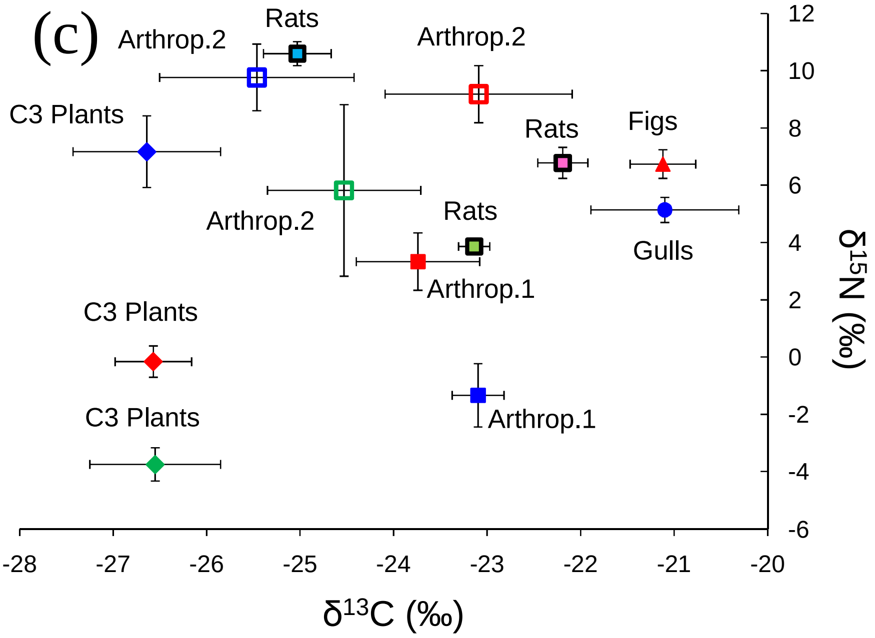


**Figure 19.** Mean isotopic signatures (carbon and nitrogen ratios, $\delta^{13}$C and $\delta^{15}$N respectively) of black rats and their preys with standard errors, in three habitats (blue symbols: gull habitat; red symbols: iceplant habitat; green symbols: scrubland habitat) during three seasons: May 2006 (a), September 2006 (b) and February 2007 (c). Preys were identified by analyses of rat fecal contents.

Centroid hierarchical cluster analyses revealed the same three main clusters for each season (Figure 20). Each cluster was mainly composed of individuals captured in one of the three study habitats. Overall, very few marginal individuals were identified to switch habitats in one week or one month time scale: only 3 rats trapped in a habitat other than *GU* or *IC* were clustered for their liver isotopic signatures with individuals trapped in *GU* or *IC* (Figure 20a, c, e), and the isotopic signatures of 4 rats shifted from a habitat to another between tissues (Figure 20b, d, f). For each season, some individuals trapped in *IC* were clustered with some individuals trapped in *SC*.

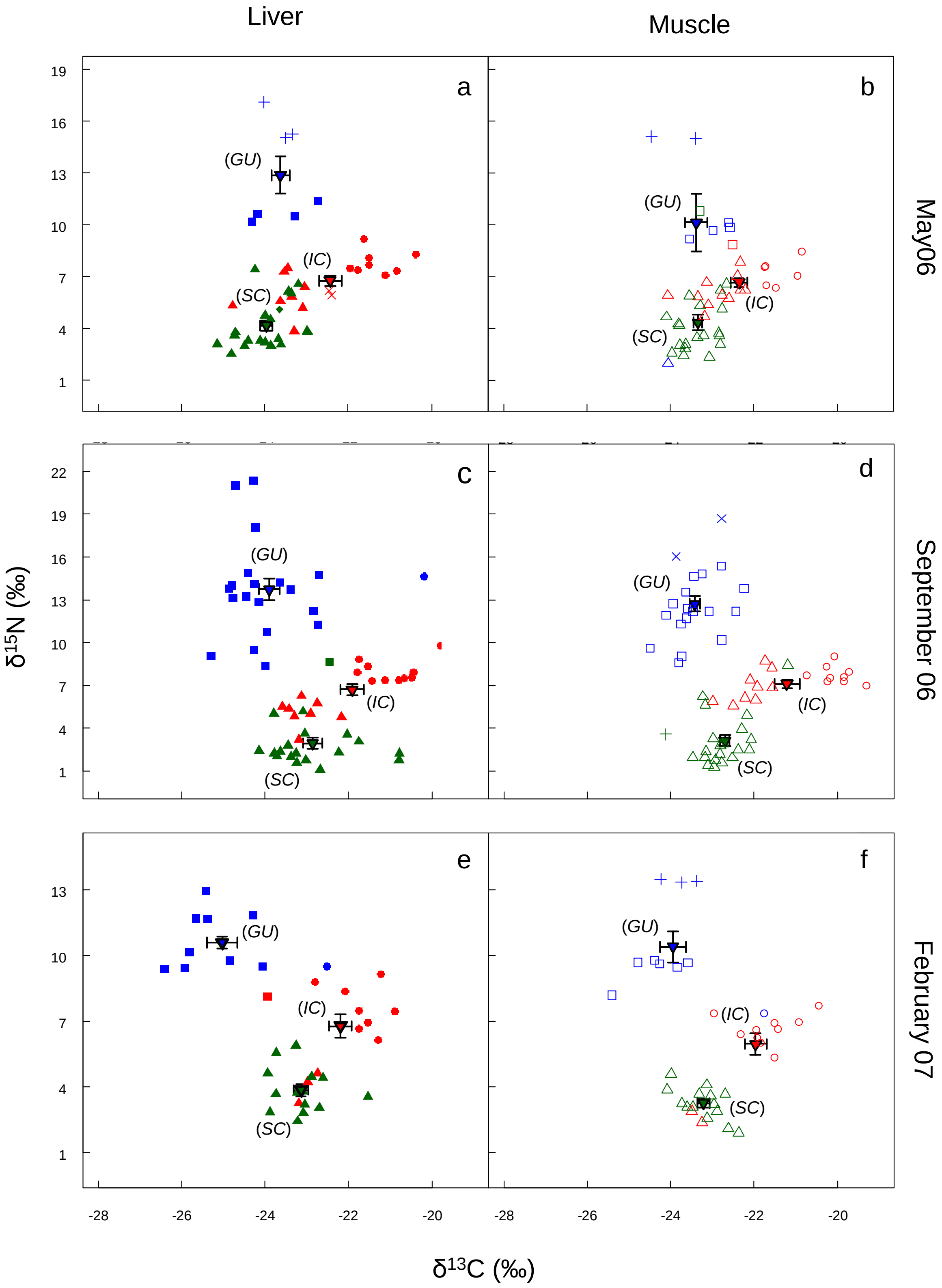


**Figure 20.** Results of centroid distance clustering analyses on stable isotope signatures of liver (filled symbols; a, c, e) and muscle (open symbols; b, d, f) of rats trapped in each of the three habitats (blue: gull habitat, red: iceplant habitat, green: scrubland habitat) during three seasons (May 2006: a, b; September 2006: c, d; February 2007: e, f). Similarity between each pair of plots indicates little change in individual diet in one month scale. Identical symbols are clustered in the same group.

To run SIAR models, *IC* was split in two groups (Table 9), according to the hierarchical cluster analysis results (see above). *IC*-1 was related to individuals trapped in *IC* whose isotopic signatures were clustered in an independent group (red triangles in Figure 20), whereas *IC*-2 was related to individuals trapped in *IC* but whose isotopic signatures were clustered with those of individuals trapped in SC (red circles in Figure 20). SIAR estimates showed that rats from adjacent *IC* and *SC* significantly diverged in the assimilated proportions of figs across seasons. In particular, the model estimated a large relative contribution of figs in rat diet for *IC*-1 for all seasons, but more specifically for SEP, and a very low proportion of figs in the diet of rats from *IC*-2 and adjacent *SC* (Table 9).

| Season | | May 06 | | | | September 06 | | | | February 07 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | Group | Mode | Mean | CI 2.5% | CI 97.5% | Mode | Mean | CI 2.5% | CI 97.5% | Mode | Mean | CI 2.5% | CI 97.5% |
| *IC* | 1 | 0.34 | 0.36 | 0.08 | 0.64 | 0.43 | 0.47 | 0.20 | 0.77 | 0.36 | 0.39 | 0.14 | 0.66 |
| | 2 | 0.03 | 0.13 | 0.00 | 0.35 | 0.02 | 0.07 | 0.00 | 0.18 | - | - | - | - |
| | 1+2 | 0.20 | 0.20 | 0.00 | 0.40 | 0.31 | 0.28 | 0.02 | 0.50 | 0.26 | 0.23 | 0.00 | 0.44 |
| *SC* | | 0.01 | 0.04 | 0.00 | 0.10 | 0.03 | 0.08 | 0.00 | 0.21 | 0.02 | 0.09 | 0.00 | 0.22 |

**Table 9.** Estimates of relative contribution (with 95% credible intervals) of iceplant figs in the assimilated diet of rats trapped in the iceplant (*IC*) and scrubland (*SC*) habitats during three seasons. *IC* was split in two groups, according to the hierarchical cluster analysis results (Figure 18): *IC*-1 is for individuals represented by red triangles in Figure 18, and *IC-2* is for individuals represented by red circles in Fig.ure 18 (see Result-Resource use for further details).

Variation in isotopic ratio values between rat tissues (i.e. variation through the previous four weeks before sampling: D$\delta^{13}$C and D$\delta^{15}$N) was lower than 1‰ for all habitat-season combinations, except in *GU* for D$\delta^{15}$N in MAY and SEP and for D$\delta^{13}$C in FEB (Figure 21a, b). Through April (i.e. MAY), during the middle of the gull nesting period, the enrichment in mean $\delta^{15}$N of rats trapped in *GU* was significantly higher compared to the two other habitats during the same season and the two other seasons for *GU* (Figure 21b). In summer (i.e. SEP), during the peak of fig ripening, the depletion in mean $\delta^{13}$C of rats trapped in *IC* was significantly higher than the two other habitats, especially *SC* (Figure 21a). No correlation was found between empty body mass of individuals and both D$\delta^{13}$C (Spearman $r_s = 0.14$, $N$ = 138) and D$\delta^{15}$N (Spearman $r_s = -0.01$, $N$ = 138). Neither D$\delta^{13}$C nor D$\delta^{15}$N were significantly different between sexes (Mann Whitney tests, $P > 0.05$).

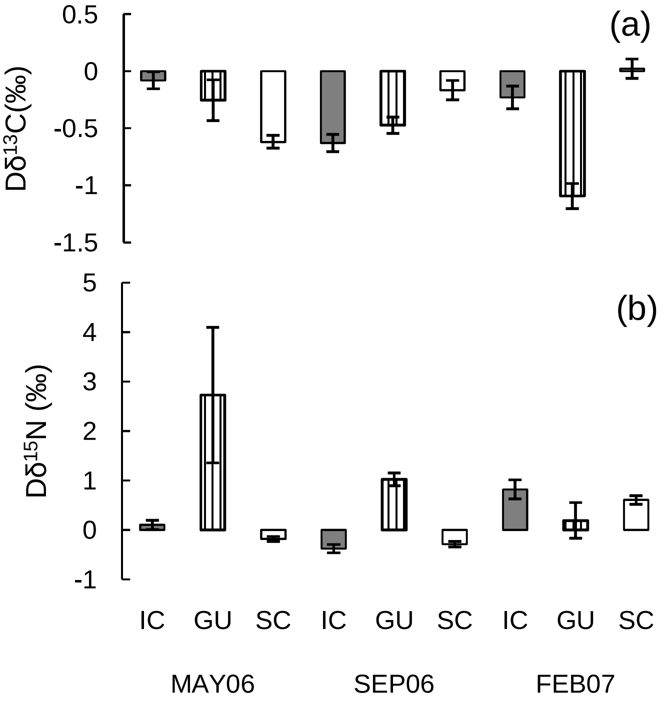


**Figure 21.** Variation in $\delta^{13}$C (D$\delta^{13}$C: 3a) and $\delta^{15}$N values (D$\delta^{15}$N: 3b) between muscle and liver of rats from each habitat (*GU* = gull, *IC* = iceplant, *SC* = scrubland) – season (MAY06 = May 2006; SEP06 = September 2006; FEB07 = February 2007) combinations.

### 4.1.3.2. Habitat use

From April 2007 to April 2009, 19 capture-recapture sessions gave 2236 captures and 610 rats marked. Nearly half the marked rats were recaptured in at least two different trapping sessions. Mean and maximum distances moved by rats between subsequent captures were respectively 30 m (*SD* = 37) and 451 m. Mean distances moved between subsequent captures were significantly higher for males than for females (mean $\text{dist}_{\text{Male}}$ = 36 m ± 42 *SD*, $N_M = 210$; mean $\text{dist}_{\text{Female}}$ = 23 m ± 30 *SD*; $N_F = 196$, $Z = -3.9$, $P < 0.001$). Mean distances moved between subsequent captures were significantly higher ($Z = 9.4$, $P > 0.001$) for animals trapped during different sessions (33 m ± 40 *SD*, *N* = 290) than trapped within the same session (14 m ± 15 *SD*, *N* = 402). Spearman rank correlations showed a slight correlation between distances moved between sessions and time between subsequent captures (*N* = 596, Spearman $r_s = 0.22$, $P < 0.001$).

The habitat transition matrix revealed low probabilities of movement between habitats (Table 10). However, the probability for rats of staying within the same habitat between subsequent captures was greater than 0.87 in each habitat. The 50% FK core areas of all radio-tracked individuals remained in the same habitat where they were collared and trapped by capture-recapture. Estimated 100% MCP showed a mean home-range width of 133 m ± 51 *SD*. The seven rats collared further than 100 m from the iceplant patch were never recorded in the patch.

| **Estimates** | **Mean** | **SD** | **CI 2.5%** | **CI 97.5%** |
|---|---|---|---|---|
| $\psi_{GU,GU}$ | 0.93 | 0.02 | 0.89 | 0.96 |
| $\psi_{GU,SC}$ | 0.05 | 0.02 | 0.02 | 0.08 |
| $\psi_{GU,IC}$ | 0.02 | 0.01 | 0.01 | 0.04 |
| $\psi_{SC,GU}$ | 0.07 | 0.02 | 0.03 | 0.12 |
| $\psi_{SC,SC}$ | 0.87 | 0.03 | 0.80 | 0.92 |
| $\psi_{SC,IC}$ | 0.06 | 0.02 | 0.03 | 0.11 |
| $\psi_{IC,GU}$ | 0.02 | 0.01 | 0.00 | 0.04 |
| $\psi_{IC,SC}$ | 0.02 | 0.01 | 0.00 | 0.04 |
| $\psi_{IC,IC}$ | 0.97 | 0.01 | 0.93 | 0.99 |

**Table 10.** Posterior probabilities ($\psi$) of rat movement between habitats (*GU* = gull, *SC* = scrubland, *IC* = iceplant) with standard deviation (SD) and 95% credible intervals (CI).

### 4.1.4 Discussion

At a small spatial scale, the isotopic signatures of resources varied locally among habitats on Bagaud Island. Gulls substantially enriched local trophic webs in $^{15}$N during their breeding season in spring and iceplant produced figs enriched in $^{13}$C during summer. These nutrient enrichments seemed to persist in the local food webs even when gull and fig resources were much less or no longer available. For each season, rat isotopic signatures were similar to the isotopic value of their immediate habitat and the high $^{15}$N and $^{13}$C enrichment in their tissues indicated that high-order consumers like invasive rats on islands were locally subsidized by gulls and figs, respectively.

Faecal content and stable isotope analyses from our study both agreed with the generalist foraging behavior (diet breadth) of *R. rattus* and the ability of the species, as a whole, to exploit a wide range of resources and establish in habitats of variable quality (Clark 1981; Harper *et al*. 2005; Towns *et al*. 2006; Caut *et al*. 2008a). The dietary and habitat breadth of the species should have facilitated its success of invasion on islands of various environmental conditions, even when drastic (e.g. Caut *et al*. 2008a). On Bagaud Island, within each habitat, rats selected different food items across seasons, probably in relation to their seasonal phenology, abundance, nutritional value and palatability (Clark 1981; Grant-Hoffman *et al*. in press). However, diet plasticity of rats was far narrower at the individual level. Surprisingly, even when habitats were only tens of meters apart, the diet of rats was substantially distinct among adjacent habitats for each season. Moreover, very few individuals moved among adjacent habitats in pursuit of higher-quality resources when they became available, despite the marked influence of gull-derived resources and, to a lesser extent figs, on rat population dynamics (e.g. higher individual growth rates, higher reproductive output and density; L. Ruffino unpublished), especially during drastic climate conditions (i.e. dry years with low terrestrial productivity). This specific pattern of resource use was consistent over successively larger time scales (i.e. days, weeks, and months) and reflected the specific or even exclusive use of resources by rats found in the habitat that they closely occupy. Gull and fig resources, in particular, were extensively used by rats when they became available but only benefit resident individuals.

Live-trapping studies are prone to biases when estimating habitat use by animals and their home range span with successive records of trapping events. Here, the possible biases in estimating distances moved by rats with live-trapping studies were overcome by combining a long-term capture-recapture survey with the monitoring of individual movements by radio-tracking at a finer spatio-temporal scale. Our radio-tracking results reinforced the apparent high residency rate of black rats and showed that although rats had a home-range span large enough to reach alternative habitats during the dry summer, they remained in the surrounding scrubland. Even though our capture-recapture survey indicated higher mean travel distances by rats with time between captures, distances moved remained low (< 40m), suggesting no apparent range shift with time. Unfortunately, individual-based movement studies on rodent populations covering a long period of time with seasonal fluctuating resources remain scarce (but see Moller & Craig 1987), although very useful to highlight habitat or dietary shifts over time. The apparent low distances moved by black rats between captures and low individual dispersal towards unfamiliar areas (i.e. outside their home range area) were consistent with some other capture-recapture studies on rodents (e.g. Moller and Craig 1987; Jones 1989). However, the capacity of small mammals to move among different habitats and disperse long distances may depend on the spatial distribution (i.e. patchiness) and temporal availability of resources (Dowding & Murphy 1994; Tobin *et al*. 1996; Gauffre *et al*. 2008), the presence of geographical corridors or barriers (Krohne & Hoch 1999), or metapopulation dynamic processes (Krohne 1997; Lin & Batzli 2001).

The variation in isotopic ratios of the same rats over one month scale (i.e. variation between tissues) was low and only a few individuals were identified to switch habitats when the availability of high-quality resources was the greatest. This switching by some individuals was not linked to either age or sex, and may be an outcome of other population processes such as being forced out of territories. Even the rats dwelling in the immediate interface between scrubland and the iceplant patch only slightly used figs during the dry summer, while the resident rats from the fig patch strongly relied on this resource at that time (Figure 18, Table 10). Food supplementation experiments and manipulations of habitat quality in the field often encourage immigration towards food supplemented areas or higher-quality habitats and increase residential times of newly established individuals (Boutin 1990), especially omnivorous rodents (Banks & Dickman 2000; Lin & Batzli 2001; Van Aarde & Jackson 2007). Therefore, our finding is counterintuitive for a generalist invasive forager which may have had access to higher-quality resources in close proximity throughout the year. These unexpected findings are likely to be related to other population processes, such as intraspecific territorial interactions, that may limit the access of high-quality resources to subordinates.

There is extensive evidence that some species of ecological generalists, which use a large diversity of resources, are in fact formed by heterogeneous groups of individuals using narrower ranges of resources (Bolnick *et al*. 2003; Brooke MacEachern *et al*. 2006; Bolnick *et al*. 2007; Quevedo *et al*. 2009). However, studies demonstrated distinct foraging strategies in individuals of generalist species occupying small habitat patches in close proximity are rare (but see Brooke MacEachern *et al*. 2006). Decrease in niche breadth in individuals of generalist species may minimize intra-specific competition by reducing resource use overlap (Bolnick *et al.* 2007), and is observed in heterogeneous landscapes and patchy habitats, and in individuals exhibiting a strong territoriality (Angerbjorn *et al*. 1994; Urton & Hobson 2005). *R. rattus* tend to be strongly bounded to their feeding sites, remaining within their territory boundaries to defend food and mates (Worth 1950; Telle 1966). Territory defense (e.g. through scent marks) and/or agonistic behavior towards unfamiliar conspecifics may provide a plausible explanation for the low mobility of rats and the privileged access to enriched resources by dominants and residents, as predicted by the ideal despotic distribution (Fretwell & Lucas 1970) and already demonstrated for other rodents (Spencer & Cameron 1983; Gray *et al*. 2002; Jensen *et al*. 2005). Moreover, when the high-quality food source is clumped in space, e.g. patchy habitats, dominant individuals may tend to monopolize food sources (Boutin 1990). In this sense, the larger body mass of rats foraging on gull-subsidized resources on Bagaud Island (compared to rats that did not have access to these enriched resources; L. Ruffino unpublished) could favor social dominance and aggression (i.e. Spencer & Cameron 1983).

By combining diet and trophic analyses at various time scales with an intensive individual-based movement monitoring all over several rat generations, we were able to examine how habitat heterogeneity at a small spatial scale and the seasonal fluctuation of resource quality within habitats affect diet breadth and plasticity at the individual and population levels, in a generalist forager. The diet-switching ability of introduced rodents to benefit from seasonal high-quality resources is often proposed to explain their wide invasion success and diverse impact from arctic to tropical islands (Stapp 2002; Stapp & Polis 2003; Major *et al*. 2006; Towns *et al*. 2006). Caut *et al*. (2008a) recently demonstrated a dietary shift in *R. rattus* diet on a dry tropical island between seasons, but did not track individual rats. Whether diet plasticity is attributable to marked shifts in individual diet, or alternatively differences between sub-populations remains unclear. Conversely, on Bagaud Island, we found that individual rat diet was relatively consistent with the resources available in their immediate habitat across seasons, despite the very close proximity of fluctuating resources of differential quality in the wider environment. The differences observed between the two systems may be related to multiple intrinsic and extrinsic factors such as rat local population density, the attractiveness of resources, climate conditions or intraspecific interactions.

### 4.1.5. Conclusions and implications

The pattern of resource use observed in our study could be considered surprising for such a successful invader, renowned for its ecological flexibility and diet plasticity. Although our results support high species- and population-level diet breadth and plasticity, they show a much narrower diet and habitat breadth of individuals, constrained by complex mechanisms probably related to social organization and territory defense behavior. Restricted diet breadth of *R. rattus* individuals along with limited rat movements between habitats may promote differentiation among sub-populations in dynamics and structure, reinforcing the benefits of enriched resources (L. Ruffino unpublished). On the other hand, our results add to growing evidence that invasive black rats can occupy various habitats, even those of low quality, which should explain their wide invasion success on islands, especially on drastic environments. Our results also suggest that even on a small island, the accessibility of patchy and high-quality resources to rats from the whole population is not systematic, a result which has important implications when quantifying invasive rat impact on patchily distributed species, especially when studies use indirect methods such as diet analyses as a substitute for direct observations of feeding habits. To conclude, we underline here the usefulness of coupling methods and the need of carrying out more long-term individual-based monitoring studies to assess both resource and habitat use of invasive species at different spatio-temporal scales in changing environments.

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# - Partie 4.2. -

## 4.2. CLIMATE MEDIATE THE EFFECTS OF ALLOCHTHONOUS SUBSIDIES ON AN INSULAR INVASIVE RAT POPULATION

4.2. Les conditions climatiques modulent les effets des apports de resources d'origine allochtone sur une population insulaire de rats introduits

**Résumé:**

L'identification des facteurs susceptibles d'affecter les dynamiques de populations d'espèces envahissantes et d'accroître leurs impacts revêt un intérêt majeur en matière de conservation des communautés insulaires indigènes des îles. Au cours des dernières décennies, l'accroissement des activités humaines s'est traduit par d'importants changements trophiques au niveau des écosystèmes insulaires. En particulier, les apports anthropiques de nutriments d'origine allochtone ont modifié la structure trophique des communautés insulaires. Ces apports sont susceptibles de fertiliser les consommateurs de derniers ordres en déclenchant un contrôle des chaînes trophiques de type « bottom-up », surtout sur les îles de faible productivité trophique aux conditions climatiques sèches. Dans le cadre de ce travail, nous avons testé l'effet des ressources anthropiques d'origine allochtone sur une population insulaire d'une des espèces les plus ravageuses au monde, le rat noir, *Rattus rattus,* sur une île oligotrophique de Méditerranée, Bagaud (S-E France). Un suivi par capture-marquage-recapture des dynamiques de population du rat noir a été réalisé durant deux années aux conditions climatiques contrastées, dans le but d'étudier (1) la réponse des dynamiques de populations du rat noir aux apports de ressources d'origine allochtone, (2) le rôle du climat dans la modulation des effets de ces ressources allochtones, et (3) le rôle de l'hétérogénéité et de la proximité spatiale des habitats dans le transport des nutriments allochtones par les rats. Nos résultats montrent un effet plus prononcé des ressources allochtones sur les dynamiques de populations des rats durant l'année sèche. Les effets des apports de nutriments par les goélands anthropophiles sur les dynamiques de populations de rats apparaissent plus forts que ceux des plantes succulentes envahissantes, en particulier sur les taux de croissance des individus, et dans une plus faible mesure, sur les paramètres reproducteurs et les densités de rats. Cependant, ces effets sont spatialement limités, suggérant que sur Bagaud, les rats noirs sont de faibles vecteurs de nutriments allochtones à travers les habitats, même lorsqu'ils sont spatialement proches. Dans une perspective d'aridification du climat en Méditerranée, le fort potentiel des apports de ressources d'origine allochtone dans l'atténuation des effets négatifs des conditions environnementales drastiques pourrait participer à stabiliser les fluctuations inter-annuelles des dynamiques de populations de rats, maintenir les populations sur le long terme et indirectement, accroître l'impact des rats sur les communautés insulaires.

**Cette partie correspond à l'article en préparation suivant :**

**Ruffino L., Russell J. & Vidal E. Climate mediate the effects of allochthonous subsidies on an insular invasive rat population. En préparation pour *Oecologia*.**

### 4.2.1. Introduction

Island systems, even the most isolated ones, rarely function independently with neighboring ecosystems (Polis *et al.* 1996, 2004). Ecologists are increasingly recognizing the important direct and indirect effects that inputs of nutrients (e.g. carbon, nitrogen, phosphorous) and energy from outside the focal site (i.e. allochthonous inputs) have on recipient abiotic and biotic components (Polis and Hurd 1996; Anderson & Polis 1999; Wait *et al*. 2005; Stapp &Polis 2003b; Ellis 2005; Marczak *et al*. 2007; Paetzold *et al*. 2008). Allochthonous inputs on islands come from marine (e.g. marine sprays, algae drift, marine carrions, seabird guano; Polis *et al*. 2004) and/or terrestrial areas (e.g. natural establishment of terrestrial organisms, species introductions by humans). The transport of materials and nutrients occurs from organisms either naturally dispersing across ecosystem boundaries (e.g. birds, insects, mammals or reptiles, Polis *et al.* 1997a) or transported by humans (i.e. species introductions), and/or from abiotic factors (e.g. wind, tidal action, Polis *et al*. 1997a, 2004).

During the last decades, many studies have documented the important role of allochthonous (mainly marine) subsidies in enhancing bottom-up controls of island trophic dynamics (Polis & Hurd 1996; Sanchez-Pinero & Polis 2000; Anderson *et al.* 2008) and in subsidizing native island communities, such as plants (Farina *et al*. 2003; Ellis 2005; Ellis *et al.* 2006), arthropods (Sanchez-Pinero & Polis 2000; Markwell & Daugherty 2002; Paetzold *et al.* 2008), reptiles (Markwell & Daugherty 2002; Barrett *et al*. 2005), marsupials (Wolfe *et al.* 2004), small (Stapp & Polis 2003a, 2003b) and large mammals (Iason *et al*. 1986). The potential for allochthonous resources to subsidize recipient food webs should vary with the productivity gradient between donor and recipient compartments (Polis *et al.* 1997a; Catenazzi & Donnelli 2007; Paetzold *et al*. 2008) and climate conditions (Stapp *et al*. 1999; Stapp & Polis 2003a; Anderson *et al*. 2008). On islands where the net *in situ* primary productivity is low (e.g. arid and/or oligotrophic islands), a shift in trophic structure and community functioning is expected between climatically-contrasted years (Stapp *et al*. 1999; Anderson *et al*. 2008). During wet years, when heavy rainfall pulses stimulate terrestrial productivity and increase the overall resource availability for high-order consumers, allochthonous resources should contribute little to island population dynamics. Conversely, during dry years, island communities should rely to a greater extent on inputs of enriched allochthonous resources that may help the persistence of island consumers, sometimes by allowing large population densities that would not be possible based on low productive terrestrial resources alone (Stapp & Polis 2003a).

In the Mediterranean, human-induced changes in land use and increased trade activities have accelerated the rate of anthropogenically-driven flows of allochthonous nutrient inputs on islands, modifying the trophic structure of island communities. For example, the anthropogenically-driven demographic increase in yellow-legged gull (*Larus michahellis*) populations in the north-western Mediterranean basin (Vidal *et al*. 1998a) indirectly lead to substantial changes in native plant (Vidal *et al*. 1998b) and arthropod communities (Orgeas *et al*. 2003) in guano-fertilized areas on offshore islands. Food scraps, cracked eggs, dead chicks or adults also fuel scavengers. In addition, the widespread introduction and expansion of alien succulent plants (e.g. *Carpobrotus* spp., *Opuntia* spp., *Agave* spp., Hulme 2004) along continental and island coastal sites of the Mediterranean have provided new allochthonous resources to island consumers, especially during summer, when fleshy fruits ripen (Bourgeois *et al*. 2005). Given the wide distribution of alien invasive mammals on islands, their overall generalist foraging behavior and large impact on native island communities (e.g. Courchamp *et al.* 2003), the potential for allochthonous resources of anthropogenic origin to help them persist in the long-term despite sometimes low productive environments, and hence to increase their overall impact may have important implications for island conservation.

We selected a dry Mediterranean island, Bagaud Island, where anthropogenic allochthonous resources were found in close spatial proximity, to conduct a long-term capture-recapture survey on one of the most pervasive introduced mammals on the world's islands, the black rat (*Rattus rattus*). The potential effects of ongoing climate change, with expected longer dry season in summer and more frequent drastic events in the Mediterranean, on invasive rat population dynamics were investigated over two years of contrasting climate conditions (the driest and one of the wettest years of the last decade). The aims of the study were three fold. First, we assessed the effects of super-abundant gulls and introduced iceplant both occurring seasonally on Mediterranean islands, on rat population dynamics and structure. Given their generalist foraging behavior and their high-elevated trophic position on Bagaud Island, black rats are expected to be strongly bottom-up driven by allochthonous subsidies. Second, we investigated the role of climate in modulating the effects of allochthonous resources on rat population parameters. We hypothesized that rats would benefit much more from allochthonous inputs during dry (i.e. low *in situ* productivity) than during wet conditions (i.e. high *in situ* productivity). Third, we assessed the effects of habitat heterogeneity in structuring the spatial distribution of allochthonous subsidies. Given the very close spatial proximity of different allochthonous resources on Bagaud Island and the generalist foraging behavior of black rats, we expected that rats would be an effective vector of allochthonous nutrients across adjacent habitats.

## 4.2.2. Materials and methods

### 4.2.2.1. Study site

This study was conducted on Bagaud Island (58ha, 1.48 km long, 0.59 km wide), a natural reserve of the Port-Cros National Park in the Mediterranean Sea, lying 7.5 km from the southeast coast of France and 500 m from the nearest island (Figure 20). The island is mainly composed by acid rock substrate and reaches 57 m above sea level at its higher point. The black rat was probably introduced during the Roman times (Ruffino *et al.* 2009) but persists as the only non-volant mammal on the island, despite no permanent fresh water.

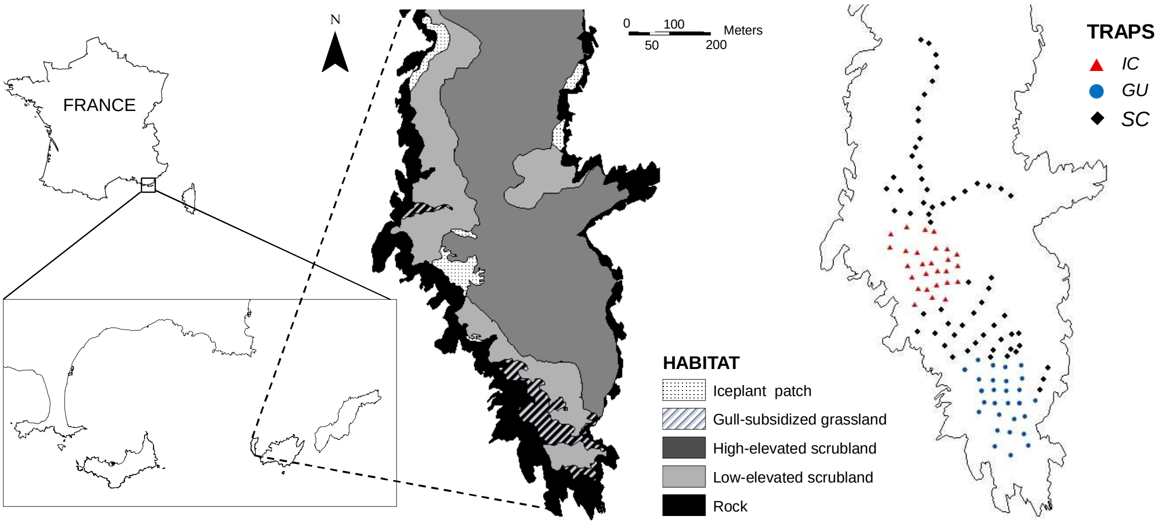

**Figure 22.** Map of Bagaud Island (43°00’42 N; 6°21’45 E), Port-Cros National Park, south-east France, showing the main habitats and trap location (*IC* = iceplant habitat, *GU* = gull habitat, *SC* = scrubland habitat).

### 4.2.2.2. Habitat description

The southern study site was selected for the close proximity of three distinct habitats differing in their resource availability and seasonality (Figure 22). First, the gull habitat (hereafter *GU*) comprises a yellow-legged gull (*Larus michahellis*) colony with a ruderal grassland mainly composed of Fabaceae, Poaceae and Juncaceae. In this habitat, plant and arthropod communities are substantially enriched in nitrogen (especially in $^{15}$N; Ruffino L. submitted) due to high guano deposition (Vidal *et al*. 1998b; Orgeas *et al.* 2003). March through May is the gull breeding period and, thus, are the three months of the year when gull influence is maximum (e.g. high input of marine-derived nutrients, adults feeding chicks, egg/chick carcasses). Second, the iceplant habitat (hereafter *IC*) was identified as a 1 500 m² patch of the mat-forming *Carpobrotus* spp. (Aizoaceae). This succulent invasive plant abundantly produces large fleshy figs, enriched in $^{13}$C (Ruffino L. submitted), energy (310 kJ/100g dry mass$^{-1}$) and water (80% water; Vila & D'Antonio 1998) that mature during the dry Mediterranean summer season. Third, the scrubland habitat (hereafter *SC*), a native dry Mediterranean mattoral, does not receive any allochthonous inputs and was identified as the non-subsidized habitat. This habitat is composed of a dense high-elevated mattoral dominated by *Pinus halepensis*, *Erica arborea*, *Myrtus communis*, *Arbutus unedo* and *Phyllirea* spp (Médail 1998) and a much less dense low-elevated scrubland, dominated by *Pistacia lentiscus* and *Juniperus phoenicea* (Figure 22). In each habitat, resources were seasonal, unavailable at the same time and differentially enriched in nutrients (e.g. marine-derived nutrients in *GU*; fresh water and energy in *IC*).

### 4.2.2.3. Rainfall patterns

The study was conducted during two years with contrasted climate in the total amount and timing of rainfall. The annual rainfalls for 2007 and 2008 were 403.4 mm and 803.6 mm respectively (Figure 23). The mean annual rainfall for the decade 1999-2008 was 625.1 ± 187.1 *SD* mm (Levant Island Meteorological Office). 2007 was the driest year of the last decade. 2007 had also the driest summer of the last decade (15.8 mm for June-September in 2007; mean summer rainfall for 1999-2008 = 105.4 ± 62.8 *SD* mm) and the driest autumn of the last decade (133.8 mm for October-December; mean autumn rainfall for 1999-2008 = 351.0 ± 151.3 *SD* mm). 2008 was among the rainiest years of the last decade, particularly in autumn with a total rainfall of 502 mm (Figure 23). In addition, spring 2008 had more homogenous monthly fresh water inputs and during a longer period of time, while spring 2007 had lower monthly rainfall with sudden large fresh water input.

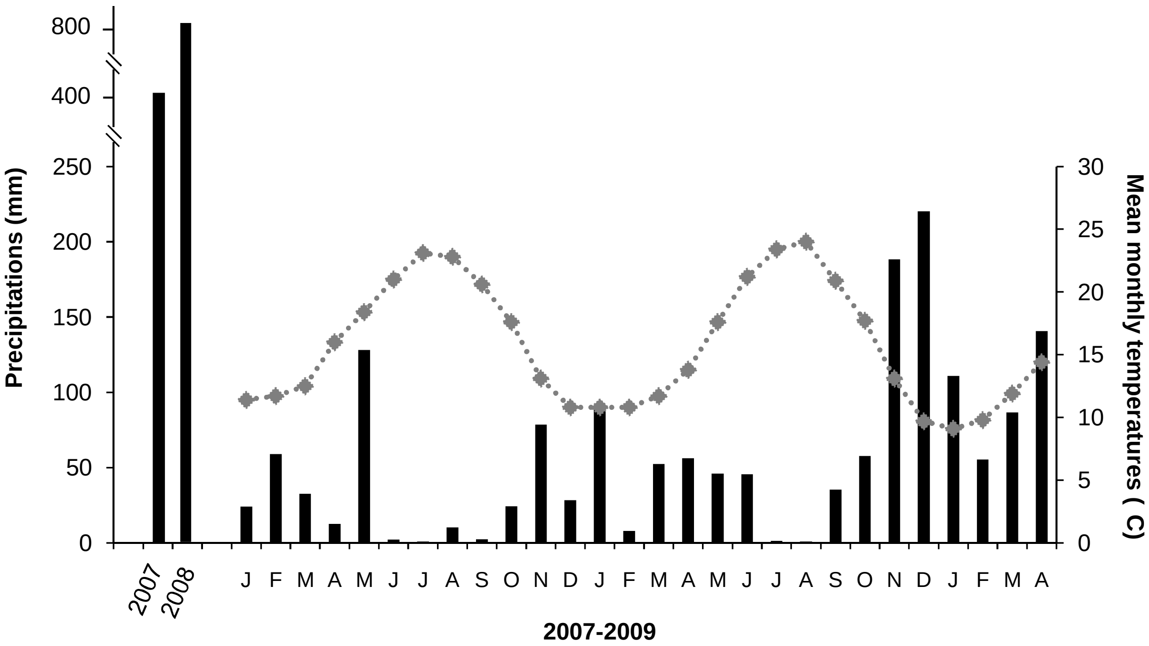

**Figure 23.** Monthly precipitations and mean monthly temperatures on Bagaud Island (data courtesy of Levant Island Meteorological Office). Bars show total monthly precipitations and the line shows mean monthly temperatures.

### 4.2.2.4. Rat isotopic signatures

In 2006-2007, three rat trapping sessions were conducted to analyze the isotopic signatures of rats within the three study habitats (*GU*, *IC*, *SC*) during three seasons (spring: early May 2006, summer: early September 2006, winter: early February 2007). BTS-Mécanique cage traps (29 x 10 x 10 cm, Manufrance, Saint-Etienne, France) were baited with peanut butter before dusk, checked and closed each morning. In total, 163 rats were captured (51 rats in May, 76 in September, 36 in February) and euthanized. Samples of liver were collected for stable isotope analyses and preserved in 70% alcohol. All samples were dried and ground in fine powder. Analyses of stable isotope ratios of carbon ($^{13}C/^{14}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) were performed by a spectrometer Delta V Plus (Service Central d'Analyses, CNRS Solaize, France). Ratios were expressed as $\delta^{13}C$ or $\delta^{15}N$ = $[(R_{sample}/R_{standart}) - 1] \times 1000$ when $R$=$^{13}C/^{12}C$ or $^{15}N/^{14}N$ for $\delta^{13}C$ or $\delta^{15}N$ respectively. The standard for C is the IAEA-NBS 21 (graphite: –28·13‰) and for N the IAEA-N1 (+0·4‰) and IAEA-N2 (+20·3‰). Ten replicate assays of intemal laboratory standards indicated measurement maximum errors (SD) of ± 0·15‰ and ± 0·2‰ for stable carbon and nitrogen isotope measurements, respectively. For all the individuals sampled, the effects of habitat and season on their mean trophic level (mean $\delta^{15}$N signature of liver samples) were tested with a multivariate ANOVA. As $\delta^{15}$N may vary with nutritional stress (Hobson *et al*. 1993) and indicate diet preferences between sexes, a GLM was used to investigate the effects of habitat, season, empty body mass (i.e. digestive tract removed) and sex on $\delta^{15}$N of individuals larger than150g (considered as adults).

#### 4.2.2.5. Rat population dynamics

##### 4.2.2.5.1. Rat trapping

To investigate the influence of allochthonous resources on rat population dynamics, 117 permanent trap stations with one BTS-Mécanique live trap were set from April 2007 to January 2009, covering the three study habitats (*GU*, *IC*, *SC*). Fourteen trapping sessions were undertaken, separated by1-3 months and repeated at the same period of year during the two years. Traps were set every 20-25 m, depending on the vegetation cover. Traps were baited with peanut butter before dusk, set between 3 and 8 consecutive nights depending on weather conditions, and all checked before 9am to avoid releasing rats too late in the day. During cold and humid seasons, bedding material was provided inside traps. Rats were individually marked using subcutaneous passive integrated transponder tags (type FDX-B, IER Paris, France), sexed, weighted to the nearest 2.5 g, checked for sexual maturity and released after capture. Reproductive activity was assessed for males by the record of the testis position (abdominal *vs* scrotal) and for females by the observation of their vagina (perforate or not) and nipples (developed or not). Gestating and lactating females were systematically recorded.

##### 4.2.2.5.2. Rat population demography

Variation in rat population density (D) across seasons was estimated in the three study habitats for each trapping session. Maximum-likelihood spatially explicit capture recapture D was used to estimate D from closed population capture-recapture data using program DENSITY (Borchers & Efford 2008). By incorporating a spatial detection function, the model estimates the probability of detection of individuals in relation to the center of their home ranges. Home range centers follow a Poisson distribution, while the probability of capture from home range centers ($g_0$) to variably located trap locations ($\sigma$) follow a normal distribution. This approach overcomes the many problems related to the estimation of an effective trapping area and can be reliably applied to non-standardized trapping layouts such as on Bagaud (Figure 22).

#### 4.2.2.5.3. Reproductive output and juvenile dispersal

100 % of females and 75 % males autopsied in 2006-07 were considered as immature individuals when weighting less than 120g. This weight was therefore used as a threshold below which individuals were considered juveniles. The number of juvenile recruits was recorded for each trapping session and reported as a proportion of the total number of individuals trapped during each session. Young black rats weighting 30-40g were estimated to be 3 weeks old, and to weight 70-80g at 8 weeks old (Faugier & Pascal 2006). We used these age-weight relationships to evaluate the approximate age of young rats, newly trapped in each habitat, and estimate the most likely period of their birth. The relative age of each recaptured individual was then estimated by taking into account the time between two captures. We focused on the timing of births rather than reproduction since lactation is more energy demanding for females than gestation (Randolph *et al*. 1977; Millar 1978) and hence could be related to resource richness and availability. The effects of habitat, season and year on the proportions of juveniles trapped were investigated with a multivariate ANOVA. Prior to analysis, proportions were arcsin-transformed to meet normality. We also investigated the importance of juvenile dispersal from the two subsidized habitats (*GU* and *IC*) and we searched for any recaptures of rats first trapped as juveniles in *GU* and *IC*.

#### 4.2.2.5.4. Body mass and growth rate

The growth rate (g.day$^{-1}$) of the juveniles was assessed as the mean change in body mass of the same individuals between two subsequent captures throughout their first six months of life. Since some individuals could be captured more than once during each trapping session, we used the body mass at first capture of each session as the reference body mass for the session considered. The effects of habitat, year and sex on the mean growth rate of juveniles were tested with a multivariate ANOVA for repeated measures, with habitat, year and sex as independent fixed effects and individual incorporated as an independent random effect. The effect of habitat on the growth rate of individudas was assessed by performing slopes of linear regression between rat body mass and their relative age for *GU* and *SC* during the driest year

(2007) with a Student *t*-test. The relative age was determined with an abacus on the basis of data found in the literature (e.g. Faugier & Pascal 2006, see above for details) and successive recaptures of the same individuals. Not enough recaptures were available to calculate a regression equation for *IC*.

### 4.2.3. Results

### 4.2.3.1. Rat trophic level and resource use

Results of ANOVA revealed no significant effect of season on $\delta^{15}$N of rat liver but a significant effect of habitat ($F_{2,129}$ = 186.7, $P < 0.001$) and a significant interaction between habitat and season ($F_{4,129}$ = 4.4, $P < 0.01$). Post Hoc Scheffe tests showed that, for each habitat-season combination, mean $\delta^{15}$N of rat liver coming from *GU* was significantly higher compared to *IC* and *SC*. Mean $\delta^{15}$N of rat liver coming from *IC* was significantly higher compared to *SC* for May06 and September06 (Figure 24). GLM on mean $\delta^{15}$N for rats >150g revealed the same habitat and habitat-season effects as did the previous ANOVA. However, no significant effect of sex or empty body mass was found on mean $\delta^{15}$N.

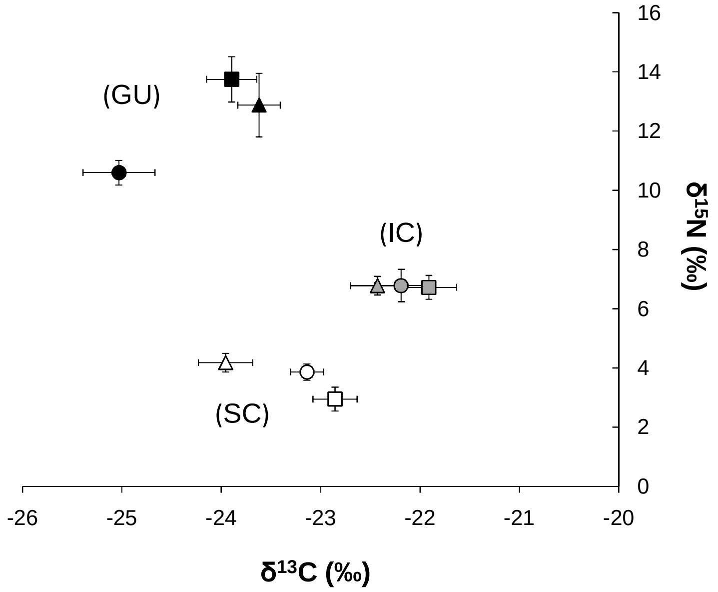

**Figure 24.** Mean stable isotope ratios of carbon (d$^{13}$C (‰)) and nitrogen (d$^{15}$N (‰)) of rat liver from the three habitats (*GU* = gull; *IC* = iceplant; *SC* = scrubland) during three seasons (triangles = May 06; squares = September 06; circles = February 07).

### 4.2.3.2. Rat population dynamics

From April 2007 to January 2009, 14 capture-recapture sessions gave 1972 captures of 582 marked rats. 66% ($N_{\text{female}} = 187$, $N_{\text{male}} = 197$) of marked individuals were recaptured at least once and 66% ($N_{\text{female}} = 131$, $N_{\text{male}} = 122$) were recaptured during at least two different trapping sessions. Maximum number of captures of the same individual was 20 (during six different sessions) and the maximum number of sessions where the same individual was trapped was 11 (17 captures). 24% ($N = 138$) of all marked individuals were recaptured at least 5 times, and 5% ($N = 32$) at least 10 times during the 14 capture-recapture sessions.

#### 4.2.3.2.1. Demography

Estimates of rat densities in the three habitats ranged from 3 to 37 rats.ha$^{-1}$ and varied little across habitats (Figure 25). Rat densities were significantly higher in *GU* in June 07 (*95%CI* = 12.3-29.3) compared to *IC* (*95%CI* = 2.5-8.8) and *SC* (*95%CI* = 6.8-12.0), higher in *GU* in July 07 (*95%CI* = 10.2-24.4) compared to *IC* (*95%CI* = 2.7-9.2), higher in *GU* in July 08 (*95%CI* = 27.8-50.4) compared to *IC* (*95%CI* = 8.8-26.3) and *SC* (*95%CI* = 7.9-14.6), and higher in *GU* in August 08 (*95%CI* = 12.6-27.7) compared to *IC* (*95%CI* = 1.5-8.7). A peak in rat density was recorded in the three habitats in January 2009 of the high rainfall year but did not appear during the previous driest year (Figure 25).

#### 4.2.3.2.2. Reproductive output and juvenile dispersal

Results of ANOVA on proportions of juvenile recruits showed a significant effect of season ($F_{3,24} = 11.6$, $P < 0.001$) and nearly significant effects of habitat ($F_{2,24} = 2.9$, $P = 0.07$) and year ($F_{1,24} = 4.0$, $P = 0.07$). Juvenile recruitment during each year peaked in spring (Figures 26, 27). An important birth pulse occurred during autumn 2008 in the three habitats. In *GU*, juvenile recruitment seemed to be more related to a seasonal pattern compared to the two other habitats. During spring 2007, reproductive output was higher in *GU* but this pattern was not clearly observed during the following spring (2008). In *IC*, young individuals were recorded throughout almost all the year. Nearly all young individuals born during summer were trapped in *IC*.

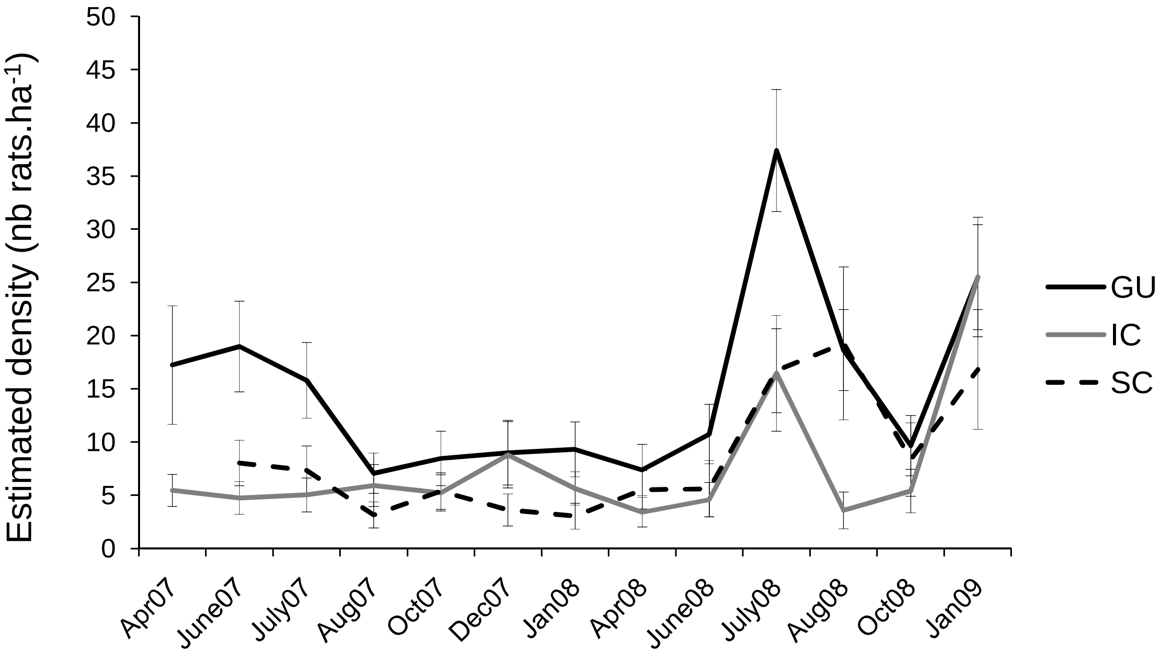

**Figure 25.** Estimated rat density from closed population capture-recapture data using maximum-likelihood spatially explicit capture recapture implemented in program DENSITY. Densities are calculated for each of the 14 trapping sessions in the three habitats (*GU* = gull; *IC* = iceplant; *SC* = scrubland). Bars indicate standard errors.

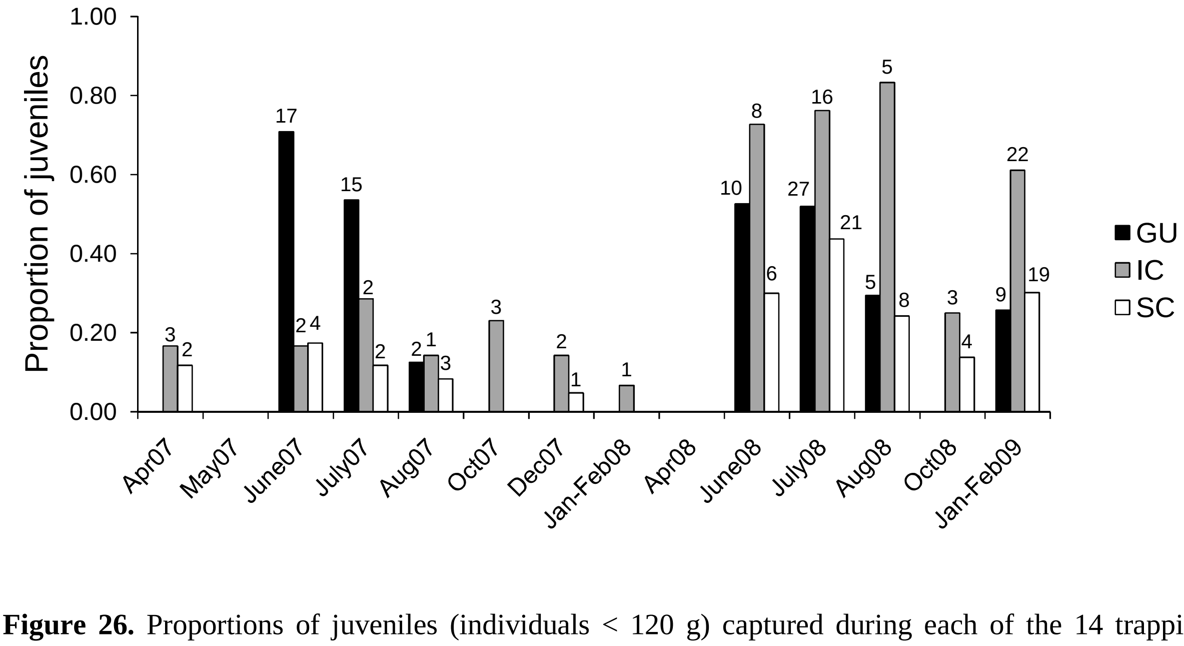

**Figure 26.** Proportions of juveniles (individuals < 120 g) captured during each of the 14 trapping sessions in the three habitats (*GU* = gull; *IC* = iceplant; *SC* = scrubland).

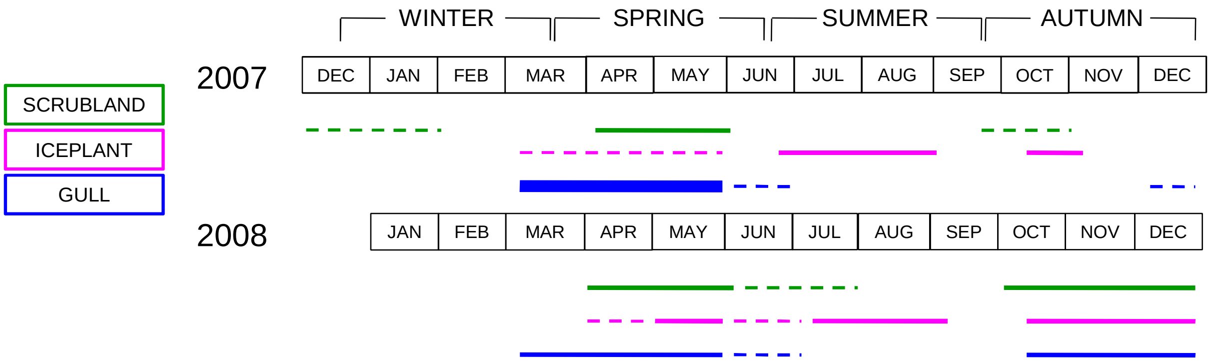

**Figure 27.** Proportions of rat births estimated for both years in the three habitats (*GU* = gull; *IC* = iceplant; *SC* = scrubland). Relative proportions are calculated over the total number of births for each year. Large bars indicate relative proportions of births > 15%, medium bars between 5 and 15% and dashed lines < 5%.

During both years, 49% of the 95 young rats trapped in *GU* for the first time were never recaptured in any of the three habitats. Rats recaptured at least once were trapped on average during 3.6 different sessions in 2007 and 2.8 sessions in 2008, spanning an average of 7.6 months in 2007 and 4.8 months in 2008. Only one rat (a male of 130g) was recorded 150 m (in *SC*) away from *GU*, 13 months after its first capture in this habitat. 50% of the 48 young rats first captured in *IC* during the two years were never recaptured in any of the three habitats. All the recaptured rats from *IC* were recaptured within the 50m-boundary strip around *IC*.

#### 4.2.3.2.3. Body mass and growth rate

Results of the ANOVA on growth rates of young rats revealed a significant effect of habitat ($F_{2,147} = 8.8$, $P < 0.001$), year ($F_{1,147} = 44.7$, $P < 0.001$), sex ($F_{1,147} = 4.7$, $P < 0.05$) and the interactions habitat*year ($F_{2,147} = 25.5$, $P < 0.001$) and sex*year ($F_{1,147} = 5.6$, $P < 0.05$). During the dry 2007, the mean growth rate (g.day$^{-1}$) of young rats (all sex combined) was significantly higher in *GU* compared to *IC* and *SC*, and significantly higher in *IC* compared to *SC* (Figure 28). Conversely, there was no significant difference in the mean growth rate of the young rats of the rainy year 2008 among habitats. Males (all habitats combined) grew faster in 2008 than in 2007 compared to females. The slopes of regression equations of rat body mass on their relative age were significantly different between *GU* and *SC* (*GU*: $y = -2886.50 + 28.99x$; *SC*: $y = -1189.68 + 12.59x$, $t = 8.9 > t(0.95, 159)$, $P < 0.05$). At 8-10 months-old, the mean body mass of rats from *GU* was 215.4g (*SD* = 28.8; max = 278g) compared to 159.4g (*SD* = 23.4; max = 230g) for rats from *SC* (Table 11).

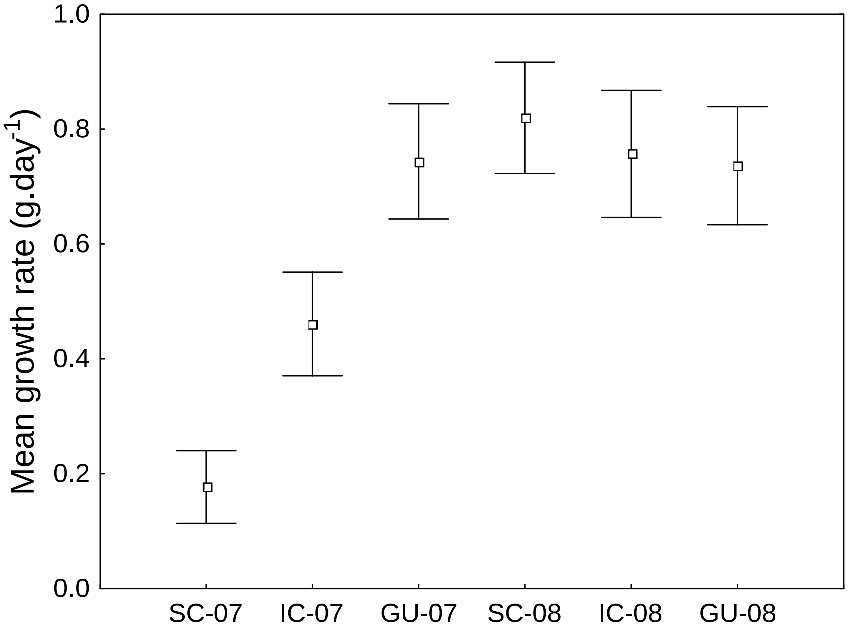

**Figure 28.** Mean growth rates of young rats during the six first months of their lives in the three habitats (*GU* = gull; *IC* = iceplant; *SC* = scrubland) during two years (07 = 2007; 08 = 2008).

| | | **GULL** | | | | | | | **ICEPLANT** | | | | | | | **SCRUBLAND** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Month | *N* | 0-150 | 151-250 | >250 | Mean body mass | SE | Max | *N* | 0-150 | 151-250 | >250 | Mean body mass | SE | Max | *N* | 0-150 | 151-250 | >250 | Mean body mass | SE | Max |
| **2007** | **Apr** | 23 | 0.00 | 0.35 | 0.65 | 264.5 | 9.1 | 310 | 21 | 0.33 | 0.62 | 0.05 | 207.9 | 10.4 | 275 | 16 | 0.25 | 0.56 | 0.19 | 216.7 | 12.0 | 295 |
| | **May** | 6 | 0.17 | 0.33 | 0.50 | 262.5 | 24.7 | 295 | 8 | 0.00 | 1.00 | 0.00 | 183.8 | 8.7 | 210 | 2 | 0.50 | 0.50 | 0.00 | 230.0 | 0.0 | 230 |
| | **June** | 30 | 0.70 | 0.20 | 0.10 | 231.7 | 13.8 | 315 | 14 | 0.21 | 0.50 | 0.29 | 218.2 | 14.1 | 300 | 8 | 0.00 | 0.88 | 0.13 | 214.4 | 10.1 | 260 |
| | **July** | 33 | 0.67 | 0.33 | 0.00 | 177.2 | 7.5 | 225 | 12 | 0.50 | 0.42 | 0.08 | 216.7 | 15.3 | 270 | 10 | 0.00 | 0.80 | 0.20 | 225.5 | 15.4 | 320 |
| | **Aug** | 17 | 0.35 | 0.65 | 0.00 | 196.5 | 9.2 | 230 | 11 | 0.73 | 0.27 | 0.00 | 196.7 | 13.7 | 200 | 26 | 0.31 | 0.62 | 0.08 | 203.3 | 7.8 | 280 |
| | **Oct** | 15 | 0.60 | 0.40 | 0.00 | 190.8 | 5.4 | 220 | 13 | 0.46 | 0.54 | 0.00 | 200.4 | 9.0 | 227 | 25 | 0.48 | 0.52 | 0.00 | 186.1 | 6.5 | 230 |
| | **Dec** | 15 | 0.33 | 0.47 | 0.20 | 232.9 | 11.8 | 283 | 12 | 0.17 | 0.83 | 0.00 | 188.7 | 7.7 | 238 | 16 | 0.31 | 0.69 | 0.00 | 186.7 | 6.0 | 228 |
| **2008** | **Jan** | 19 | 0.11 | 0.42 | 0.47 | 245.0 | 7.6 | 295 | 16 | 0.25 | 0.75 | 0.00 | 206.3 | 6.7 | 242 | 19 | 0.05 | 0.89 | 0.05 | 198.9 | 8.7 | 280 |
| | **Apr** | 14 | 0.14 | 0.36 | 0.50 | 256.9 | 12.3 | 300 | 8 | 0.38 | 0.50 | 0.13 | 227.6 | 15.3 | 270 | 20 | 0.00 | 0.95 | 0.05 | 207.3 | 6.5 | 250 |
| | **June** | 19 | 0.74 | 0.00 | 0.26 | 253.4 | 22.0 | 307 | 10 | 0.70 | 0.20 | 0.10 | 226.7 | 42.1 | 310 | 16 | 0.31 | 0.31 | 0.38 | 248.1 | 13.6 | 305 |

| | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **July** | 53 | 0.74 | 0.23 | 0.04 | 205.9 | 9.9 | 275 | 18 | 0.67 | 0.28 | 0.06 | 240.2 | 21.7 | 300 | 37 | 0.51 | 0.38 | 0.11 | 231.1 | 8.2 | 290 |
| | **Aug** | 32 | 0.44 | 0.53 | 0.03 | 195.4 | 8.3 | 290 | 10 | 0.60 | 0.40 | 0.00 | 205.0 | 20.6 | 246 | 33 | 0.58 | 0.36 | 0.06 | 216.0 | 10.7 | 263 |
| | **Oct** | 16 | 0.19 | 0.81 | 0.00 | 188.3 | 8.5 | 235 | 13 | 0.31 | 0.54 | 0.15 | 207.9 | 13.1 | 270 | 26 | 0.50 | 0.42 | 0.08 | 197.7 | 11.4 | 273 |
| **2009** | **Jan** | 35 | 0.40 | 0.34 | 0.26 | 234.5 | 13.7 | 300 | 37 | 0.89 | 0.08 | 0.03 | 204.0 | 11.7 | 255 | 46 | 0.37 | 0.61 | 0.02 | 211.2 | 5.3 | 270 |

**Table 11**: Body masses (g) of black rats from the three habitats during the 14 capture sessions. The table indicates the percentage of individuals belonging to each of the three body mass classes (0-150g; 151-250g; >250g), mean body masses with standard errors (SE) and maximums (Max).

### 4.2.4. Discussion

#### 4.2.4.1. The role of climate in modulating the effects of allochthonous resources

We found strong support for a subsidizing effect of anthropogenic allochthonous resources on rat population dynamics. However, the way that rats responded to these allochthonous resources varied between years. The benefits provided by allochthonous subsidies were particularly striking during the dry 2007 year for the mean growth rate of young rats, substantially lower in the unsubsidized habitat. To a lesser extent, the gull subsidies allow rats to achieve higher reproductive outputs and densities in spring 2007 compared to the very low levels supported elsewhere during the same year. The ability of trophic subsidies, especially those of marine origin, to positively affect the population dynamics of consumers has been demonstrated to be particularly strong in unproductive systems (Polis & Hurd 1996; Polis *et al.* 1997b; Sanchez-Pinero & Polis 2000; Catenazzi & Donnelli 2007). In such systems of low *in situ* productivity, the net primary productivity and population dynamics cannot be sustained without inputs of allochthonous nutrients (Polis *et al.* 1997a). Therefore, by providing energy and nutrients of high quality and abundance to fuel a diverse array of consumer populations, enriched allochthonous resources may be central to the dynamics and functioning of oligotrophic island systems by helping species dampening the negative effects of low productive trophic webs, especially during dry years (Stapp & Polis 2003b; Anderson *et al.* 2008).

The marked effect of internal allochthonous resource input variation on rat population dynamics recorded between habitats during the dry 2007 year were not evident during the wet

2008 year, driving more homogenous monthly rainfall in spring, a shorter summer drought period and substantially rainier autumn and winter. During the wet 2008 year, growth rates of young rats nearly reached the same levels within the three habitats, suggesting that rats were no longer food-limited in the less productive scrubland habitat during rainy conditions. Previous studies conducted on arid seabird islands in Baja California have shown that rainfall pulses can release a larger amount of guano-derived nutrients compared to drier climate conditions (Stapp *et al*. 1999; Anderson *et al*. 2008) and, hence, translate into larger increases in consumer numbers during fresh water pulses (Stapp & Polis 2003a). We found that these results are not limited to Baja California and are emergent to other dry island systems such as in the Mediterranean. On Bagaud Island, rat densities peaked higher in the gull-subsidized habitat after spring breeding in 2008 compared to the previous year. However, whether such differences were related to two distinct patterns of rainfall and resource availability in spring (more homogenous monthly fresh water inputs during a longer period of time in 2008 *vs* lower monthly rainfall with sudden large fresh water input in 2007) or to intrinsic-rat-population regulating factors remain unclear. Conversely, subsidized habitats did not experience higher rat densities after rainfall pulses in winter 2008. This may be related to a differential timing between winter rainfall pulses and the periods of maximum availability of allochthonous resources (i.e. spring for gull and summer for iceplants), or rats may have already reached carrying capacity in subsidized habitats in winter 2008.

The rapid response of rat populations to rainfall pulses confirms the potential for the population dynamics of a high-level and generalist consumer to be strongly bottom-up driven by increases in terrestrial productivity, by growing faster, adjusting its timing of reproduction and increasing in numbers. Rodent population dynamics have already been related to pulses of primary productivity lagging behind heavy precipitations in arid systems (Clark 1980; Madsen & Shine 1999; Ernest *et al*. 2000) or on islands experiencing El Nino events (Stapp & Polis 2003a). Even though it has often been assumed that precipitation leads, with relatively short time lags, to germination, growth, and reproduction of plants, and the resulting increase in food supply in the form of seeds, fruits, and leaves lead to increase in rodent populations, the relationship between the three components (rainfall - primary productivity - consumer abundance) often remains non linear and complex (Ernest *et al*. 2000), especially when long-term time series are considered (Brown *et al*. 1992; Meserve *et al*. 2003).

#### 4.2.4.2. Population responses to allochthonous resources

Because of their capacity to exploit a broad range of resources and the cumulative enrichment of nutrients up trophic chains, top-level and generalist consumers are known to be strongly affected by enriched allochthonous resources (Rose & Polis 1998; Stapp & Polis 2003a; Catenazzi & Donnelli 2007; Darimont *et al*. 2009). We found that gull-subsidized resources, and to a lesser extent iceplant figs, affected many rat population dynamic parameters, such as the growth rate of young rats and body mass of adults, the timing and intensity of reproduction and local population density. Rapid growth of young rats may stem from an energy maximizing strategy driven by selection for rapid reproductive maturity to increase reproductive success before cold season arrives and reproduction ceases (Eifler *et a*l. 2003). However, this was not likely to occur on Bagaud Island since no juveniles were observed to breed during the first months of their lives. A more likely hypothesis may be that young individuals dwelling in subsidized habitats may invest relatively more energy into growth, allowing them to persist during harsh seasons, whereas young rats that did not have access to subsidized resources suffered from dry and hot summer and cold and resource-scarce winter by growing slower, losing weight and eventually dyeing off. Rats foraging in the gull-subsidized habitat frequently reached body masses up to 300 g after one year (Table 11). Such large body masses have been reported for rats dwelling in seabird areas (J. Russell & G. Harper, pers. comm ) and may favour social dominance and aggression (e.g. Spencer & Cameron 1983), helping competition for resources on Bagaud Island.

Food supplementation experiments, fruit or seed mast events, and marine-subsidized resources have generally been reported to produce an increase in rodent population size, due to a combination of enhanced reproductive output and immigration into high-quality areas (Doonan & Slade 1995; King & Moller 1997; Lin & Batzli 2001; Banks & Dickman 2002; Stapp & Polis 2003b; Ruscoe *et al*. 2004). On Bagaud Island, the fluctuations in rat population densities followed breeding periods. Rat densities always peaked higher in the gull-subsidized habitat after spring breeding compared to the two other habitats. Peaks in density in early summer can only be attributed to recruitment of juveniles in spring since, on Bagaud Island, rats did not often move among habitats according to resource availability (Ruffino L. submitted) and immigration of new individuals in each habitat was rarely recorded (Ruffino L. unpublished). Given that rodent fecundity is highly sensitive to the level of available nitrogen and soluble amino acids (e.g. White 2002), our results suggest that the high-quality of seabird-derived resources can enhance high reproductive output and hence high local population densities during maximum availability of gull resources. Interestingly, in the fig habitat, spring breeding extended throughout summer for both years. Even though the number of births recorded was quite low, breeding in summer in the Mediterranean is rare enough to warrant explanation. High temperatures, water and food stress during summer in the Mediterranean are the main factors for explaining why breeding ceased during this season. It is possible that adult rats that have access to figs in early summer may take advantage of this source of water, energy and protein to allocate it to reproduction, especially during the energy-expensive period of lactation for small rodent females (Randolph *et al*. 1977; Millar 1978).

#### 4.2.4.3. Transport of allochthonous nutrients by rats across habitat boundaries

The transport of allochthonous nutrients across habitat boundaries by island consumers depends in part on the spatial scale under consideration (Polis & Hurd 1996; Stapp & Polis 2003b), the life-history traits of individuals (i.e. mobility, degree of diet specialization; Stapp & Polis 2003b; Farina *et al*. 2003; Paetzold *et al.* 2008), community structure and competition for resources (e.g. Stapp & Polis 2003b). Surprisingly, the effects of allochthonous resources on the trophic level and population dynamics of rats were spatially limited among nearby habitats, even when only tens of meters apart. Long-term movement and diet analyses of black rats on Bagaud showed a low level of individual diet plasticity and a low probability of movements among adjacent habitats when high-quality resources became available, which could be related to intra-specific relationships (Ruffino *et al*. submitted, see also **Partie 4.1**.). This suggests that, on Bagaud Island, rats are poor conduits of subsidized nutrients across habitats. The hypothesis that seabird-subsidized habitats, by providing high-quality resources, may be a source of rat-assisted dispersal to lower quality areas has often been put forward (Stapp 2002; Mayor *et al*. 2006). From our data, it is difficult to conclude on the capacity for young rats to disperse substantially further inland and to transfer subsidized nutrients over longer distances since nearly half of the juveniles marked in these habitats were never recaptured anywhere (whereas the other half was only recaptured in the same habitats).

### 4.2.5. Conclusion – Implications for invasives’ impact

Our results add to growing evidence to the contribution of allochthonous resources, especially seabird-derived nutrients, to insular food webs worldwide (Iason *et al*. 1986; Ellis

2005; Anderson *et al*. 2008). We show in this paper that invasive rodents such as black rats can substantially benefit from allochthonous inputs on Mediterranean islands, where the native scrubland habitat appeared to be the less rat-productive one, especially during dry years. Our findings have three major implications. First, the strong potential for allochthonous resources to dampen the negative effects of drastic environmental conditions on rat populations may help stabilize inter-annual fluctuations in population dynamics and increase the probability of long-term persistence by providing a minimum level of resource availability (MacCann *et al*. 1998), especially for generalist invasive consumers (Holt & Barfield 2003). Second, our results reinforce the capacity of invasive species to interact with one another in their novel environment and their potential to lead to cumulative pervasive effects on native communities ('invasional meltdown'; Simberloff & Von Holle 1999, Simberloff 2006). Third, in the perspective of climate change towards extended drastic events in the Mediterranean, increase in gull population demography and expansion of exotic succulent plants, it is likely that human-induced trophic changes may indirectly contribute to potential increases in invasive rat impacts on these naturally low productive but vulnerable island native communities. Finally, our results confirm the strong propensity for invasive black rat population dynamics to fluctuate between seasons and years, but also among adjacent habitats, which emphasize the need to monitor and take into account long-term changes in population parameters when studying the impact of invasive rodents on island systems, known to be highly susceptible to strong unpredictable variation in resource availability in space and time.

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# - Partie 4.3. -

## 4.3. THE ROLE OF SPATIO-TEMPORAL RESOURCE VARIATION ON THE SURVIVAL OF ISLAND INVASIVE BLACK RATS

4.3. Le rôle de la variation spatio-temporelle de la disponibilité des ressources sur la survie de rats noirs insulaires introduits

**Résumé:**

Les fluctuations spatio-temporelles des apports de resources saisonnières au sein d'un écosystème jouent un rôle déterminant dans les dynamiques de populations des consommateurs. Les effets de ces fluctuations spatio-temporelles de ressources sont reconnus pour être très importants au niveau des écosystèmes insulaires, dont le fonctionnement semble être majoritairement contrôlé par des processus de type « bottom-up », dont le maillon « prédateurs » fait souvent défaut, et qui subissent une variation saisonnière et inter-annuelle importante des conditions trophiques. Dans le cadre de ce travail, les variations de la survie mensuelle des individus d'une population de rats noirs *Rattus rattus* introduits et consommateurs de niveau trophique élevé ont été analysées sur une île oligotrophe de Méditerranée. Un modèle multi-états pour populations fermées couplée à une approche bayésienne hiérarchique a été développé dans le but d'évaluer l'influence relative de la variation spatiale (entre habitats) et temporelle (entre saisons) des ressources sur la survie des individus. Nos résultats montrent que la survie des individus varie significativement en fonction des précipitations mensuelles. L'apport d'eau douce en grande quantité (fortes précipitations) semble gommer les effets mineurs de la variation spatiale des ressources entre habitats. Nous suggérons ainsi que les conditions climatiques constituent un facteur primordial gouvernant les dynamiques de populations de rongeurs sur les îles oligotrophes, et que les effets des variations spatiales de la qualité des ressources sur la survie des individus sont susceptibles d'être atténués par les variations saisonnières des ressources gouvernées par les patrons de précipitations. Ces résultats ont une implication forte en termes de gestion des espèces envahissantes et de conservation des espèces vulnérables occupant des environnements aux ressources saisonnières, et gagneraient à être testés sur d'autres espèces introduites de niveaux trophiques supérieurs.

**Cette partie est tirée du travail suivant :**

**Russell J. & Ruffino L. The role of spatio-temporal resource variation on insular rat population dynamics. Soumis à *Ecological Applications*.**

### 4.3.1. Introduction

Recent research has highlighted the cascading role resource subsidies, and their spatio-temporal variation, play in the regulation of communities (Orr *et al*. 2005; Bissonette & Storch 2007; Marczak *et al*. 2007; Yang *et al*. 2008). The population dynamics of any given species in a community will be governed by its trophic position and the dominant mode of regulation at that trophic level (Hunter &Price 1992). Island ecosystems tend to be strongly bottom-up regulated environments, with marked seasonal and multi-annual variation in resource inputs, often driven by marine-terrestrial interfaces in resource exchange, such as seabird-driven allochthonous resource inputs (Sánchez-Piñero & Polis 2000) and climatic patterns (Polis *et al*. 1997b). The impact of these inputs on population dynamics can differ among habitats with resource quality and availability (Stapp & Polis 2003; Rayner *et al*. 2007). The population dynamics of higher-order consumers on such islands is therefore likely to be strongly driven by spatial and temporal variation in these resource inputs (Anderson *et al*. 2008), although the relative contribution of each to community regulation is less well known (Holt 2008). Spatial heterogeneity in resource distribution can also influence individuals by affecting their foraging behaviour, reproductive output, densities and dispersal rates (Marczak *et al*. 2007). Individual movement among habitats also has an important role in subsidy dynamics (Polis *et al*. 1997a; Holt 2008). Establishing movement rates between habitats and populations is therefore imperative when investigating population dynamics. The interaction between spatial and temporal resource variation, with animal movement, can lead to especially complex impacts on island biotas such as dietary shifts (Caut *et al*. 2008) and ecological facilitations such as seed dispersal (Bourgeois *et al*. 2005).

Introduced rats are a generalist higher-order consumer found on many islands throughout the world. The population dynamics of small rodents are well-studied, and hence they are a common model for investigating population regulation. Where small rodent populations have co-evolved with higher-order predators, such as on high-latitude continents, predator-mediated cycles generally dominate population processes (Hanski *et al*. 2001). In tropical continental regions however, rainfall-mediated cycles appear to dominate (O'Connell 1989, Madsen & Shine 1999). In this paper we model the monthly survival of black rats (*Rattus rattus*), the highest-order consumer, on a dry Mediterranean island. Black rats were introduced to most Mediterranean islands over 2,000 years ago (Ruffino *et al.* 2009). Despite their historical introduction, they continue to have an ongoing negative impact on island ecosystems (e.g. Martin *et al*. 2000). Over the last century, the nature of these impacts has changed due to direct and indirect anthropogenically-driven changes upon islands. Human land-use and its intensity has increased on many islands, increasing introductions of alien plants, and subsidising gull populations, whose disturbances on their roosting and nesting areas lead to substantial changes in native flora (Vidal *et al*. 1998). These changes can be interactive, possibly leading to facilitated ecological meltdown on some islands (Bourgeois *et al*. 2005).

We test the relative contributions of bottom-up driven spatial (habitat) and temporal (climatic) resource fluctuations by modelling their contributions to rat survival, while accounting for additional variation due to age, sex or unexplained individual effects. We fit a multi-strata model; one where at any time each individual exists in a uniquely distinguishable and identifiable, although not always fully observed, series of states, such as age-classes, and habitats (Brownie *et al*. 1993; Shwarz *et al*. 1993; Dupuis 1995). Multi-strata models allow us to realistically consider the spatial and temporal structure of the complex island environment in which the rats live. We take a fully individual-based approach where survival depends upon biological (sex and age), temporal (month) and spatial (habitat) states. We take a hierarchical approach which facilitates coping with complexities in the data such as non-constant between session times and modelling both session and monthly specific covariates upon them. The entire model allows us understand the underlying survival process in the population. We fit the model using recently developed Bayesian hierarchical methods (Gimenez *et al*. 2007; Royle 2008; Calvert *et al.* 2009; Schofield *et al*. 2009). Bayesian hierarchical approaches allow complex systems to be broken down into a series of more simple conditional relationships, where the likelihood can be broken down into tractable conditionings upon only certain components (e.g. Schofield *et al.* 2009).

### 4.3.2. Materials and methods

#### 4.3.2.1. Data

Black rats were capture-mark-recaptured on Bagaud Island (43°01″N, 6°22″E, 58 ha; Figure 29) in Port-Cros National Park (SE France) over 14 sessions spanning 22 months from April 2007 to January 2009 (Appendix 2), in 81 permanent trap stations (BTS–Mécanique, Manufrance, Saint Etienne, France) over three distinct habitats (4.25 ha). Sessions were separated by 26 to 122 days, and within each trapping lasted from 3 to 8 nights. All rats captured were marked with a unique sub-cuticle pit tag (FDX-B, IER Paris, France), weighed, sexed, assigned as either juvenile or adult, and released. A total of 395 unique individuals were captured 685 times. The open yellow-legged gull (*Larus michahellis*) (1.00 ha) and iceplant (*Carpobrotus* sp.) (1.25 ha) habitats are highly subsidized zones, with seasonally varying pulses of enriched resource input from gull reproduction (spring) and plant fruiting (summer) respectively. The intermediate scrubland (2.00 ha) habitat does not provide any marked annual variation in resource availability and serves as a baseline. Rainfall was measured monthly on nearby Levant Island Meteorological Station.

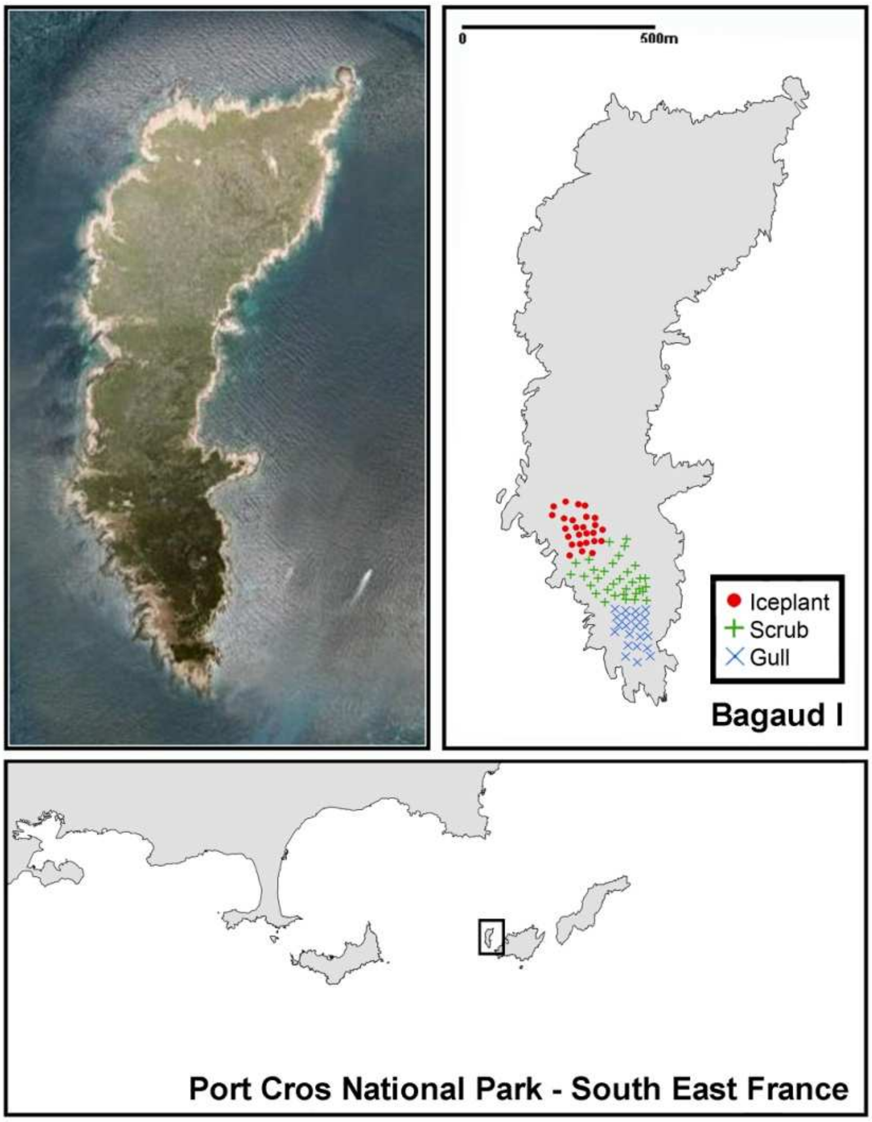

**Figure 29.** Bagaud Island in Port-Cros National Park.

#### 4.3.2.2. Model

We constructed an individual effects hierarchical multi-state model of capture probability and survival over our 14 primary sessions. The model incorporates survival rates and capture probabilities for each session, and movement probabilities between each of the three habitats that are assumed constant through time. Both survival and capture probabilities may be affected by age, sex, habitat, and individual random effects, while rainfall is allowed to impact survival but not capture.

Our model formulation follows Royle (2008) where for $i$ individuals over $j$ sessions we treat $X_{ij}$ as the binary detection (capture) matrix, and $Z_{ij}$ as the underlying binary state matrix of alive or not. We wish to make inference on $\Phi_j$, survival from time $j$ to $j + 1$. We note similarities with Gimenez *et al.* (2007) and Schofield *et al.* (2009). The $Z_{ij}$ matrix is only partially observed as an individual's state is only known if it is captured. Similarly, we treat age class, $A_{ij}$, and habitat, $H_{ij}$, as additional partially observed state variables, observed upon capture. For age classes we can impute missing (unobserved) values based on the well-known rapid maturation of rats relative to our time between sessions. Sex, $S_i$, is assigned upon first capture. To account for potential additional individual heterogeneity in survival and capture probability, we considered random effects in our model. Random effects were assumed to be $N(0,\sigma^2)$, but because of poor mixing we re-parameterised them to $\sigma.N(0,1)$ in our model.

We model the fixed effects, $\beta$, of sex (FEMale), age (JUVenile) and habitat (GUll, SCrubland & ICeplant), and individual random effects, $\varepsilon$, as covariates on capture and survival. This is achieved using a logistic generalised linear mixed models framework:

$$\log\left(\frac{\hat{\theta}_{ij}}{1-\hat{\theta}_{ij}}\right) = \alpha_j + \beta_{sex}S_i + \beta_{age}A_{ij} + \beta_{hab}H_{ij} + \varepsilon_i \quad \text{where } \theta = p \text{ or } \Phi$$

and the intercept $\alpha_j = \log\left(\frac{\theta_j}{1-\theta_j}\right)$ (i.e. the log-odds ratio when all covariates are zero)

Because the time between sessions is not constant our estimates of survival are not directly comparable, and so we transform them to comparable monthly rates ($\Phi_{mj}$ for $j = 1,\ldots,12$), although these estimates are not associated with any month in particular. This is achieved by taking the $k^{\text{th}}$ root of between session survival estimates:

$$\phi_{mj} = \sqrt[k]{\phi_j}$$

where $k$ is the fraction of months between sessions

Monthly survival estimates were strongly correlated with *log*(rainfall) (range 0 – 5.15, $r$ = 0.49, $P$ = 0.10, monthly rainfall weighted by time between sessions; Appendix 1). Therefore, we included *log*(rainfall) as a covariate on survival. Rainfall is modelled as a fixed effect on the logit scale of our monthly survival estimates, to estimate a monthly survival rate incorporating the effect of rainfall ($\phi^{r}_{mj}$ for $j$ = 1,…,12 sessions):

$$\log\left(\frac{\hat{\phi}^{r}_{mj}}{1-\hat{\phi}^{r}_{mj}}\right) = \alpha_j + \beta_{rain}\log(rain^*_j) \qquad \text{where rain* = weighted rainfall}$$

and the intercept $\alpha_j = \log\left(\frac{\phi_{mj}}{1-\phi_{mj}}\right)$ (i.e. the log-odds ratio when rainfall is zero)

We then estimate a mean monthly survival across our entire study weighted by the time between sessions ($\phi^{r}_{m\bullet}$) and incorporating the effect of monthly rainfall.

Model selection in a Bayesian framework is difficult when missing data or random effects are present in a model specification (Celeux *et al.* 2006; Schofield *et al.* 2009), both of which we have. We focused on building a biologically realistic model incorporating covariates which are reasonably expected to have an influence on rodent population dynamics (and where data were available). For the random effects, however, we used the model selection method proposed by Royle (2008 Web Appendix 5), whereby we include binary indicator variables for the random effects and allow the model to choose them as required.

In our population, migration in to or out of our study area during the two year study is confounded with capture probability and survival respectively, but we assume such movements on the boundaries of our arbitrary study area are random and rare, only affecting our precision without bias (Kendall 1999). Temporary emigration between primary sessions will negatively bias capture probability (Kendall *et al.* 1997), but we treat capture probability only as a nuisance parameter. We assumed a closed state population within secondary surveys, i.e. that an individual did not move between states (i.e. habitats). This was not true for individuals (*n* = 18) who did move between habitats within sessions, where we took the first location of capture within a session as the animal's closed state for that session. By discarding within session trapping information from this closed model we lose only the extra information to more accurately estimate the probability of capture accounting for all *N* possible individuals (Kendall *et al*. 1997). Our estimates of capture probability are only applicable to those *n* individuals captured within our study, and will be affected by the number of trapping nights within each secondary session. Additionally, confounding in the last session prevents estimation of the final survival and capture probabilities (Royle 2008)

Our model formulation gives a total of 40 independent parameters to estimate. Following others (Dupuis 1995; Gimenez *et al*. 2007; Royle 2008), we use uniform priors for base-line monthly survival rate and capture probability. Perceivably uninformed priors on covariates of logistic models can substantially alter the distribution of the response (bi-modally weighting it towards extremes; Van Dongen 2006). We do not expect survival or capture to change drastically (greater than ±1 on logit scale) with covariates, and so we use conservative prior distributions appropriate to our binary state variables in order to retain relatively uninformed prior distributions on survival rate and capture probability when incorporating covariates (Appendix 3); N(0,1) priors for fixed effects parameters and Uniform(0,5) for random effect variances. We ran the model as two chains for 55,000 iterations discarding the first 5,000 iterations of each chain as burn-in. We performed model analysis entirely in WinBUGS (v. 1.4), followed by a suite of standard MCMC diagnostics (Cowles and Carlin 1995), and testing sensitivity to covariate priors. We considered fixed effects significant if their 95% credible interval did not include zero. From the results of our survival model we are able to estimate the mean life-span and maximum age (< 1% survival) of black rats on Bagaud Island.

### 4.3.3. Results

Rainfall-inclusive monthly survival estimates ranged from 0.63 to 0.96 (Table 12), with seasonal variation (Figure 30). Model selection for random effects showed full support (100%) for unexplained heterogeneity in capture probability, but almost no support for unexplained heterogeneity in between session survival (9%). We therefore only included a random effect for capture probability in our full model (Appendix 4). Mean session-specific capture probabilities for the *n* individuals in our study ranged from 0.10 to 0.42 (Table 12;

Figure 30), most commonly around the average of 0.32, but significantly lower in Spring (April).

| **Capture** | **Mean** | **SD** | **CI 2.5%** | **CI 97.5%** | **Survival** | **Mean** | **SD** | **CI 2.5%** | **CI 97.5%** |
|---|---|---|---|---|---|---|---|---|---|
| $p_1$ | 0.1 | 0.06 | 0.03 | 0.24 | $\phi_{m1}^{r}$ | 0.81 | 0.14 | 0.49 | 0.99 |
| $p_2$ | 0.15 | 0.07 | 0.05 | 0.33 | $\phi_{m2}^{r}$ | 0.89 | 0.12 | 0.59 | 1 |
| $p_3$ | 0.36 | 0.11 | 0.17 | 0.58 | $\phi_{m3}^{r}$ | 0.63 | 0.11 | 0.42 | 0.86 |
| $p_4$ | 0.39 | 0.1 | 0.21 | 0.6 | $\phi_{m4}^{r}$ | 0.72 | 0.09 | 0.54 | 0.89 |
| $p_5$ | 0.41 | 0.1 | 0.23 | 0.6 | $\phi_{m5}^{r}$ | 0.94 | 0.04 | 0.84 | 1 |
| $p_6$ | 0.42 | 0.1 | 0.23 | 0.63 | $\phi_{m6}^{r}$ | 0.87 | 0.06 | 0.74 | 0.97 |
| $p_7$ | 0.42 | 0.1 | 0.23 | 0.61 | $\phi_{m7}^{r}$ | 0.96 | 0.04 | 0.86 | 1 |
| $p_8$ | 0.41 | 0.11 | 0.21 | 0.64 | $\phi_{m8}^{r}$ | 0.87 | 0.05 | 0.77 | 0.97 |
| $p_9$ | 0.2 | 0.07 | 0.08 | 0.37 | $\phi_{m9}^{r}$ | 0.86 | 0.09 | 0.66 | 0.99 |
| $p_{10}$ | 0.31 | 0.09 | 0.16 | 0.5 | $\phi_{m10}^{r}$ | 0.92 | 0.06 | 0.76 | 1 |
| $p_{11}$ | 0.37 | 0.1 | 0.19 | 0.57 | $\phi_{m11}^{r}$ | 0.74 | 0.09 | 0.58 | 0.92 |
| $p_{12}$ | 0.31 | 0.09 | 0.16 | 0.51 | $\phi_{m12}^{r}$ | 0.83 | 0.09 | 0.63 | 0.99 |
| $\beta\text{-}FEM_p$ | 0.06 | 0.29 | -0.52 | 0.64 | $\beta\text{-}FEM_{\Phi}$ | 0.03 | 0.18 | -0.32 | 0.4 |
| $\beta\text{-}JUV_p$ | -0.56 | 0.31 | -1.19 | 0.04 | $\beta\text{-}JUV_{\Phi}$ | 0.33 | 0.37 | -0.34 | 1.12 |
| $\beta\text{-}GU_p$ | 0.12 | 0.33 | -0.55 | 0.76 | $\beta\text{-}GU_{\Phi}$ | -0.09 | 0.24 | -0.56 | 0.38 |
| $\beta\text{-}IC_p$ | -0.17 | 0.37 | -0.9 | 0.55 | $\beta\text{-}IC_{\Phi}$ | -0.05 | 0.27 | -0.57 | 0.48 |
| $\sigma_p$ | 1.25 | 0.26 | 0.77 | 1.81 | $\beta\text{-}log(RAIN^*)_{\Phi}$ | 0.69 | 0.21 | 0.31 | 1.11 |

**Table 12.** Posterior parameter summaries for capture and survival estimates with standard deviations (SD) and 95% credible intervals (CI).

Capture probabilities did not depend on the number of trapping nights in each session (Spearman's correlation, $\rho$ = -0.13, $p$ = 0.68,). Of the fixed effects for sex, age, habitat and rainfall, only *log*(rainfall) on survival was significantly different from zero (95% credible interval; Appendix 3), although this variable also had high auto-correlation within the MCMC chains. Juvenile rats had a lower probability of capture, and higher probability of survival, although with some confounding ($r$ = -0.25). Habitat and sex had no significant effect on rat survival or capture probability (Table 12). Fixed and random effects were robust to more uninformed prior distribution specifications (N(0,10) for fixed effects, Unif(0,10) for random effects) and although more uninformed prior distributions on logistic model covariates heavily informs the prior distribution of the response (Appendix 3), estimates of survival rates and capture probabilities remained the same. Based on our mean monthly survival estimate, the mean life-span of rats on Bagaud Island is 6 months, and rats seemed not to live longer than 28 months.

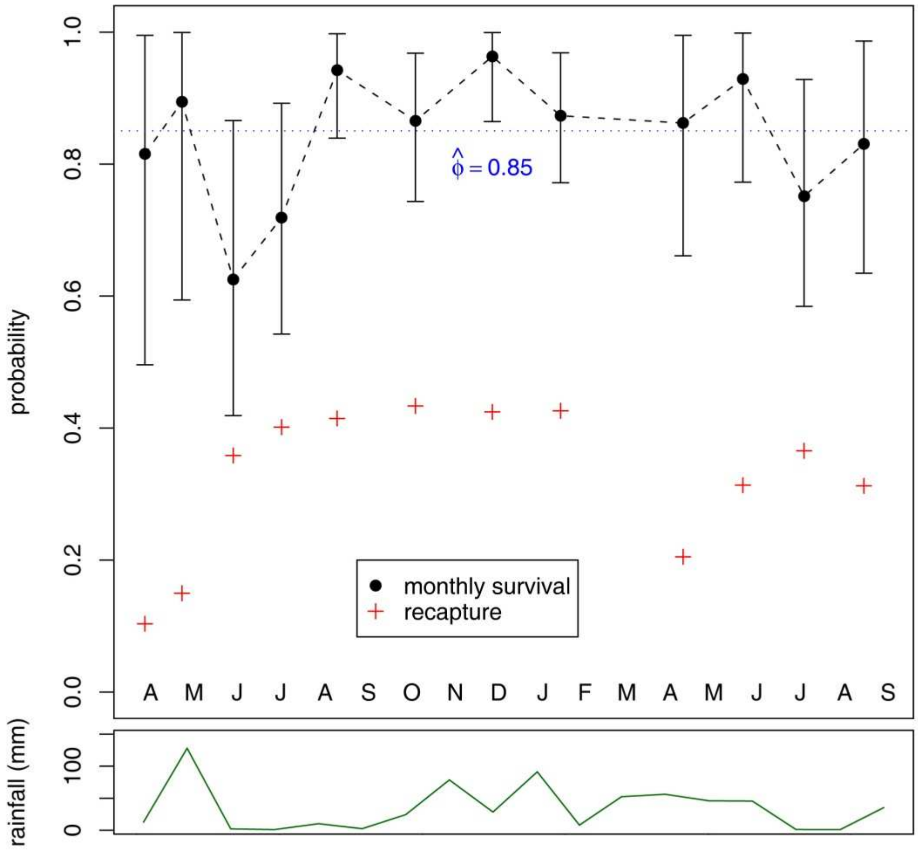

**Figure 30.** Upper plot: Rat survival including the significant effect of rainfall and capture probability estimates. Error bars indicate 95% credible intervals. Lower plot: Monthly rainfall. April 2007 – September 2008 (months indicated).

### 4.3.4. Discussion

Although both spatial and temporal resource pulses were regular in our study, the temporal resource subsidy external to the island system, rainfall, had the strongest effect on survival of a higher-order consumer. Spatial resource variation due to habitat had no discernable effect on survival. The absence of a significant influence of spatial resource variation may in part be because plant and lower-order consumers in the different habitats were themselves simultaneously responding in a similar manner to external temporal resource pulses. Studies of dry islands in the Gulf of California have shown that pulsed rainfall events and seabird colonies interact to impact the growth of plant populations (Anderson *et al.* 2008), and trapping rates of rodent populations are spatially heterogeneous, and increase by a factor of 1.5 to 4 during years of intense rainfall, leading to invasion of less preferred habitats (Stapp & Polis 2003). However, in the Galapagos correlations between rainfall pulses and rodent abundances were not systematic within the same island but depended mostly on habitat characteristics, such as vegetation cover or local climate (Clark 1980). In their study of insular rodent responses Stapp & Polis (2003) similarly found that the generalist species *Peromyscus maniculatus* responded most strongly to temporal rainfall subsidies, while the specialist *Chaetodipus rudinoris* depended more strongly on spatial habitat subsidies.

By constructing a hierarchical model of a rat population on a small Mediterranean island, we were able to determine the relative roles of extrinsic and intrinsic resource subsidies on survival. The hierarchical modelling approach allowed us to partition complex model components into simple conditional components to which we could specify relationships (Calvert *et al*. 2009). Rat survival increased by a factor of up to 1.5 with intense rainfall events, which could vary by a factor of up to 200 from winter to summer. This relationship was logarithmic (i.e. non-linear), suggesting that rainfall immediately enhances rat survival, but this effect rapidly becomes saturated. The amount and timing of this pulsed freshwater input may benefit rats by enhancing plant and arthropod abundances. Studies on arid continental systems have also shown a boost in primary productivity lagging behind rainfall pulses and generating bottom-up processes, such as increases in rodent abundances, when propagating up trophic chains (Ernest *et al*. 2000; Brown & Ernest 2002, Previtali *et al*. 2009). In contrast, habitat variation, and associated resource fluctuations, accounted for only small variation in the odds of rat survival (0.91 and 0.94 fold between scrubland to gull and iceplant habitat respectively; back-transformed logit fixed effects). This lesser impact of habitat dependent resource enrichment is not surprising as local food supplementation does not usually lead to an increase in rodent survival (Gilbert & Krebs 1981; Banks & Dickman 2000). Perhaps because spatial variation in resource subsidies varied simultaneously with external temporal subsidies, individual black rats did not benefit from moving among habitats tracking resources (Holt 2008), contrary to other consumers who may increase mobility in response to pulsed resources (Yang *et al*. 2008). The random effect for capture probability compensated for significant unexplained heterogeneity due to non-random trap placement, where individuals were exposed to different levels of trapping intensity. Incorporating individual-based effects and model selection was necessary to encompass otherwise unmodelled heterogeneity.

Introduced rats play a major role in island ecosystems. Not only do they have direct effects on other species, both as predators (e.g. Towns *et al*. 2006) and prey (Bonnaud *et al*. 2007), but through these strong direct effects they have cascading top-down indirect effects on other ecosystem components, such as invertebrates (Towns *et al.* 2009) and plants (Mulder *et al*. 2009). The magnitude of these indirect effects can also vary spatially (Rayner *et al*. 2007). Given dominant bottom-up regulation of introduced rats on islands, resource pulses leading to rat irruptions may generate strong direct effects such as extinctions of vulnerable native species (Harper 2005), and also indirect effects such as increased food abundance for higher-level introduced predators, where present (Bonnaud *et al*. 2007). On Bagaud Island, the low probability of movements recorded among habitats dampens the potential for rats to disperse iceplant seeds over long distances, reducing the potential for invasional facilitation (Bourgeois *et al*. 2005), but vulnerable seabirds no longer breed, possibly attributable to the abundant black rats (Martin *et al*. 2000; Ruffino *et al.* 2009). Our work suggests the rat population is most limited during the dry summer months, which would be the optimal time for an eradication program.

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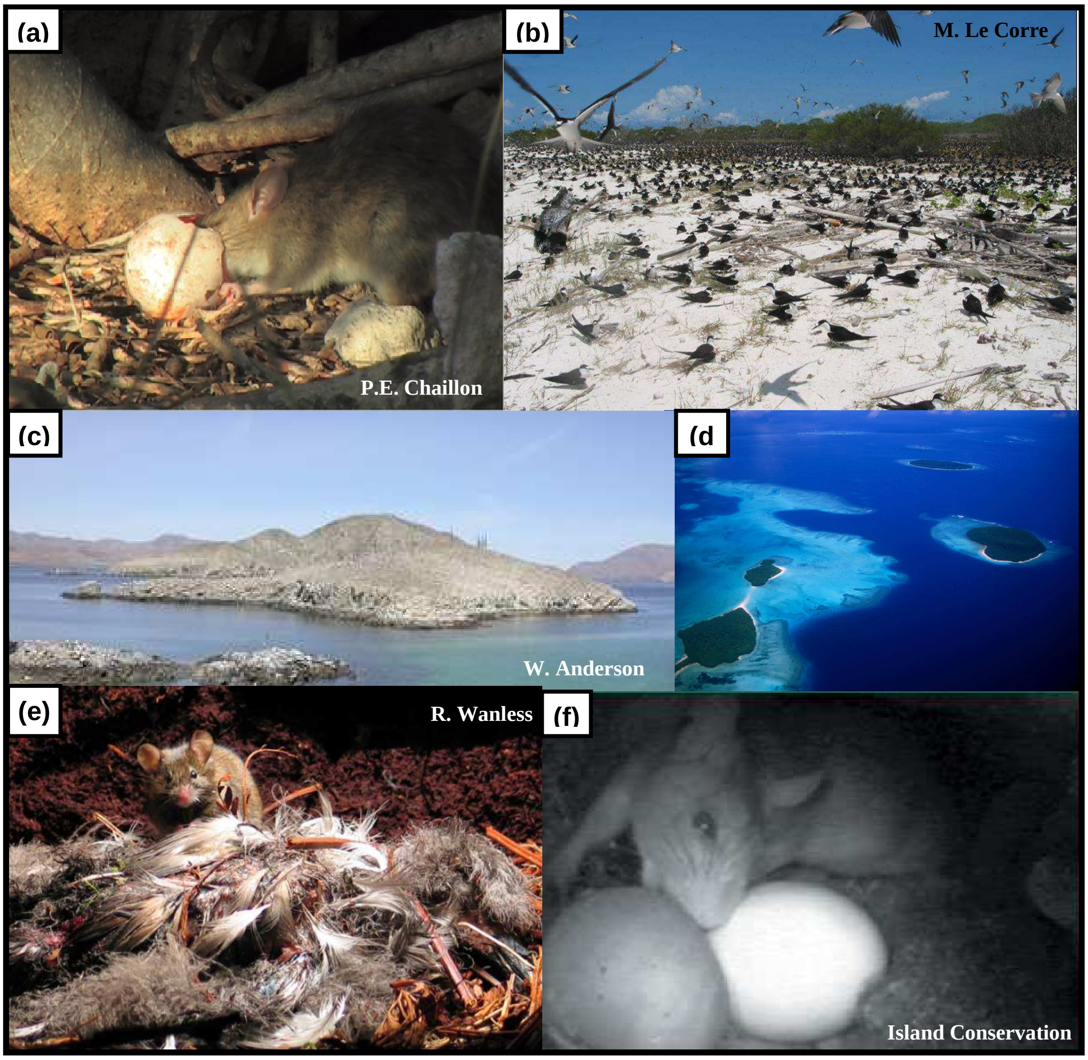
# Chapitre 5.

## SYNTHÈSE, DISCUSSION GÉNÉRALE ET PERSPECTIVES DE RECHERCHE



(a) rat noir consommant un œuf de paille-en-queue sur l'île Europa ; (b) colonie de sternes fuligineuses *Onychoprion fuscatus* sur l'île Juan de Nova, Océan Indien ; (c) îles désertiques du Golfe de Californie ; (d) îles pacifiques ; (e) souris grise *Mus musculus* devant une carcasse de pétrel atlantique *Pterodroma incerta* sur l'île Gough ; (f) prédation enregistrée par vidéo.

# 5. SYNTHESE, DISCUSSION GENERALE ET PERSPECTIVES DE RECHERCHE

## 5.1. Synthèse et discussion générale

### 5.1.1. Intégrer la dimension temporelle des introductions d'espèces permet de mieux comprendre leurs effets sur le long terme, et les mécanismes favorisant la persistance des espèces natives

La synthèse des connaissances archéozoologiques faisant mention de restes de rats noirs datant d'âges anciens sur les îles de Méditerranée a permis d'appuyer sans équivoque l'un des postulats majeurs de ce travail de thèse reposant sur une présence ancienne et généralisée du rat noir sur les îles de Méditerranée (**Partie 2.1.**). Même si la période exacte d'arrivée de l'espèce sur les rives orientales du bassin méditerranéen ainsi que celle de son accession au statut d'espèce commensale restent encore à débattre, il ne fait aucun doute que le rat noir a débuté sa colonisation des îles du bassin Méditerranéen dès l'époque romaine, occupant à l'heure actuelle 99% des îles de Méditerranée occidentale dont la surface est supérieure à 30 ha (**Partie 2.2.**).

***Comment se traduisent alors les effets du rat sur la structuration actuelle des populations d'oiseaux marins après une présence aussi ancienne du rat sur les îles ?***

En travaillant à une large échelle géographique, sur un lot important d'îles et ilots aux caractéristiques physiques, écologiques et anthropiques variées, nous avons pu mettre en évidence qu'après 2 000 ans de présence du rat noir en Méditerranée, sa présence actuelle sur les îles ne conditionnait pas celle des quatre espèces de pétrels et puffins. Ce schéma est particulièrement frappant pour les trois espèces de puffins qui nichent quasi exclusivement sur des îles qui hébergent des rats, parfois même en larges densités. Seules les abondances de la plus petite espèce, le pétrel tempête, semblent être sensiblement affectées par la présence du rat, confirmant ainsi le statut de vulnérabilité plus accru des oiseaux de petite taille pour lesquels tous les stades démographiques peuvent être affectés par la prédation (Imber 1984 ; Jones *et al*. 2008). Les différentes analyses de ce jeu de données régionales nous permettent de suggérer le rôle important des contextes insulaires variés dans le maintien de certaines populations d'oiseaux sur des îles présentant des secteurs moins accessibles aux prédateurs introduits, comme des falaises élevées et escarpées, des cavités profondes (*P. yelkouan* est reconnu pour avoir de fortes affinités cavernicoles) ou des grottes calcaires (*P. mauretanicus, P. yelkouan* et *H. pelagicus* nichent fréquemment dans des grottes calcaires). Cette hypothèse de cantonnement en « secteurs moins risqués » rejoint les observations faites sur les patrons de structuration des communautés d'oiseaux marins des archipels du Pacifique, ayant subi, comme en Méditerranée, des perturbations anciennes et récurrentes par l'Homme et son cortège d'espèces introduites (Steadman 2006). De même, la sélection préférentielle par les puffins yelkouan de Port-Cros de cavités profondes et sinueuses, où le succès reproducteur est meilleur que dans des cavités plus accessibles (Bourgeois & Vidal 2007), laisse penser que cette stratégie ait pu permettre de limiter l'intensité des interactions avec les rats noirs introduits (**Partie 3.1.**). Toutefois, même si l'on peut très probablement penser que ces zones marginales et ces cavités confinées offrent aujourd'hui des secteurs à l'abri des prédateurs introduits, il ne nous est pas possible de nous prononcer sur le rôle exact du rat dans le cantonnement des oiseaux au niveau de ces secteurs. De nombreux autres facteurs de dérangement ont également pu conduire les oiseaux à s'y réfugier, comme la présence d'autres prédateurs introduits (e.g. chats) mais aussi celle de l'Homme, qui en Méditerranée exerce une pression anthropique forte depuis plusieurs millénaires (destruction de l'habitat, chasse, et plus récemment dérangement par les activités multiples sur terre et en mer). Enfin, malgré cette situation d' « apparent équilibre » actuel, il n'est évidemment pas à exclure que les rats aient joué, en synergie ou en addition avec d'autres facteurs de dérangement, un rôle régulateur important dans la régression des effectifs globaux de populations d'oiseaux et l'extinction de populations sur certaines îles au cours de l'histoire de son invasion (Vigne *et al*. 1991 ; Alcover & Florit 1992).

***Quels sont alors les processus qui ont permis aux quatre espèces de pétrels et puffins de Méditerranée de persister durant si longtemps à l'échelle du bassin méditerranéen malgré une présence ancienne du rat ?***

L'approche que nous avons entreprise au travers de l'analyse des patrons de distribution et d'abondances des oiseaux à une échelle régionale (**Partie 2.2.**), ainsi que des patrons de sélection des cavités par les puffins yelkouan (**Partie 3.1.**), ne nous permet pas d'identifier les mécanismes exacts qui ont permis aux oiseaux de se maintenir durant plusieurs centaines d'années de présence du rat, et notamment de distinguer entre une sélection « passive » des sites de reproduction par les oiseaux (i.e. non basée sur l'évaluation par les oiseaux du risque de prédation comme un critère de bonne ou mauvaise qualité de l'habitat), et au contraire une sélection « active » (i.e. le risque de prédation est considéré par les oiseaux comme un critère de bonne ou mauvaise qualité dans le choix des sites).

Une première hypothèse serait que la structuration des populations d'oiseaux marins actuelle résulterait d'une « sélection passive » des sites de reproduction face aux risques liés à la présence de prédateurs introduits (Schlaepfer *et al*. 2002 ; Battin 2004 ; Igual *et al*. 2007). Les Procellariidés sont des oiseaux qui peuvent changer de cavités ou terriers assez fréquemment après un échec reproducteur tout en restant dans la même colonie (Bried & Jouventin 1999 ; Igual *et al*. 2007). Ainsi, après avoir subit plusieurs échecs reproducteurs dans les cavités moins confinées, un couple peut se retrouver à nicher dans une cavité de meilleure qualité (moins accessible aux rats), mais uniquement par hasard. L'effet négatif de la prédation n'est pas perçu comme un signal qui va orienter le choix des oiseaux vers une cavité « plus sûre », mais agit plutôt comme un déclencheur de changement de cavité, dont le choix s'opère de manière aléatoire.

Une seconde hypothèse impliquerait une « sélection active » des sites et cavités pour la nidification des oiseaux, face aux risques liés à la présence de prédateurs introduits (e.g. Schlaepfer *et al*. 2005). Dans le but de maximiser la fitness des individus, le coût nécessaire à opérer ces choix vers des secteurs préférentiels ne devrait pas être plus important que le coût induit par la prédation que l'oiseau pourrait subir s'il choisissait de nicher dans des secteurs plus « à risque » (si le coût est plus important, l'habitat choisi devient alors sub-optimal, Schlaepfer *et al*. 2002). Par ailleurs, une sélection active impliquerait que les individus perçoivent au travers de stimuli variés (échec reproducteur, stimuli visuels et/ou olfactifs) le risque lié à la prédation, pour ne pas se reproduire dans les secteurs les plus « à risque », et suggèrerait donc le développement de mécanismes adaptatifs (Stockwell *et al*. 2003 ; Schlaepfer *et al*. 2005).

En absence de prédateurs sur les îles, la sélection des sites de reproduction par les oiseaux se base essentiellement sur des stimuli relatifs à une bonne qualité de l'habitat (e.g. la qualité des cavités, la compétition pour les cavités avec d'autres espèces d'oiseaux, l'attraction sociale, la philopatrie natale, la présence de perturbations) et ayant conduit, au cours des temps évolutifs, à une meilleure fitness (Lack 1968 ; Danchin *et al*. 1998 ; Warham 1996 ; Bried & Jouventin 2002 ; Parejo *et al*. 2005). La modification de l'environnement par l'Homme, et en particulier l'arrivée d'un prédateur introduit, modifie la qualité de l'habitat (il devient de moins bonne qualité pour les oiseaux). Ainsi, des individus qui ne parviendraient pas à s'adapter à la présence de cette nouvelle menace ne percevraient pas le risque associé à la prédation et reviendraient se reproduire sur les mêmes secteurs, jusqu'à présent de bonne qualité. On dit alors que ces individus sont pris dans des pièges évolutifs, et cette théorie permet, entre autres, d’expliquer pourquoi les espèces indigènes des îles sont si vulnérables aux prédateurs introduits (Schlaepfer *et al*. 2005). Les récentes études qui ont été menées sur les colonies de puffins cendrés des îles Chafarines (au large du Maroc) tendent à suggérer une « sélection passive » des sites de reproduction (Igual *et al*. 2007). En effet, les auteurs suggèrent, au moins sur ce site des îles Chafarines, que les puffins ne parviendraient pas à distinguer les zones à fort risque de prédation par les rats des zones les moins sensibles. Ainsi, certaines populations continueraient à se reproduire sur des secteurs où le risque de prédation est important (densités de rats élevées). Comment alors ces populations se maintiennent-elles ? La clé pourrait résider dans le fonctionnement méta-populationnel des puffins, les fluctuations temporelles fréquentes des densités de rats sur une même île, et la faible sensibilité de la fitness des oiseaux longévifs à un affaiblissement du succès reproducteur. Sur les îles, la dynamique de populations de rats est fortement sujette aux fluctuations liées à la variabilité saisonnière et inter-annuelle des ressources du milieu (Clark 1980 ; Moller & Craig 1987 ; Miller & Miller 1995 ; Russell *et al*. 2009a). Ainsi, les colonies de puffins pourraient profiter de périodes temporaires de moindre impact (liées à de faibles densités de rats ou à une abondance plus importante de ressources alternatives pour les rats) pour se « rétablir » grâce à un meilleur succès reproducteur et un apport d’immigrants (i.e. prospecteurs pour la reproduction). De plus, l’impact de la prédation des rats sur des espèces de tailles moyenne à grande (de 350 à 800 g) comme les trois espèces de puffins présentes en Méditerranée, affectant principalement le succès reproducteur (œufs, jeunes), la survie des adultes et leurs capacités de dispersion ne sont que peu touchées (Doherty *et al*. 2004 ; Le Corre 2008 ; Igual *et al*. 2009), ce qui pourrait apporter une hypothèse additionnelle pour expliquer la persistance des populations d’oiseaux marins sur le long terme.

### 5.1.2. Rats et oiseaux marins : interactions aux cavités, capacités de prédation et évaluation de l’impact

#### *Des interactions limitées aux cavités entre rats noirs et puffins yelkouan. La situation atypique de l’île de Port-Cros*

Sur l’île de Port-Cros, les six années de suivi fin de l’évolution de la dynamique de population du puffin yelkouan suggèrent un impact du rat noir très limité sur le succès reproducteur des oiseaux, alors même qu’après suppression du prédateur apical, le chat haret, la fréquence d’interactions potentielles aux cavités entre rats et oiseaux s’accentue significativement (**Parties 3.1. et 3.2.**). La situation de cette île pourrait paraître originale et inattendue au regard du statut de prédateur redoutable que possède ce mammifère envahissant. Toutefois, les informations complémentaires suivantes peuvent permettre de nous éclairer sur les mécanismes mis en jeu dans la persistance de cette colonie de puffins : (1) le rendement de piégeage des rats sur l'île reste faible à modéré suivant les années (de 0.008 à 0.354 rats par nuit*piège aussi bien avant, pendant et après le contrôle des chats), (2) la probabilité d'immigration et de dispersion des puffins entre colonies semblent être forte (Bonnaud *et al.* 2009), (3) les rats noirs de l'ile de Bagaud, île voisine de 500 m de Port-Cros, présentent une grande difficulté à consommer des œufs intacts d'une taille similaire à ceux de puffins yelkouan (**Partie 3.3.**), et (4) la production de glands de chêne verts semblent jouer un rôle important dans les préférences alimentaires des rats sur Port-Cros (Cheylan 2006). En ce qui concerne ce dernier point, même si des ressources telles que des œufs et poussins d'oiseaux présentent un apport énergétique élevé, leur acquisition représente un coût non négligeable (engagé par la recherche de ces ressources difficilement accessibles, la confrontation avec les parents quand ils sont présents, et les moyens mis en œuvre pour consommer la ressource), il serait particulièrement plausible d'envisager que des rats qui auraient facilement accès à une ressource prédictible et abondante, comme des fruits ou graines, puissent éviter d'aller se risquer dans les cavités d'oiseaux pour augmenter leurs bénéfices énergétiques. Le cas de l'île de Port-Cros n'est pas unique et fait échos à d'autres situations de par le monde où le rat n'occasionne qu'un impact très faible sur d'autres espèces de Procellariidés, comme par exemple sur les îles Falkland (prion de Belcher, Catry *et al.* 2007 ; Quillfeldt *et al.* 2008) et en Nouvelle-Zélande (puffin fuligineux, Gaze 2000, Harper 2007 ; puffin à pieds pâles, Gaze 2000). Globalement, les situations de faible impact du rat sur les oiseaux marins restent encore trop rarement répertoriées et étudiées, certainement car elles ne sont pas considérées comme un intérêt majeur pour la conservation des espèces menacées (**Partie 3.4.**). Cependant, occulter ces situations de « coexistence » pourrait revenir non seulement à passer à côté de processus clé de persistance des oiseaux, mais aussi à contribuer à surestimer l'ampleur générale de l'impact des rats et fournir une estimation biaisée des risques d'extinctions.

### *Prendre conscience des différents biais méthodologiques - Préconiser des approches adaptées à une meilleure estimation du degré de vulnérabilité des oiseaux face aux rats.*

Le statut actuel de conservation alarmant de nombreuses espèces d'oiseaux marins et l'identification des rats comme l'un des facteurs majeurs de risque d'extinction de ces espèces, plus particulièrement des puffins et pétrels, fournissent des arguments de taille pour la mise en place d'opérations de gestion et de conservation. Durant les deux dernières décennies, 332 éradications des quatre espèces de rongeurs introduits ont été entreprises sur les îles de la Planète (Howald *et al*. 2007) et la surface des îles dératisées ne cesse de s'accroître. Chaque opération de gestion représente un coût considérable (en termes de moyens financiers  mais aussi de temps et d'efforts humains). Il est donc essentiel d'avoir recours à des études d'impact pertinentes et rigoureuses (que cherche t-on à montrer et/ou à quantifier?) et adaptées aux espèces cibles (traits d'histoire de vie, facteurs intrinsèques et extrinsèques de fluctuations de leurs populations) afin d'évaluer au mieux le degré de vulnérabilité des populations d'oiseaux, concentrer les efforts et moyens sur les situations les plus « à risque », accroître l'efficacité des opérations de conservation et préserver au mieux la biodiversité. La synthèse des méthodologies couramment employées depuis les 30 dernières années pour évaluer l'impact du rat (**Partie 3.4.**) révèle avant tout que toutes les approches expérimentales ne permettent pas d'identifier avec certitude les mécanismes d'impact (comment les rats affectent-ils les populations d'oiseaux ? Les effets observés sont-ils liés à de la prédation ou à d'autres types d'interactions ?), de quantifier précisément cet impact (quelle est l'ampleur de l'impact sur les populations d'oiseaux ?) et souvent d'estimer la part relative de l'impact du rat dans le déclin des populations par rapport aux effets des facteurs intrinsèques et extrinsèques additifs et/ou synergiques. En outre, certaines méthodologies, comme celles des études de régime alimentaire, ne permettent en aucun cas de conclure sur le moyen d'acquisition de la ressource : y a-t-il eu prédation ou consommation de cadavres ou d'œufs non viables/abandonnés ? Or, une erreur d'interprétation à ce stade critique d'évaluation est susceptible de conduire à des conclusions erronées sur le rôle du rat dans le déclin des populations d'oiseaux.

Par ailleurs, nous avons souligné l'intérêt du recours à des méthodologies jusqu'à présent très peu usitées, comme l'utilisation d'équipements vidéo ou les expérimentations comportementales en situation contrôlée (**Partie 3.3.**) ; ces dernières représentent une alternative possible aux méthodologies indirectes d'évaluation de l'impact, et permettent de pallier les difficultés d'observations directes et de quantification du phénomène de prédation en milieu naturel. Il convient cependant de rester prudent dans l'extrapolation des résultats des études comportementales en situation contrôlée aux conditions *in natura*, du fait notamment des biais possibles liés au stress engendré par le maintien en captivité des individus, de la quantification de l'impact en conditions naturelles à partir de données expérimentales (Meyer & Shiels 2009), des caractéristiques d'œufs proposés aux animaux testés différentes de celles présentes en conditions naturelles (Haskell 1995 ; Yahner & Mahan 1996 ; Lindell 2002) ou de l'utilisation d'individus de laboratoire au lieu d'individus sauvages pour les tests comportementaux (e.g. Massei *et al*. 2002). De manière générale, le couplage systématique des sources d'information corroboratives est fortement recommandé afin de limiter les erreurs d'interprétation et d'affiner les estimations d'impact (Harper 2007 ; Caut *et al*. 2008).

### *Rats, prédateurs d'œufs ou charognards ?*

Grâce à la mise en place de tests comportementaux sur des individus sauvages, nous avons pu tester les capacités de prédation réelles d'un grand nombre de rats noirs sur des œufs (**Partie 3.3.**). La réponse des rats noirs testés quant à leurs capacités de prédation sur des œufs intacts et préalablement perforés est particulièrement bien tranchée. En effet, quelle que soit leur masse corporelle, leur sexe et leur habitat d'origine, les rats ont montré une difficulté très importante à casser et consommer des œufs intacts de tailles similaires à ceux d'oiseaux marins de taille moyenne (assimilable au puffin yelkouan) et même de petite taille (assimilable au pétrel tempête). La simple présence, cependant, d'une petite perforation ou fêlure au niveau de la coquille suffit à augmenter très largement le taux de réussite à la consommation, qui passe de 2% pour les œufs intacts à 90% pour les œufs perforés. Ces résultats sont à la fois quelque peu inattendus, si l'on se reporte au statut dévastateur des rats sur l'avifaune marine et aux mentions assez fréquentes de prédation sur les œufs (e.g. Atkinson 1985), mais ils sont également en accord avec les quelques études expérimentales qui ont mis en évidence l'incapacité de certaines espèces de rongeurs, comme *Peromyscus* sp. (DeGraaf & Maier 1996 ; Marini & Melo 1998 ; Rangen *et al*. 2000), *R. rattus* (Prieto *et al*. 2003) et *R. norvegicus* (Massei *et al*. 2002) à consommer des œufs intacts de caille (cas de *Peromyscus* sp.) et poule (cas de *Rattus* spp.). Par ailleurs, nos résultats accordent plus de poids à l'hypothèse alternative d'un comportement partiellement charognard fréquent chez les rats introduits, avérée, mais pourtant trop souvent négligée dans les études d'impact car difficilement quantifiable (**Partie 3.4.**). Ces résultats renforcent avant tout la légitimité des recommandations de prudence quant aux interprétations souvent équivoques des restes d'œufs consommés trouvés à proximité des cavités et des résultats de régime alimentaire conventionnel. Plus globalement, ils légitiment fortement les récents questionnements émis au sujet de l'intensité de l'impact de la prédation du rat sur les oiseaux marins (Prieto *et al*. 2003 ; Towns *et al*. 2006 ; **Partie 3.1.**). Par contre, ces résultats n'écartent pas la possibilité de l'existence d'un comportement d'apprentissage de techniques particulières de prédation (Grant *et al.* 1981 ; Booth *et al.* 1996 ; Seto & Conant 1996), la plus forte vulnérabilité des œufs laissés sans protection qui pourraient être facilement déplacés hors des cavités (Imber 1984 ; Booth *et al.* 1996) et un taux de prédation élevé sur les très jeunes poussins d'oiseaux marins (Thibault 1995 ; Igual *et al.* 2006), et les adultes d'oiseaux marins (Major & Jones 2005) et œufs d'oiseaux terrestres de petite taille (Robertson *et al.* 1994 ; Penloup *et al.* 1997 ; Robinet *et al.* 1998 ; Kerbiriou *et al.* 2004).

### 5.1.3. Influence de l'hétérogénéité de l'habitat, des ressources d'origine allochtone et des apports hydriques épisodiques sur l'écologie trophique, la dynamique et la structuration spatiale des populations des rats insulaires.

L'identification des facteurs susceptibles de favoriser le maintien et les abondances des populations envahissantes et d'accroître leurs impacts sur les communautés insulaires est essentielle afin de mettre en place des solutions adaptées pour la gestion des espèces envahissantes. Au travers des travaux exposés au chapitre 4, nous avons montré que les apports trophiques d'origine allochtone (ressources dérivées des populations de goélands leucophées nicheurs et d'une plante envahissante, la griffe de sorcières) exerçaient une influence nette sur la dynamique de population de rats noirs d'une petite île de Méditerranée, en particulier sur les taux de croissance des individus, les taux de reproduction et les densités (**Parties 4.2.** et **4.3.**). En outre, les effets de ces nutriments allochtones sont particulièrement plus marqués durant l'année sèche, comparativement à l'année pluvieuse, suggérant fortement un rôle « compensatoire » de ces apports allochtones en période où les conditions climatiques sont drastiques, et où seule la productivité primaire endogène de l'île ne permettrait aux paramètres de la dynamique de population de rats (taux de croissance, densités de population, productivité) que de se maintenir à des niveaux faibles. De manière surprenante, les effets des ressources allochtones sont spatialement limités et restreints à chaque habitat. Malgré la proximité spatiale d'habitats de qualité variable selon les saisons sur Bagaud, les rats présentent un faible degré de plasticité alimentaire à l'échelle de l'individu par rapport à celui de l'espèce ou de la population entière de l'île, suggérant ainsi l'importance du rôle des interactions intra-spécifiques dans la structuration spatiale des populations (**Partie 4.1.**).

Les effets des apports allochtones sur la survie des individus ne sont toutefois pas significatifs (**Partie 4.3.**). Ce résultat parait plutôt surprenant car les taux de croissance des jeunes individus occupant la zone de maquis sont nettement plus faibles durant la période sèche, et la perte de poids de certains individus au cours de l'automne et hiver suivant suggère un taux de mortalité assez fort à cette période (les individus ne sont plus recapturés par la suite ; **Partie 4.2.**). L'absence d'effet significatif des ressources allochtones sur la survie des individus entre les années et les habitats est probablement liée à une taille d'échantillon réduite lorsque l'on estime les paramètres de survie par session, milieu et année (un modèle prenant en compte l'interaction année*habitat*session a été construit au préalable et n'a estimé que des paramètres de survie avec des intervalles de confiance très larges), ainsi qu'à un effet confondant des classes d'âge (seuls les jeunes de l'année issus de l'habitat non enrichi, le maquis méditerranéen, semblent subir un taux de mortalité important).

Grâce à un suivi de la dynamique de population de rats sur 21 mois, couvrant plusieurs générations, des saisons variées et deux années aux conditions climatiques contrastées, nous avons pu mettre en avant la forte propension des populations de rats noirs insulaires à fluctuer au fil des saisons et années. Nos résultats soulignent également l'existence d'une régulation forte des populations de type « bottom-up » chez cette espèce qui figure parmi les consommateurs de dernier ordre sur Bagaud. Cette régulation semble être gouvernée par l'apport soudain d'eau douce en grande quantité, facteur reconnu pour contrôler l'abondance des ressources de milieux où la productivité terrestre est faible (Clark 1980 ; Polis *et al.* 2007 ; Brown & Ernest 2002).

Ces résultats soulignent avant tout le fort potentiel des populations de rats noirs insulaires à exploiter et interagir avec des ressources issues d'autres espèces envahissantes et de milieux perturbés. Certaines populations d'oiseaux anthropophiles, comme les goélands leucophées en Méditerranée, mais aussi les goélands marins (*Larus marinus*) et cormorans à aigrettes (*Phalacrocorax auritus*) dans le nord de l'Atlantique (Ellis *et al.* 2006), les grands cormorans (*Phalacrocorax carbo*) en Scandinavie (G. Kolb, comm. pers.), les goélands argentés sur les côtes du nord et nord ouest de l'Europe (Pons 2004) ont subit depuis ces dernières décennies une explosion démographique marquée qui conduit ces oiseaux à s'installer en masse sur les îles. Ainsi, nos travaux suggèrent que la modification sensible de la composition spécifique et des chaines trophiques des îles où ces oiseaux s'installent est fortement susceptible de fournir aux populations introduites omnivores, détritivores et même herbivores ou granivores les moyens de se maintenir sur des îles, où la qualité et l'abondance des ressources sont souvent peu élevées et leur disponibilité hautement variable et non prédictible. Enfin, ces résultats suggèrent que le maintien sur le long terme des populations de rats introduits sur les îles méditerranéennes pourrait être favorisé par la prolifération des ressources anthropiques d’origine allochtone, malgré l’évolution annoncée du climat en Méditerranéen prédisant une augmentation de la fréquence des évènements climatiques drastiques (Lejeusne *et al.* sous presse).

## 5.2. Perspectives de recherche

### 5.2.1. Comment tester les stratégies de sélection de l’habitat de reproduction par les oiseaux marins?

Les mécanismes de sélection des sites de reproduction par les oiseaux marins paraissent assez complexes à appréhender (problèmes inhérents aux effets confondants, à la nécessité de disposer d’un large jeu de données couvrant plusieurs générations sur un minimum d’une dizaine d’années pour des espèces aussi longévives que les Procellariidés, e.g. Bradley *et al*. 1991 ; Cuthbert & Davis 2002 ; Jouventin *et al*. 2003). Cependant, la compréhension des patrons de sélection des sites de reproduction offre des pistes de recherche précieuses pour la conservation des oiseaux et la mise en place de stratégies pertinentes pour la gestion des facteurs de perturbation, notamment les prédateurs introduits (e.g. Bried & Jouventin 1999 ; Igual *et al.* 2006, 2007). Avant tout, il est nécessaire de pouvoir isoler les effets du rat dans le choix des sites de reproduction par les oiseaux. Un moyen simple de tester cela serait de comparer les caractéristiques des cavités sélectionnées entre deux colonies semblables en terme de couvert végétal et de disponibilité de l’habitat, mais différant par la présence du rat. Cependant, en Méditerranée le rat noir est présent sur la plupart des îles et îlots de Méditerranée (c.f. Ruffino *et al*. 2009). Une alternative serait d’effectuer la comparaison entre des secteurs dératisés et des secteurs non dératisés (mais présentant des caractéristiques physiques semblables), ou encore entre deux situations pré- et post-éradication. Dans un second temps, dans le but de distinguer entre sélections « passive » et « active » des cavités par les oiseaux, il serait nécessaire de mettre en relation des données de fitness des individus (succès reproducteur et survie) avec celles relatives à la qualité de l’habitat (condition corporelle des adultes et des jeunes, poids des œufs), et au recrutement et à la dispersion des individus (changement de cavités, de colonies) (Igual *et al*. 2007). L’acquisition d’un tel jeu de données nécessite bien évidemment la mise en place de programmes prolongés de baguage, de captures et recaptures nombreuses, et d’un suivi robuste des paramètres reproducteurs sur plusieurs générations. Enfin, il convient d’insister sur le fort potentiel des études phylogénétiques dans la compréhension des flux d’individus entre colonies et des patrons de structuration des populations de pétrels et puffins à l’échelle du bassin méditerranéen (Austin *et al*. 1994 ; Crochet 1996 ; Dearborn *et al.* 2003 ; Genovart *et al*. 2007).

### 5.2.2. Comment mieux évaluer les mécanismes et l'intensité de l'impact des rats sur les oiseaux marins ?

La compréhension des mécanismes d'impact d'un prédateur aussi cryptique que le rat sur des oiseaux aux mœurs discrètes passe obligatoirement par la mise en place de protocoles expérimentaux rigoureux et d'outils adaptés aux processus que l'on souhaite mettre en évidence. Les apports de chaque méthodologie mais aussi leurs biais respectifs, ainsi que les lacunes de nos recherches ont été traités dans la partie 4 du chapitre 3. Je souhaiterais ici pointer du doigt deux perspectives de recherche qui pourraient contribuer à affiner la compréhension des mécanismes d'interactions et d'impact du rat sur les oiseaux marins, mais qui jusqu'à présent n'ont été que très peu, voire pas du tout, examinées dans cet optique.

#### *Mieux évaluer le comportement charognard des rats et son importance dans leur mode d'acquisition des ressources*

Une première perspective de recherche concerne l'étude du comportement charognard des rats introduits du genre *Rattus* et la quantification de ce phénomène. La quantification de la part relative des ressources dérivées d'oiseaux marins (protéines animales) acquises à partir de matériel mort dans le régime alimentaire du rat n'a jamais été estimée en milieu naturel. Seules quelques mentions ou hypothèses figurent au travers de rares articles (e.g. Witmer *et al*. 2006 ; Harper 2007 ; Quillfeldt *et al*. 2008), certainement du fait de la difficulté de pouvoir quantifier ce phénomène en milieu naturel, et des sources d'erreurs inhérentes à une interprétation parfois hasardeuse des résultats de terrain, de régime alimentaire ou d'analyses trophiques (Stapp 2002 ; Harper 2007 ; Quillfeld *et al.* 2008). Or, au sein des colonies d'oiseaux marins, on trouve, parfois en grande quantité, des cadavres, carcasses, œufs abandonnés, fêlés, jonchant la proximité des cavités ou nids d'oiseaux, et il semble probable que les rats vivant à proximité de colonies d'oiseaux marins acquièrent une partie de leurs ressources à partir de matériel mort. Quantifier l'acquisition de ressources à partir de matériel mort (comportement charognard) et de proies vivantes (prédation) apparait primordial pour une première étape d'étude d'impact. En effet, la prédominance de l'un ou l'autre des comportements change complètement la donne, l'un (la prédation) impliquant un impact sur les individus, et l'autre (le comportement charognard) n'impliquant aucun impact sur les populations d'oiseaux marins. Le moyen qui parait le plus direct pour visualiser ce comportement charognard et obtenir une idée de l'ampleur du phénomène reste la vidéo. Ainsi, il serait particulièrement intéressant de disposer des systèmes d'enregistrement vidéo à proximité des cadavres frais d'oiseaux ou d'œufs abandonnés, fêlés, ouverts, sur des colonies d'oiseaux marins où les rats sont présents. Cela permettrait dans un premier temps de savoir si les cadavres et œufs laissés ou endommagés sont utilisés par les rats et d'observer leur comportement pour l'acquisition de cette ressource (la consomment-ils sur place ? quels sont les moyens mis en œuvre pour la consommer, et notamment faciliter sa consommation [déplacement, roulage des œufs en vue de les fragiliser] ?). L'installation de dispositifs vidéo près des nids et à l'intérieur des cavités (bien que plus compliquée à mettre en œuvre) doit également être favorisée afin de visualiser les confrontations entre rats et oiseaux (parents ou jeunes) et les moyens développés par les rats pour extirper la ressource hors de la cavité (Booth *et al.* 1996 ; Sanders & Maloney 2002 ; Jonhston *et al.* 2003 ; Thompson & Burhans 2004 ; Wanless 2007). L'utilisation d'équipements vidéo reste cependant coûteuse et demandeuse en temps (notamment pour le tri des images). De plus, cette méthodologie reste sensible à la faible probabilité d'occurrence de la prédation et donc d'enregistrement vidéo du phénomène, ainsi qu'à la difficulté d'obtenir une taille d'échantillons assez large afin de pouvoir quantifier le phénomène (voir cependant Innes *et al.* 1994 ; Sanders & Maloney 2002 ; Thompson & Burhans 2004). De manière alternative et afin d'obtenir une taille d'échantillon plus large, le comportement charognard pourrait être visualisé par l'intermédiaire de nids ou terriers artificiels posés dans le milieu naturel mimant les caractéristiques des nids et terriers naturels, dans lesquels seraient disposés la ressource proposée (œufs intacts, perforés, cadavres) et munis d'un dispositif vidéo. Un système d'identification individuelle des rats pénétrant dans les cavités pourrait être également envisagé afin d'enregistrer les fréquences de passages et d'identifier des individus spécialistes. Enfin, comme nous avons pu le mettre en évidence, les tests comportementaux sur individus sauvages en situation contrôlée sont des moyens intéressants pour tester les capacités de prédation et les mécanismes impliqués (DeGraff & Maier 1996 ; **Partie 3.3.**). Les tests de prédation sur des œufs gagneraient à être étendus à d'autres espèces de rongeurs introduits plus petites que le rat noir, comme *R. exulans* et *M. musculus*, reconnues pour être des prédateurs redoutables d'oiseaux marins, et des espèces plus grosses, comme *R. norvegicus* dont la taille d'ouverture de mâchoires et la force musculaire pourraient leur faciliter la consommation d'œufs intacts de petite et moyenne tailles.

### *Agents de stress physiologique et compétition pour l'habitat : deux alternatives à l'impact causé par la prédation ?*

Une seconde perspective de recherche intéressante à développer concerne le rôle d'interactions autres que la prédation pour expliquer l'impact des rats sur les oiseaux marins, comme par exemple celui du stress induit par la perception (visuelle ou olfactive) d'un prédateur, et celui de la compétition pour l'habitat. Ces phénomènes n'ont jamais été testés dans le cas d'interactions rats-oiseaux marins, ni même réellement formulés en tant qu'hypothèses complémentaires à l'impact de la prédation, mais reposent pourtant sur des bases théoriques cohérentes. Chez les animaux qui ont évolué en présence de prédateurs et/ou compétiteurs, la détection de leur présence induit chez l'animal un stress physiologique et une réponse comportementale de défense ou de fuite (Kats & Dill 1998 ; Schleuerlein *et al.* 2001 ; Cockrem & Silverin 2002). Au contraire, les animaux qui n'ont pas évolué en présence de prédateurs et compétiteurs (animaux dits naïfs), comme les espèces indigènes des îles, ne sembleraient pas capables de s'adapter à l'arrivée de prédateurs ou compétiteurs introduits, et de ce fait ne développeraient pas de comportement anti-prédateur (Blumstein 2002 ; Blumstein & Daniel 2005). Chez les iguanes marins des Galapagos (*Amblyrhynchus cristatus*), Röld *et al.* (2007) ont montré que le stimulus induit par la présence d'un nouveau prédateur ne générait pas de réponse physiologique chez ces reptiles naïfs ayant vécu entre 5 et 15 millions d'années en absence de prédateurs. Par contre, une confrontation répétée au facteur de stress permettait rapidement aux reptiles de développer une réponse physiologique, mais n'induisait pas de réponse comportementale pour échapper à la menace. Les auteurs suggèrent ainsi que même si les espèces indigènes des îles qui ont longtemps évolué en l'absence de prédateurs pouvaient être douées d'une certaine plasticité physiologique, leur plasticité comportementale restait certainement réduite. Un stress accru et répété, n'induisant pas de réponse comportementale pour l'éviter, pourrait générer des troubles physiologiques et comportementaux (e.g. perturbation du succès reproducteur, Schleuerlein *et al.* 2001). Des pistes de recherches intéressantes se dessinent ainsi dans le domaine des interactions prédateurs introduits-oiseaux marins. En effet, les oiseaux marins de l'ordre des Procellariiformes sont reconnus pour posséder un sens de l'olfaction particulièrement développé, qu'ils utilisent notamment pour identifier leurs terriers et partenaires (Bonadonna *et al.* 2003; Bonadonna & Nevitt 2004) et localiser leurs ressources alimentaires (Nevitt & Bonadonna 2005). Il serait donc probable que les traces olfactives laissées par les prédateurs introduits (urine, fèces) lors de leur prospection au niveau des sites de reproduction des oiseaux puissent être perçus par les Procellariiformes comme signaux de « danger », et puissent induire un stress physiologique chez les oiseaux, se traduisant par une baisse des paramètres reproducteurs, de la condition corporelle ou par un évitement des sites occupés par les prédateurs. Ainsi, il serait intéressant d'étudier la réponse physiologique des oiseaux marins à la vue et l'odeur d'un prédateur tel que le rat par la mesure de la production de corticostérone suite à une exposition seule et répétée au prédateur, et de déterminer si cette réponse correspond à un réel agent de stress (e.g. Sapolsky *et al.* 2000 ; Rödl *et al.* 2007). Si la perception du prédateur induit une réponse de stress physiologique chez l'oiseau, et le facteur de stress a bien été identifié (la vue d'un prédateur, un/des composé(s) chimique(s) émis par ces prédateurs), il deviendrait alors particulièrement intéressant de conduire une expérimentation en milieu naturel, en soumettant aux oiseaux marins les agents de stress identifiés (un composé chimique, de l'urine ou fèces de prédateur), puis en mesurant leurs effets sur les paramètres reproducteurs ou la sélection des sites de reproduction par exemple. La mise en place de ce type d'expérimentation sous-entendrait de travailler au niveau de colonies d'oiseaux marins de grands effectifs et sur ces espèces peu ou pas menacées pour éviter les effets négatifs des agents stressants sur la dynamique de population. A ce stade de la réflexion, tout cela n'est que de l'ordre de la spéculation mais ces quelques pistes paraissent prometteuses.

Enfin, outre les effets de la prédation et du stress physiologique, l'impact des rats sur les oiseaux marins pourrait également se manifester par l'intermédiaire d'une compétition pour l'habitat. En effet, dans leur comportement de recherche de nourriture et d'abris, les rats affectionnent tout particulièrement les terriers, cavités et crevasses, qui représentent des endroits de choix pour la nidification de la plupart des pétrels et puffins (Ruffino *et al.* 2008 ; voir aussi **Parties 3.1. et 3.2.**). L'hypothèse soulevée ici est que les oiseaux pourraient être capables d'identifier les indices de présence de rats pour éviter les cavités déjà occupées ou prospectées par des compétiteurs supérieurs que pourraient représenter les rats (cette réponse induirait donc une réaction comportementale d'évitement et pourrait être considérée comme une réponse adaptative, contrairement à ce qui a été développé précédemment). Ces hypothèses pourraient être testées par la mise en place de dispositifs expérimentaux en « labyrinthe » (Bonadonna *et al.* 2004) et l'observation du comportement de l'oiseau qui, placé à la base à l'embranchement du dispositif, pourrait être confronté à deux tunnels, l'un comportant l'odeur de sa cavité, et l'autre, l'odeur de sa cavité à laquelle serait ajoutée l'odeur du compétiteur.

Les impacts attendus des deux processus - l'influence du stress physiologique et de la compétition pour l'habitat - sur les populations d'oiseaux marins seraient sans doute moins intenses mais additionnels à ceux de la prédation. David (2003) et Gurevitch & Padilla (2005) soulignent que les interactions de compétition induites par les espèces introduites ont rarement été identifiées comme agents d'extinction d'espèces indigènes et notamment d'oiseaux, et suggèrent ainsi que le phénomène de compétition demanderait un temps très long pour conduire une espèce à l'extinction complète, ou que les extinctions seraient plus susceptibles d'être provoquées par de la prédation ou transmission de pathogènes par exemple. En plus des capacités de dispersion des oiseaux et de la moindre sensibilité des espèces longévives à une réduction du succès reproducteur, de telles interactions impliquant un impact moins fort sur les populations que celui de la prédation, pourraient peut-être expliquer pour partie la persistance de certaines populations et espèces d'oiseaux marins en présence de rats durant plusieurs centenaires ou millénaires. Ces processus liés au stress et à la compétition pour l'habitat pourraient notamment être impliqués dans les réactions fortes des populations d'oiseaux marins enregistrées en réponse à l'éradication des rats (augmentation importante du succès reproducteur des oiseaux, augmentation du taux d'occupation des sites favorables à la reproduction, recolonisation de sites délaissés par les oiseaux en présence de rats) en situation de coexistence ancienne, comme sur les îles méditerranéennes (Amengual & Aguilar 1998 ; Corbi *et al*. 2005 ; Igual *et al*. 2006 ; Pascal *et al*. 2008).

### 5.2.3. Mieux comprendre les processus d'extinctions et le rôle des « invasives » dans les extinctions passées afin de mieux évaluer les risques futurs

Le groupe des oiseaux insulaires a subi depuis les temps préhistoriques un taux d'extinctions d'espèces liées à l'impact direct ou indirect de l'Homme très important (Steadman 2006). La vulnérabilité de ces oiseaux face aux prédateurs introduits, en particulier aux rats, qui ont été introduits sur la plupart des îles de la Planète, est mondialement reconnue. Sur les 134 espèces d'oiseaux éteintes depuis 1500, 71 cas seraient liés aux prédateurs introduits, dont 58% ($n$ = 41) directement liés aux rats (Birdlife International 2008). Toutefois, du fait de la variabilité de leurs traits d'histoire de vie, le groupe des oiseaux insulaires présente des degrés de vulnérabilité variables suivant les taxa. Par exemple, les oiseaux terrestres (e.g. râles, passereaux, pigeons, perruches), aux capacités de dispersion limitées, ont subi sur les îles du Pacifique un taux d'extinction d'espèces équivalent à 30% si l'on se base sur le nombre d'extinctions d'espèces identifiées, et allant jusqu'à 78% si l'on prend en compte le grand nombre d'espèces éteintes à la taxonomie indéterminée, alors que seulement de 7% à 14% des espèces d'oiseaux marins se seraient éteintes (Table 13). Plus globalement, l'UICN répertorie cinq espèces d'oiseaux marins éteintes depuis 1500, contre 129 espèces d'oiseaux terrestres éteintes (UICN 2008). Ce constat semble aller à l'encontre des estimations de risques d'extinction d'espèces d'oiseaux marins imputés aux rats (d'après les critères UICN, les trois espèces de rats introduits sont identifiées comme un facteur de risque majeur d'extinction chez 70% des espèces de pétrels et puffins). Les oiseaux marins seraient-ils moins vulnérables à l'extinction ? Ou bien les processus d'extinction sont-ils plus longs que pour des espèces aux capacités de dispersion limitées ? La vulnérabilité des oiseaux marins face aux rats introduits se serait-elle accrue durant ces dernières décennies avec l'intensification des activités humaines ?

| | **Oiseaux terrestres** | | | **Oiseaux marins** | **Toutes espèces** |
|---|---|---|---|---|---|
| | **Non passereaux** | **Passereaux** | **Total** | | |
| (A) Nombre d'espèces vivantes | 261 | 246 | 507 | 130 | 637 |
| (B) Nombre d'espèces éteintes connues | 152 | 25 | 177 | 10 | 187 |
| (C) Estimation du nombre total d'espèces éteintes[1] | 623-1758 | 102 | 725-1860 | 22 | 747-1882 |
| (D) Estimation du nombre total d'espèces (A+C) | 884-2019 | 348 | 1232-2367 | 152 | 1384-2519 |

**Table 13.** Estimation du nombre d'espèces d'oiseaux insulaires vivantes et éteintes sur tous les archipels de l'Océanie, excepté les îles hawaiiennes (d'après Steadman 2006). [1]L'estimation intègre l'ensemble des taxa reconnus comme éteints mais à la taxonomie non identifiées.

Les processus d'extinctions sont souvent complexes car ils découlent rarement d'un seul facteur (Burbidge & Manly 2002 ; Burney & Flannery 2005 ; Trevino *et al*. 2006). Les facteurs d'extinctions, aussi multiples qu'ils puissent être, sont souvent confondants, agissant en synergie ou addition d'autres facteurs, si bien que la quantification du rôle de chaque facteur dans l’extinction de la population ou de l’espèce en question apparait souvent énigmatique  (Steadman 2006). C’est particulièrement vrai pour les oiseaux marins qui sont soumis aux menaces et dérangements à la fois en mer mais aussi sur terre (Gaze 2000 ; Oro *et al.* 1999, 2004 ; Buckelew 2007 ; Igual *et al.* 2009). Par ailleurs, le temps nécessaire pour qu’un prédateur introduit conduise une population ou une espèce à l’extinction complète varie selon les traits d’histoire de vie des espèces introduites et menacées (temps de renouvellement des générations, capacités de fuite, d’expansion), du/des stade(s) démographique(s) affecté(s), et des différentes « vagues » d’introductions (arrivée de différentes espèces à des périodes différentes, ou introductions répétées de la même espèce dynamisant ainsi son invasion) (e.g. Steadman 2006 ; Buckelew 2007). C’est pourquoi, en l’absence d’études robustes ou d’écrits rapportés par les témoins des extinctions passées, la détermination des causes d’extinctions devient un vrai challenge. La solution alternative pour une meilleure compréhension des déterminismes des extinctions passées et futures reste l’analyse et la modélisation de bases de données à une large échelle afin de pointer du doigt les groupes d’espèces les plus à risque, les traits d’histoire de vie de ces taxa qui les rendent vulnérables, mais aussi ceux qui favorisent leur maintien, ainsi que les caractéristiques des îles favorisant l’extinction, comme les facteurs abiotiques (surface de l’île, topographie, substrat, isolement, climat), biotiques (diversités animale et végétale, présence de mammifères terrestres) et culturels (présence de l’Homme et intensité de son occupation, présence d’espèces introduites) (Jones *et al.* 2003 ; Duncan & Forsyth 2006 ; Trevino *et al.* 2006 ; Steadman 2006 ; Table 14 ). La recherche des déterminants et processus d’extinctions est grandement facilitée par la mise à disposition par l’UICN d’une base de données (liste rouge) listant le statut de conservation d’un grand nombre d’espèces animales et végétales, ainsi que les espèces reconnues comme éteintes depuis 500 ans. Enfin, les territoires d’outre-mer français, répartis dans les principaux océans du monde, occupent une place de choix parmi les hot-spots de biodiversité insulaire et figurent comme des sites de privilégiés pour l’étude des patrons de raréfaction et d’’extinction d’espèces.

| | Favorisent potentiellement l'extinction | Retardent potentiellement l'extinction |
|---|---|---|
| **FACTEURS ABIOTIQUES** | | |
| - Surface de l'île | Petite | Grande |
| - Topographie | Plat, faible altitude | Altitude élevée, présence de falaises |
| - Substrat | Sablonneux, non calcaire | Calcaire ou volcanique abrasif |
| - Type de sol | Riche en nutriments | Pauvre en nutriments |
| - Isolement | Très isolée | Peu isolée |
| - Climat | Aridité saisonnière | Climat peu sec toute l'année |
| **FACTEURS BIOTIQUES INDIGENES** | | |
| - Diversité végétale | Pauvre | Riche (retard sur le court terme seulement) |
| - Diversité animale | Pauvre | Riche (retard sur le court terme seulement) |
| - Présence de mammifères terrestres | Absence | Présence |
| - Présence de ressources marines | Pauvre, accès difficile | Riche, accès facile |
| - Traits d'histoire de vie des espèces | Aptérisme, mœurs terrestres, grande taille, naïveté, plumage coloré | Espèces ailées, de petite taille, comportement anti-prédateurs, vivant dans la canopée, plumage peu coloré |
| **FACTEURS CULTURELS** | | |
| - Occupation humaine | Permanente | Temporaire |
| - Intensité de l'occupation | Etendue | Restreinte |
| - Accroissement de la Population humaine | Croissance rapide, densités élevées | Croissante lente, densités faibles |
| - Présence de plantes introduites | Beaucoup d'espèces, populations envahissantes | Peu d'espèces, populations non envahissantes |
| - Présence d'animaux introduits | Beaucoup d'espèces, populations envahissantes | Peu ou pas d'espèces, pas de populations envahissantes |

**Table 14.** Facteurs favorisant et retardant les extinctions anthropogéniques de vertébrés sur les îles océaniques du Pacifique (d'après Steadman 2006).

### 5.2.4. Eclaircir les facteurs favorisant le maintien des populations de rats introduits sur les îles et leurs impacts sur les oiseaux marins

Dans le cadre des travaux présentés au chapitre 4, nous avons pu démontrer les effets importants des ressources d'origine allochtone sur les populations de rats noirs et les capacités des rats à répondre rapidement aux apports de ressources pulsées. Cependant, deux axes essentiels restent à approfondir. (1) Les apports d'origine allochtone (e.g. dérivés d'oiseaux anthropophiles ou d'espèces proies introduites) ainsi que les ressources épisodiques prédictibles (e.g. pluie de graines ou de fruits, émergences d'insectes) ou imprédictibles (e.g. accroissement de l'abondance des ressources suite à des précipitations intenses) pourraient-ils indirectement accentuer l'impact des rats introduits sur les communautés insulaires ? Cette augmentation de l'intensité de l'impact pourrait se manifester par une amélioration de la dynamique de population de rats par rapport aux populations qui n'auraient pas accès à ces ressources allochtones ou épisodiques enrichies et abondantes. Pour tester ces hypothèses, l'idéal serait de pouvoir travailler à l'échelle d'un archipel présentant à la fois des îles recevant des apports substantiels de nutriments allochtones (par exemple via la concentration de larges colonies d'oiseaux pélagiques ou marins anthropophiles) ou recevant une production massive de graines, fruits ou insectes, et des îles ne recevant pas ces apports (e.g. Markwell & Daugherty 2002 ; Stapp & Polis 2003 ; Barrett *et al.* 2005). Ces îles devront également héberger des populations d'espèces vulnérables à l'impact du rat, à la fois sur les îles recevant ces apports enrichis et sur celles n'en recevant pas. (2) Par ailleurs, il serait fortement enrichissant d'étendre l'étude des mécanismes favorisant le maintien des populations de rats sur des îles aux conditions environnementales particulièrement drastiques (peu de ressources, climat aride) en approfondissant le rôle de deux types de facteurs sur la survie des individus : (1) celui des ressources d'origine allochtone (d'origine anthropique ou non) et des ressources épisodiques (d'origine exogène ou non), et (2) celui de la plasticité trophique individuelle des rats, en particulier leur capacité à opérer des changements (« shifts ») alimentaires pour compenser l'absence temporaire d'une ressource principale. Les expérimentations menées sur Bagaud nous ont fourni un aperçu intéressant des mécanismes susceptibles de jouer un rôle important dans le maintien des populations de rats sur le long terme, mais semblent aller à l'encontre d'autres contextes insulaires (comme l'île Surprise dans l'Océan Pacifique, où le maintien des rats noirs semble être lié à leurs capacités à s'orienter vers des ressources alternatives lorsque les ressources principales sont absentes et à se déplacer d'un habitat vers un autre; Caut *et al.* 2008). C'est pourquoi, notre connaissance mériterait de s'étendre à d’autres systèmes, en particulier beaucoup plus drastiques en termes de conditions environnementales, en vue d’une meilleure évaluation des mécanismes de maintien des populations introduites et de leurs impacts sur les communautés indigènes.

Enfin, au vu de la forte structuration spatiale des individus observée sur l’île de Bagaud, il serait intéressant de poursuivre les recherches sur les mécanismes d’interactions intraspécifiques, mais aussi interspécifiques (dans le cas de coexistence entre plusieurs rongeurs introduits) dans les patrons d’utilisation de l’habitat et des ressources par les rongeurs introduits. Quels sont les facteurs du milieu indicateurs d’une bonne ou mauvaise qualité d’habitat (couvert végétal, abondance et/ou qualité nutritionnelle des ressources) ? Les interactions entre individus sont-elles gouvernées par de la compétition pour l’exploitation des ressources (effets indirects de l’utilisation mutuelle de ressources limitées), ou par de la compétition par interférence (agression ou défense du territoire ; e.g. Harris & MacDonald 2007) ? Ces différentes questions pourraient être abordées par la mise en place d’expérimentations en milieu naturel. Tout d’abord, la manipulation expérimentale de la qualité et quantité des ressources du milieu et/ou de l’habitat permettrait d’enregistrer les réponses démographiques des individus ou espèces à ces changements, et d’identifier les compétiteurs (classes d’âges, sexe, espèces) supérieurs (Banks & Dickman 2000 ; Lin & Batzli 2001 ; Harris & MacDonald 2007). Par ailleurs, la suppression progressive (par piégeage léthal) des compétiteurs d’un habitat ainsi que le suivi successif du temps nécessaire à la recolonisation et des réponses des autres espèces, en termes de dynamiques de populations, fitness et patrons d’exploitation des ressources et de l’habitat, est susceptible de fournir des informations complémentaires sur la nature et l’intensité des interactions intra- et inter-spécifiques (Harris & MacDonald 2007). Enfin, l’utilisation de l’outil génétique serait à préconiser afin d’identifier les relations de parenté entre individus et groupes sociaux (Russell *et al*. 2009b), les phénomènes de dispersion et leurs directions entre habitats hétérogènes (Gauffre *et al*. 2008), ainsi que les groupes sociaux ayant développé des stratégies particulières dans l’acquisition des ressources, comme pour la prédation sur des oiseaux marins (Abdelkrim *et al*. 2009).

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# TABLE DES MATIERES

# ANNEXES

**Annexe 1.** Top-predator control on islands boosts endemic prey but not mesopredator. Article de Bonnaud *et al*. sous presse dans *Animal Conservation* dont fait référence la **Partie 3.2.**

**Annexe 2.** Données de capture-recapture de rats noirs sur l'île de Bagaud et précipitations mensuelles (**Partie 4.3.).**

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**Annexe 4.** Distributions des probabilités *a priori* ("priors") et des probabilités *a posteriori* ("posteriors") pour les paramètres $\beta_{rainfall}$ et $\sigma_p$ du modèle bayésien de Bagaud (**Partie 4.3**.).

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# ANNEXE 1.

## Top predator control boost endemic prey but not mesopredator

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Top-predator control on islands

Sous presse dans *Animal Conservation* à la date du 20 Mai 2010.

### Abstract

Introduced predators on islands are responsible for numerous extirpations and extinctions of native species. Cat predation is particularly detrimental for seabirds, so cat control or eradication is generally the best option to reduce negative impact on native fauna. However, potential cascading effects such as the mesopredator release effect need to be monitored after cat removal. On Port-Cros Island, a cat control campaign was undertaken to eliminate the strong and recurrent threat from feral cat predation to the small yelkouan shearwater population, though allowing for the persistence of a neutered domestic cat population. To evaluate the conservation success of an endemic and endangered species, using such uncommon management campaign, the diet and impact of the remaining cats were studied through scat analysis and trapping-success. Moreover, to evaluate the recovery of the seabird population and detect any potential mesopredator release effect, shearwater and rat populations were monitored simultaneously with cat control. Although only live traps were used, most cats were trapped in the first year of cat eradication and the last incidence of cat predation on the yelkouan shearwater occurred the following year. The recovery of the shearwater population, occurring the first year of cat control, was mainly attributable to the settlement of new breeders in the colony. Simultaneously, rat population dynamics fluctuated widely (increasing and decreasing) but, even though the interactions between rats and shearwaters at breeding cavities increased, no evidence of rat predation on shearwaters was recorded. Thus, cat control on Port-Cros Island is a success for native species conservation, proving that such management strategy can induce an increase in the population of the endemic species, here the yelkouan shearwater, without any evidence of a mesopredator release effect.

**Key words**: Conservation management, Mesopredator release effect, *Rattus rattus*, *Felis silvestris catus*, *Puffinus yelkouan*, Seabirds.

## Introduction

Alien species are now recognized as one of the greatest threats to biodiversity worldwide (Vitousek, Loope & Adersen, 1997; Chapin *et al.*, 2000) and the principal threat to island biota (Williamson, 1996; Whittaker, 2007). Indeed alien mammals, especially predators, have had particularly severe effects on native island fauna, being responsible for several extirpations and extinctions of mammals, birds and reptiles (Courchamp, Chapuis & Pascal, 2003; Donlan & Wilcox, 2008). This is particularly true for domestic cats (*Felis silvestris catus*), which have been associated with humans since 9500 B.P. (Vigne *et al.*, 2004), following them to most of the world's islands, where they generally succeed in establishing feral populations (Courchamp *et al.*, 2003). Feral cats are adaptable and opportunistic predators preying on native and endemic species, but also on introduced and commensal species, like rodents (Turner & Bateson, 2000; Twyford *et al.*, 2000). The feral cat is recognized as one of the most detrimental alien predators for seabirds on islands (Moors & Atkinson, 1984; Blackburn *et al.*, 2004), particularly for petrel and shearwater species, which are often naïve and clumsy when on the ground (Mayol-Serra, Aguilar & Yésou, 2000; Ainley *et al.*, 2001; Keitt *et al.*, 2002; Martínez-Gómez & Jacobsen, 2004).

Over the past decades, conservation practitioners have developed efficient techniques and methodologies to control and remove non-native mammals on islands, providing a powerful conservation tool for endangered native species. Thus, several islands have been successfully freed from their feral cat populations (Nogales, Martin & Bernier, 2004 ; Aguirre-Munoz *et al.*, 2008; Hughes, Martin & Reynolds, 2008) with generally rapid positive effects on native biodiversity, especially with respect to seabirds (Veitch, 1985; Cooper *et al.*, 1995; Côté & Sutherland, 1997; Bester *et al.*, 2002; Keitt & Tershy, 2003; Ratcliffe *et al.*, 2009). However, some recent studies have pointed out the risk that when native species are the shared preys of several introduced predators (namely cats and rats), the removal of the introduced top-predator (cat) could possibly result in the expansion of the introduced mesopredator (rat) population (Zavaleta, Hobbs & Mooney, 2001), while rats are known to be highly detrimental for native species (Martin, Thibault & Bretagnolle, 2000; Howald *et al.*, 2007; Jones *et al.* 2008). The ecological release of the introduced mesopredator and the subsequent increase in impact on the native prey has been termed "the mesopredator release effect" (MRE) (Courchamp, Langlais & Sugihara, 1999; Zavaleta *et al.*, 2001; Elmhagen & Rushton, 2007). It would suggest that for intraguild predators, the top-predator may protect the shared prey from mesopredation, and therefore removal of top-predators alone would not be advisable (Polis & Holt, 1992; Courchamp *et al.*, 1999).

Unfortunately, MRE has mostly been investigated through pure theoretical modeling approaches and there is, to the best of our knowledge, little few convincing field evidence that such detrimental cascading effects are likely to occur after cats are removed from islands (but see Rayner *et al.*, 2007; Bergstrom *et al.*, 2009). Moreover, in the case of petrels, which are long-lived species living in age-structured populations, top-predators and mesopredators do not necessarily impact the same life-stages, which greatly complicates the prediction of a putative MRE (Le Corre, 2008; Russell *et al.*, 2009). Indeed for burrowing shearwaters, cats are likely to mainly affect the adult breeding stage (survival rate) while rats, which enter the breeding burrows, mainly impact eggs and young chicks (reproductive success). Seabirds, which have long lifespans and low reproductive rates, are generally very sensitive to changes in adult survival but less sensitive to a decrease in their reproduction rates. This may suggest that the negative impact of a possible burst in mesopredator populations is likely to be largely compensated for by the strong positive effect of top-predator control.

On Port-Cros Island, previous studies had shown that (i) cats consumed a large number of introduced rats (0.950 rat preyed day$^{-1*}$cat$^{-1}$ corresponding to 7000 rats preyed year$^{-1}$ *cat population$^{-1}$, see Bonnaud *et al.*, 2007) and preyed upon the yelkouan shearwater, a protected and endemic long-lived Mediterranean seabird and (ii) before cat control, cat predation on shearwaters was strong (0.059 shearwater preyed day$^{-1*}$cat$^{-1}$ corresponding to 431 shearwaters preyed year$^{-1}$ *cat population$^{-1}$, Bonnaud *et al.*, 2007), recurrent year after year and occurring throughout the shearwater breeding cycle (Bonnaud *et al.*, 2009). Due to the strong cat predation on rats and the apparent unlimited resources for rats represented by the large amount of acorns produced by the oak forest of the studied site, we hypothesized a top-down system, as defined by Russell *et al.* (2009). In this case MRE can occur but even if a burst of rat population appears on Port-Cros Island we argue that rat impact on the yelkouan shearwater will be less detrimental than those of cats (Le Corre, 2008; Russell *et al.*, 2009).

The aims of this study were (i) to document a campaign of feral cat control conducted on a small Mediterranean island to prevent endemic shearwater extinction, while maintaining a neutered domestic cat population for the inhabitants, (ii) to study the diet and the impacts of the remaining cats (iii) to evaluate the effects of cat control on the population dynamics and the breeding parameters of the former prey, the endemic yelkouan shearwater (*Puffinus yelkouan*) and (iv) to investigate possible changes in abundance and/or behaviour of introduced ship rats (*Rattus rattus*) following cat control.

## Materials and Methods

### *Study site*

This study was conducted on Port-Cros Island (6.40 km²), protected by National Park status since 1963 and located in the north-western Mediterranean Sea (43°00'N, 6°21'E). This hilly island has a maximum elevation of 196 m above sea level and is 15 km from the mainland. Climate is sub-humid, temperate Mediterranean with an average annual rainfall of 582.4 mm and an average annual temperature of 16.5°C (Levant Island Meteorological Office, 1997–2007). This siliceous island is 80% covered by mixed forests of the sclerophyllous oaks *Quercus ilex* and *Q. suber* and the pine *Pinus halepensis*. Port-Cros Island has long been home to introduced vertebrates, especially cats (for 2 centuries; Pasqualini, 1995) and rats (at least since Roman period, Cheylan, 1984), and a Mediterranean endemic seabird of particular conservation interest, the yelkouan shearwater.

### *Cat control*

The huge amount of bird killed per year constituted a permanent threat to this shearwater population being reduced to a very low number of individuals (only 180 breeding pairs). Despite the apparent stability of the breeding population, the risk of population extinction and its vulnerability to environmental stochasticity was high (Jones, 2002). Thus, a cat population management campaign was conducted on Port-Cros Island from January 2004.

Due to the presence of inhabitants and therefore of domestic cats, the removal of feral cats was undertaken using only non-lethal methods and complete cat eradication was not possible. The trapping campaign was initially concentrated near the shearwater colonies to catch feral cats visiting shearwater breeding sites, and then extended along all island paths, especially where cat scats were found. A sterilization campaign was simultaneously conducted on the domestic cats and all new domestic cats arriving were checked for sterilization.

### *Feral cat diet and monitoring of cat impact*

The diet of feral cats was studied through scat analysis (Konecny, 1987; Fitzgerald *et al.*, 1991; Clevenger, 1995). Scats were opportunistically collected from October 2003 to August 2008 on the same paths of the island and localised by GPS (Global Positioning System). Since all scats found in the field were removed and very old ones excluded, we assumed that each sampling set represented the diet of feral cats for the two previous months. Scats of cats were dissected, and the contents separated into prey categories. Scats were analysed by washing over a 0.5-mm sieve, separating and determining all items such as hairs, feathers, bone fragments, teeth, and insect chitin (Nogales *et al.*, 1988; Furet, 1989). To detect any change in prey consumption by cats, before and after cat control a pearson $\chi^2$ test for independent samples was used to compare the two periods, and then randomisation tests were used to compare each prey consumption, since they allow the comparison of even very small percentages (PD = observed percentage differences; Manly, 1997). We reported the number of scats removed for each sampling period (a total of 30 sampling periods during the nearly 5-year study) and a Mann-Whitney U test was run to compare the number of cat scats removed before and after cat control. Then the extent of cat predation on the yelkouan shearwater population was determined for each sampling period. This representative sample allowed us to compare cat predation patterns with the shearwater breeding phases for several annual cycles. Since no identical remains from two or more yelkouan shearwaters were found in the same scat, all shearwater remains found in one single scat were assumed to belong to one single bird. This assumption is supported by the fact that even if a cat eats only 50% of a yelkouan shearwater in weight (432g), leaving behind wings, feathers and head (Cuthbert, 2002; Keitt *et al.*, 2002), this prey supplies it with enough food for one day (mean daily biomass consumed by a Port-Cros feral cat = 201g; Bonnaud *et al.*, 2007).

### *Monitoring of shearwater and rat populations*

A set of 100 cavities suitable for shearwater breeding was monitored on colonies on Port-Cros Island during six consecutive breeding seasons (2003 to 2008) to measure the percentage of occupied cavities and the breeding success of the yelkouan shearwater. Yelkouan shearwaters, like most of seabirds, have low reproductive dynamics: they start breeding around 6 years, generally first attempts of breeding fail and they produce only one egg per year (e.g. Brooke, 1990). They arrive at their breeding sites in late October or early November (Vidal, 1985; Zotier, 1997), which corresponds to the prospecting period. Egg laying is from mid-March to early April, hatching in May and fledging in July and early August. A miniature infrared camera placed on a stiff coaxial was "snaked" down each cavity to determine the presence of pairs, eggs or chicks (Bourgeois & Vidal, 2007). Cavities were checked nine times during each breeding season (end of the pre-laying period, start, mid and end of the laying and hatching periods, 15 days before the beginning and at mid-fledging period). A last check was done at the end of the breeding season to find possible corpses and confirm chick fledging (Bourgeois, 2006). Randomisation test was used to compare the percent of occupied cavity between the first year (2003) and the last year (2008) of our census. Then, added to the present data set, older data on shearwater breeding success from previous studies conducted when the cat population was not controlled (Vidal, 1985; Zotier, 1997). Finally, we compared the data for cat predation on shearwaters, before and after cat control, by running a Mann-Whitney U test.

Even if no clear evidence of rat impact on the shearwater population before the beginning of the cat control, the high probability of a top-down ecosystem coupled with the harmful effect of rats on native species (e.g. Jones *et al.*, 2008) required rat population survey. The rat population was monitored by setting two lines of 30 traps in two different areas of the island. We used live traps set every 10 meters during four consecutive nights, for 19 trapping sessions spread from December 2004 to August 2008 at three or four months intervals. To compare trends in rat population demography before and after cat control, we used data on rat trapping success from previous studies before cat control (Granjon & Cheylan, 1993) and we ran a Mann-Whitney U test.

### *Monitoring of interactions between rats and shearwaters*

Interactions between rats and shearwaters at breeding cavities (patterns of rat visits) were investigated in the largest yelkouan shearwater colony of Port-Cros Island during (2004-2005) and after (2007-2008) cat control. Breeding cavities (n = 25 in 2004-2005, n = 23 in 2007-2008) were checked for rat visits 24 times throughout the breeding cycle of shearwaters and subsequent interbreeding exodus (6 breeding periods: prospecting, mating, egg-laying, hatching, fledging and interbreeding; and 4 consecutive survey nights). Rat visits to each cavity entrance were recorded through tracks printed in fine sand and droppings and hairs found inside cavities (Ruffino *et al.*, 2008). Results were analysed as frequencies of rat visits ($f_r$) as follows $f_r = n_r/(n_p n_c n_n)$, where $n_r$ is the number of rat visits to cavities, $n_p$ the number of periods monitored ($n_p = 6$), $n_c$ the number of cavities monitored ($n_c = 25$ or 23) and $n_n$ the number of nights monitored ($n_n = 4$). A Pearson $\chi^2$ test for independent samples was used to test the difference in frequency of rat visits to cavities from year to year.

## Results

### *Cat control*

Cat control started in January 2004, giving a total of 28 feral cats trapped over two full years. A substantial trapping-campaign was conducted, mainly during the first two trapping sessions (January–April 2004 and September–December 2004) (Fig. 1a). Then, trapping success progressively decreased, becoming nil by January 2006 despite regular new trapping sessions over the last three years. We consider that cat control was complete in August 2005 because the last two cats were caught near the village and were very young. Subsequently, only neutered domestic cats were seen wandering outside the village and were photographed by trail cameras placed near paths. Moreover, no sign of recovery of the cat population was observed, indicating that even if a few feral cats remained on the island this population was too small to reproduce.

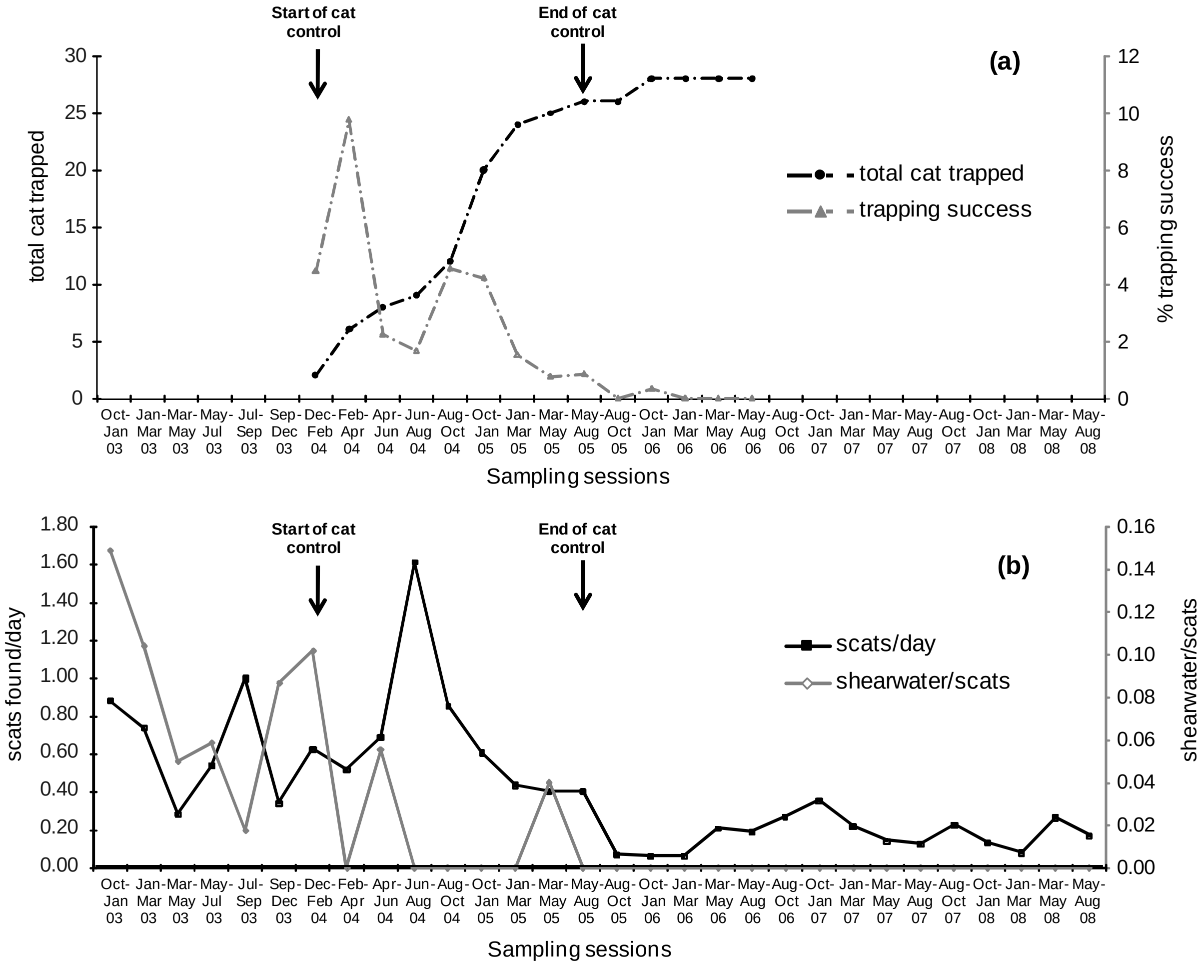


Fig. 1: (a) Cat-trapping success during the feral cat eradication and the cumulated number of cats trapped (b) Monitoring of scats collected on the paths of Port-Cros Island and number of shearwaters found per scat over five years of shearwater breeding cycle.

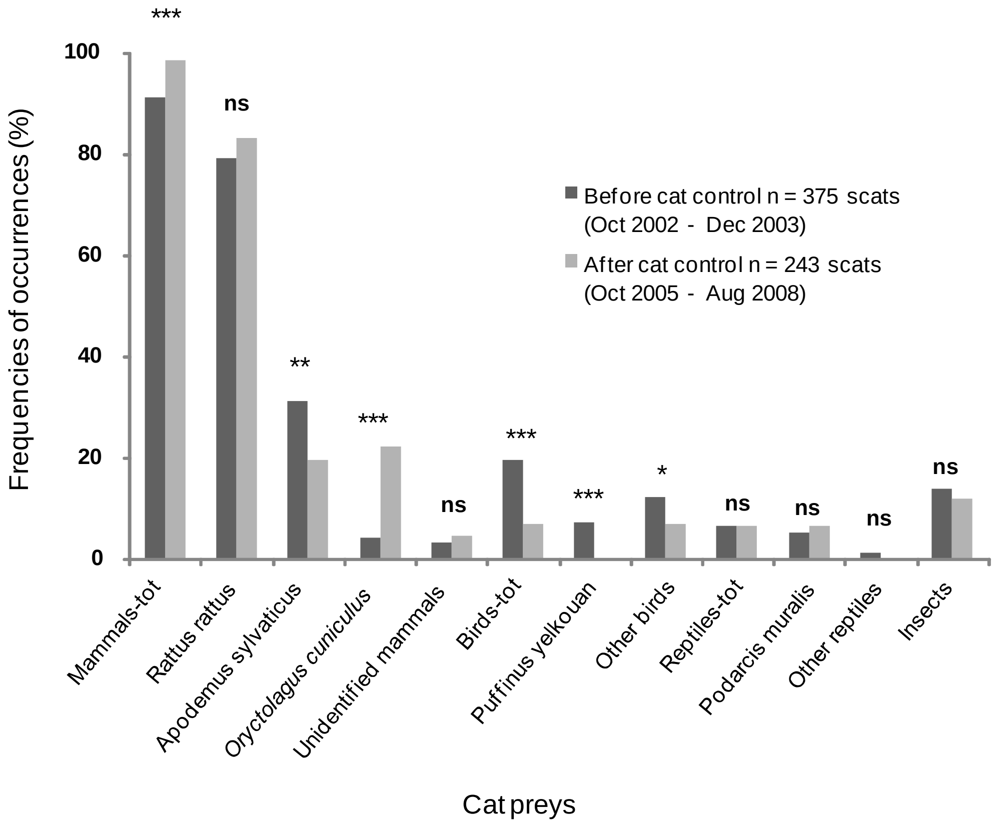
### *Feral cat diet and monitoring of cat impact*

The feral cats of Port-Cros Island preyed mainly on introduced mammals, rats being heavily preyed contrary to rabbits, and birds were secondary preys.

The diet of feral cats showed different patterns before (October 2002 to December 2003) and after (October 2005 to August 2008) cat control ($\chi^2 = 76$, $p < 0.001$). After cat control, consumption of all the introduced mammals increased, except for the *Apodemus sylvaticus*, these percentage differences being significant except for the rat and the unidentified mammals (Fig. 2a, b). Conversely, total bird consumption decreased, becoming nil for the yelkouan shearwater; these percentage differences were significant. No significant differences in prey consumption were found for reptiles and insects.

The number of scats found on sampling paths decreased from before to after cat control (respectively 0.631 ± 0.119 scats/day and 0.177 ± 0.022 scats/day; $U = 2$, $p < 0.001$). Peaks in predation on yelkouan shearwaters occurred during autumn and winter (October–November and December–February), corresponding to the prospecting period of these seabirds (Fig. 1b). After August 2005, no shearwater remains were found in cat scats and from August 2004 to August 2005 only 1 scat (May 2005) containing shearwater remains was found.

(a)



(b)

| | Mammals-tot | Rattus rattus | Apodemus sylvaticus | Orytctolagus cuniculus | Unidentified mammals | Birds-tot | Puffinus yelkouan | Other birds | Reptiles-tot | Podarcis muralis | Other Reptiles | Insectes |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PD = observed percentage differences | 0.053 | 0.075 | -0.130 | 0.128 | 0.029 | -0.054 | -0.047 | -0.050 | 0.005 | 0.016 | -0.011 | 0.030 |
| p values | 0.001 | 0.003 | <0.001 | <0.001 | 0.011 | 0.014 | <0.001 | 0.004 | 0.419 | 0.201 | 0.099 | 0.114 |

Fig. 2: (a) Diet of feral cat expressed in frequencies of occurrences before and after cat control, (b) results of the diet comparison before and after cat control using randomization tests, percentage difference and p-values are indicated.

### *Monitoring of shearwater and rat populations*

During previous monitoring (Vidal, 1985; Zotier, 1997), shearwater breeding parameters varied strongly with a decrease in 1984 (means of hatching success: 0.721 ± 0.065, fledging success: 0.806 ± 0.148 and breeding success 0.608 ± 0.141) (Fig. 3a). From 2003 to 2008 breeding parameters were high with low variations (means of hatching success: 0.849 ± 0.043, fledging success: 0.901 ± 0.021 and breeding success 0.763 ± 0.034). Between the periods before (previous studies and data from our shearwater monitoring: 2003) and after (our shearwater monitoring: 2006-2008) cat control there were no statistical differences when comparing hatching success (before and after cat control; U = 2, p = 0.101) fledging success (before and after cat control; U = 5, p = 0.453) and breeding success (before and after cat control; U = 4, p = 0.294). The percentage of occupied cavities (data only available from 2003 to 2008) was 35.7% ± 2.1 on average and increasing: 22.7% at the beginning (2003) and 38.8% the end (2008) of the study, this increase being significant (PD = 0.185, p < 0.001). The number of pairs of shearwaters was low during the previous monitoring (but these monitoring were not exhaustive), whereas our shearwater monitoring showed that the number of pairs increased by more than 40% (Fig. 3b). The number of breeding shearwaters and the percentage of occupied cavities on the monitoring colonies showed a maximum increase just after the first year of cat control.

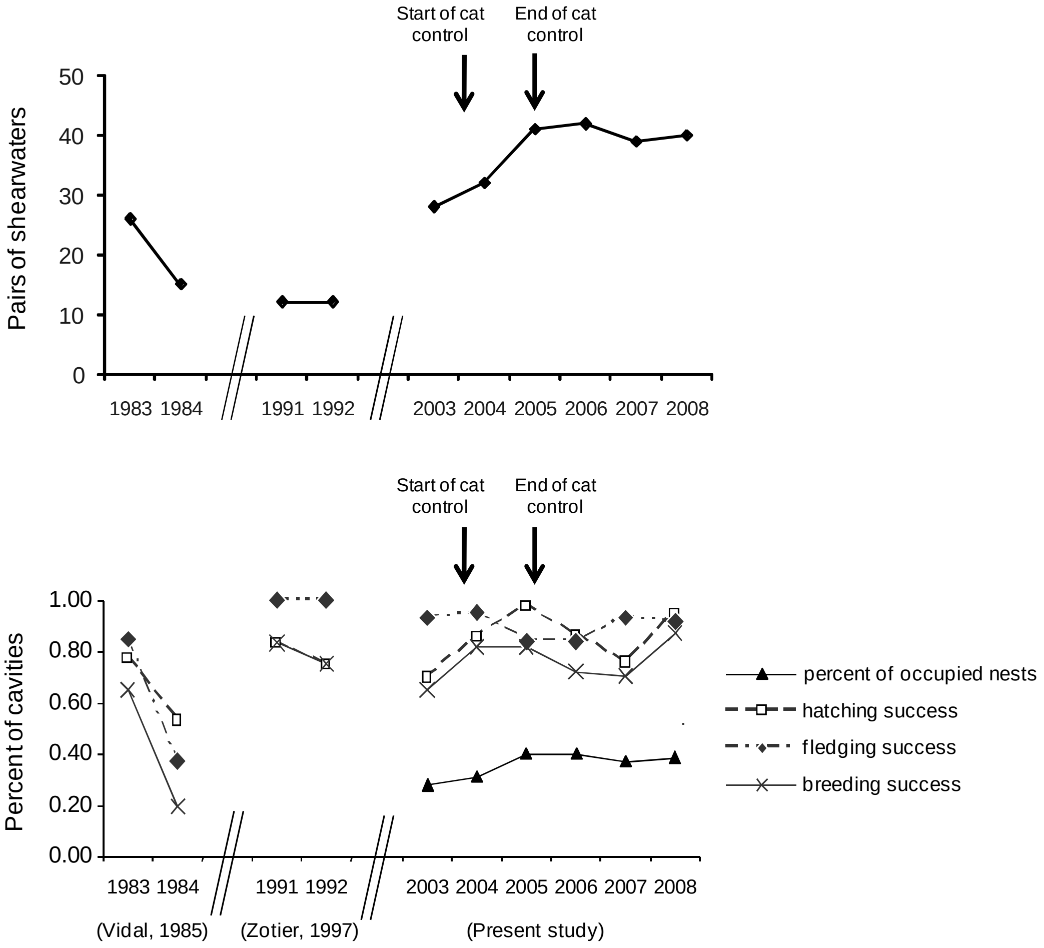


Fig. 3: Monitoring of yelkouan shearwater population (a) number of pairs of shearwaters, (b) trends of the different parameters of shearwater breeding success (1983 and 1984 data collected by Vidal (1985)).

Rat trapping success on sampling lines varied according to season and year but remained low during both previous studies and our monitoring (Fig. 4). From December 2004, peaks of rat trapping success appeared during spring and summer (except for 2005 and 2008) always followed by a significant decrease during autumn and winter. A slight increase in rat trapping success was noted after cat control began ($r^2 = 0.107$, $F = 3.149$, $p = 0.094$). Rat trapping success fluctuated over a range of value that was largely the same before (data from Granjon & Cheylan, 1993; min: 0, max: 0.220, mean: 0.068 ± 0.024 rat caught per trap-night) and after (October 2005 to August 2008; min: 0.013 max: 0.354 mean: 0.112 ± 0.026 rat caught per trap-night) cat control with non-statistical differences ($U = 44$, $p = 0.231$).

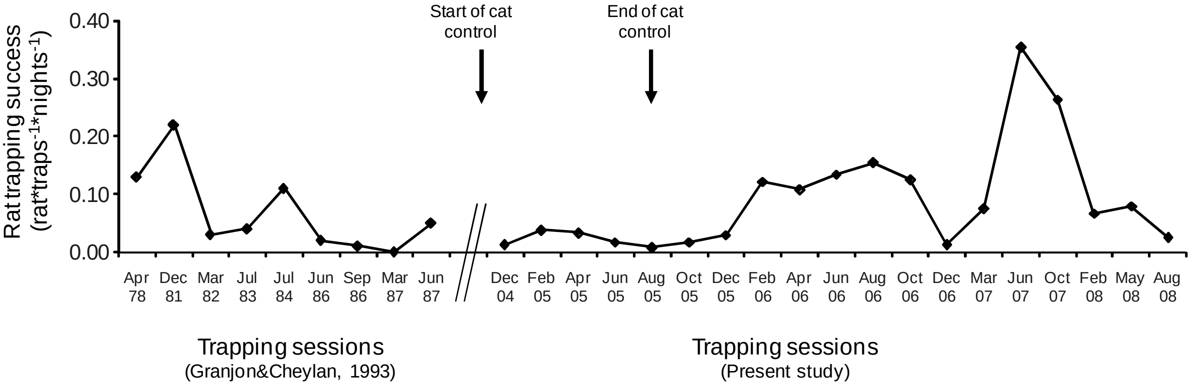


Fig. 4: Trends in rat-trapping success on Port-Cros Island, without cat control (1978-1987; Granjon & Cheylan 1993) and following feral cat eradication (2005-2008; this study).

### *Monitoring of interactions between rats and shearwaters*

The mean frequency of rat visits to shearwater breeding cavities was low in 2004-2005 ($f_r = 0.008$) and significantly increased in 2007-2008 after cat control ($f_r = 0.217$, Pearson $\chi^2 = 70$, $p < 0.001$) (Fig. 5). During the three periods of egg and chick vulnerability to rats (laying, hatching and fledging periods), only one breeding cavity (4%, n = 25 cavities monitored) was visited by rats during cat control, whereas 87% of breeding cavities (n = 23) were visited by rats at least once after cat control. During these periods, the mean frequency of rat visits to breeding cavities was significantly lower during control ($f_r = 0.003$) than after control ($f_r = 0.156$, Yates cor. Pearson $\chi^2 = 30.1$, $p < 0.001$). Six cavities (25%) exhibited breeding failure during cat control and four (17%) after cat control. In both years, no case could be conclusively attributed to rat predation, and cavities where breeding failed did not show a higher visit rate than cavities where breeding was a success, neither throughout the breeding cycle during control ($f_{r(\text{success})} = 0.002$, $f_{r(\text{failure})} = 0$) and after control ($f_{r(\text{success})} = 0.219$, $\mathrm{f}_{r(\text{failure})} = 0.208$) or during the three periods of egg and chick maximum vulnerability during control ($f_{r(\text{success})} = 0.004$, $f_{r(\text{failure})} = 0$) and after control ($f_{r(\text{success})} = 0.487$, $f_{r(\text{failure})} = 0.375$).

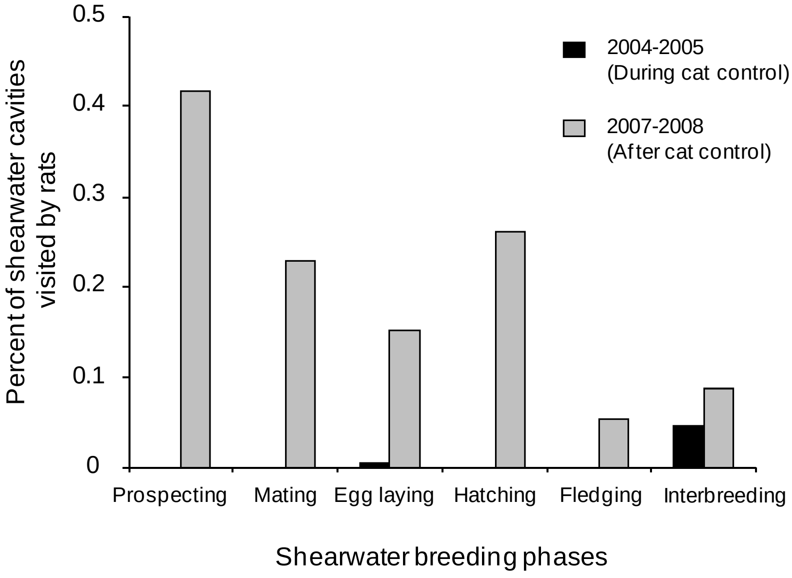


Fig. 5: Percentage of shearwater cavities visited by rats according to the different stages in the shearwater breeding cycle.

## Discussion

### *Cat control*

This feral cat management campaign was, to the best of our knowledge, one of the first conducted in the Mediterranean basin (Genovesi, 2005; Lorvelec & Pascal, 2005) and one of the few successfully developed (i) using only non-lethal trapping and (ii) conserving a domestic population of neutered pet cats on the island (Nogales *et al.*, 2004). Usually it is better to eradicate because eradication leads to permanent, more effective results and often at lower cost than control (Veitch, 1985; Bester *et al.*, 2002; Veitch & Clout, 2002; Rodríguez, Torres & Drummond, 2006). Moreover, only few cats can threatened a native population of seabirds (Keitt *et al.*, 2002; Peck *et al.*, 2007).

However in our case, where total eradication was not possible due to the presence of a domestic cat population, non-lethal trapping proved to be successful in eradicating feral cat populations and rapidly preventing cat predation on a native species, here the endemic yelkouan shearwater. No feral cats were observed or trapped on the island for the two following years (from August 2006 to August 2008), despite a reduced but continuous trapping-campaign, which provides conclusive proof of cat control success on Port-Cros Island (Copson & Whinam, 2001; Bester *et al.*, 2002).

### *Feral cat diet and monitoring of cat impact*

The analysis of cat scats shows that these predators prey mainly upon introduced mammals especially on black rat (nearly 80% frequencies of occurrences in the cat diet, Bonnaud *et al.*, 2007), and much less on rabbit due to its low abundance on the island. Thus, black rat was the staple prey of cats providing an abundant and easy food resource that probably increased the feral cat survival rate and claimed for a top-down process (Ritchie & Johnson, 2009). Simultaneously, this top-predator threatened other prey species like native seabirds, reptiles and insects.

The yelkouan shearwater, an endemic seabird of the Mediterranean basin, was the bird most preyed upon by cats. This strong predation, calculated to more than 400 birds per year (Bonnaud *et al.*, 2007; Bonnaud *et al.*, 2009), occurred especially during the prospecting period (late autumn and winter). Thus, cat predation was responsible for high predation pressure on prospecting shearwaters, limiting the settlement of potential new breeders (Cuthbert, Fletcher & Davis, 2001; Keitt *et al.*, 2002, Martinez-Gomez & Jacobsen, 2003; Bonnaud *et al.*, 2009). The diet of the remaining cats after cat control showed that the last cats consumed more introduced mammals and fewer birds than before cat control, suggesting that the cats caught first were better able to prey upon native preys, especially on birds. Indeed, cat predation on the yelkouan shearwater quickly decreased when trapping was selectively conducted around shearwater colonies, suggesting that the first cat caught might have a selective predatory behaviour focused on a specific resource, here yelkouan shearwaters. The absence of cat predation on this seabird for the past two years despite a remaining cat population (i) supports the hypothesis that some cats have a specialised predatory behaviour and (ii) confirms that most of the predation impact can be effectively removed when traps are set in selective areas.

Before cat control, cat scats were commonly found along all the island paths and on shearwater colonies. The number of scats found clearly decreased after cat control, indicating that the feral cat population was reduced to a very low number of individuals. Scat monitoring appears to be an accurate and easy field indicator of the overall trend of cat population dynamics. Regular monitoring of cat scats on paths is still being conducted on the island to detect any recovery of the cat population (Twyford *et al.*, 2000; Veitch, 2000). With respect to the last two years of the cat monitoring, it seems that the feral cat population has remained at low density, probably too low to mate (Rauzon *et al.*, 2008). Moreover the few scats recently found on the island probably belong to the domestic cats that sometimes wander outside the village and have already been caught several times in traps. This hypothesis is reinforced by the fact that no feral cat was caught after October 2005.

### *Monitoring of shearwater and rat populations*

The overall monitoring conducted during previous monitoring and this study showed that the values of the shearwater breeding parameters were high for this population (except for one “accidental” year in 1984) when compared with other related species (*Puffinus tenuirostris*: Serventy & Curry, 1983; *Puffinus auricularis newelli*: David *et al.*, 2001; *Puffinus pacificus*: Dunlop *et al.*, 2002). This seabird breeding population seems to be composed of “experimented” pairs breeding inside those cavities, which are deepest and less accessible to predators, thus ensuring a high degree of breeding success (Bourgeois & Vidal, 2007). This means that most of these birds can escape feral cat predation and survive despite several decades of predation pressure. However, the very small size of the yelkouan shearwater population (180 breeding pairs) on Port-Cros Island despite an available and suitable habitat and abundant marine food resources may indicate a possible relictual stage, and a current risk of extirpation.

Feral cat control, which mainly resulted in the rapid increase in numbers both of occupied cavities and of breeding pairs on the colonies studied, confirmed that cat predation, being mainly concentrated on the prospecting period, probably limits the recruitment of young breeders by focusing on prospecting birds (Keitt *et al.*, 2002; Massaro & Blair, 2003; Peck *et al.*, 2007). Indeed, prospecting birds are considered to be more vulnerable to cat predation due to their behaviour: wandering on the ground, cooing and calling outside burrows to find a partner, rather than entering the burrow rapidly after landing (Storey, 1984; James, 1985; Brooke, 1990; Bretagnolle, Genevois & Mougeot, 1998; Ristow, 1998; Bourgeois *et al.*, 2008; Bonnaud *et al.*, 2009). Thus, feral cat control on this island boosted shearwater population dynamics, especially since new breeders were able to settle, while the shearwater population of Port-Cros Island had been stable for over 20 years (Vidal, 1985; IMEP, unpublished data).

Rat-trapping success on Port-Cros Island remained moderate before and after cat control, compared to data from other studies (Blackwell *et al.*, 2003) and despite cyclic variations in rat population dynamics (Alterio, Moller & Brown, 1999; Blackwell, Potter & Minot, 2001). Even though a transient increase in rat-trapping success appeared a couple of years after the beginning of cat eradication, essentially due to an exceptional increase during summer 2007, rat-trapping success values were similar to previous values already recorded on the island before cat control (Granjon & Cheylan, 1993). This suggests that cat control, while diminishing predation pressure on rats, has not led to a significant increase in the rat population. Despite the top-down process exerted by high cat predation on rats, these results showed that rat population on Port-Cros Island seems to be controlled also by a bottom-up process (Russell *et al.*, 2009). Even if oak acorns represent a food resource for rats, their nutritive value appeared low and the scarcity of water, especially during the summer season, lead to limit the extend of this rat population (articles de Granjon et Chelyan).

***Monitoring of interactions between rats and shearwaters***

Despite the significant increase in interaction rates between rats and shearwaters, when rats visit breeding cavities, no breeding failure could be attributed to rat predation (no mark of rat teeth or claws on eggs). Moreover, the high values of shearwater breeding parameters showed that rat impact on shearwater breeding success was insignificant. Even if rat impact on yelkouan shearwater was not clearly demonstrated before cat control, as (i) rats were proven to be highly detrimental for seabird survival (e.g. Jones *et al.*, 2007) and (ii) interactions between rats and shearwater increased, the risk of rat predation on shearwaters was high. Thus, this study confirms that cat management does not automatically lead to a MRE (Cooper *et al.*, 1995; Girardet, Veitch & Craig, 2000, Ratcliffe *et al.*, 2009), especially when mesopredators are regulated by a bottom-up process and can access to an alternative food resource different than seabirds. Moreover, rat impact on seabirds is much lower than cat impact (Lecomte, 2007; Le Corre, 2008), contrary to what was asserted by Rayner *et al.* 2007. Despite potential rat predation on seabirds, mainly focused on eggs and chicks, it is cat predation on seabirds, mainly focused on adults, which is much more detrimental to the seabird population growth rate (Le Corre, 2008; Russell *et al.*, 2009). Thus, cat management is highly advantageous for seabird population dynamics. As rat predation is still a threat for seabirds (Jouventin, Bried & Micol, 2003; Towns, Atkinson & Daugherty, 2006; Caut *et al.*, 2007, Jones *et al.*, 2008), continuous monitoring of rat populations and their impact on native populations is advisable (Nogales *et al.*, 2004; Russell *et al.*, 2009).

## Implication for conservation

In multi-invaded islands housing both introduced predators and native preys, it is commonly admitted that the best solution is the simultaneous eradication of introduced top and mesopredators to avoid any risk of MRE (Bell, 1989; Simberloff, 2001; Zavaleta *et al.*, 2001; Courchamp *et al.*, 2003; Blackburn, 2008). When simultaneous eradications are not feasible, some studies have indicated that MRE can be more detrimental for native species (Pontier *et al.*, 2002; Zavaleta, 2002; Rayner *et al.*, 2007), but the level of risk varies depending on the species and species interactions considered (Le Corre, 2008; Russell *et al.*, 2009). When long-lived seabirds are threatened by introduced predators, top-predators like cats have more detrimental effects on these seabird population dynamics. Moreover, top-predator populations are not the only means of regulating mesopredator populations (Blackwell *et al.*, 2003). While “bursts” in mesopredator populations can appear after top-predator removal (Rayner *et al.*, 2007; Bergstrom *et al.*, 2009), several other factors can interact (self-regulation of mesopredator populations, lack of resources, disease), potentially leading to a regulation in mesopredator populations.

However, when even top-predator eradication is not feasible, this study shows that a control strategy, at first substantial and focused on specific areas and subsequently reduced and spread over the whole island, can lead to the same results as total eradication while avoiding any risk of a MRE. As Intraguild predation is complex and often multiple trophic interactions have to be taken into account (top-down or bottom up processes) (Fukami *et al.* 2006; Elmhagen & Rushton, 2007; Ritchie & Johnson, 2009), each management action should be planned after a full review of the main biotic interactions occurring in the ecosystem considered, so as to optimise native species conservation (Zavaleta, 2002; Bonnaud *et al.*, 2009, Russell *et al.*, 2009).

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# ANNEXE 2.

**Capture-recapture data and rainfall** (**Partie 4.3.**).

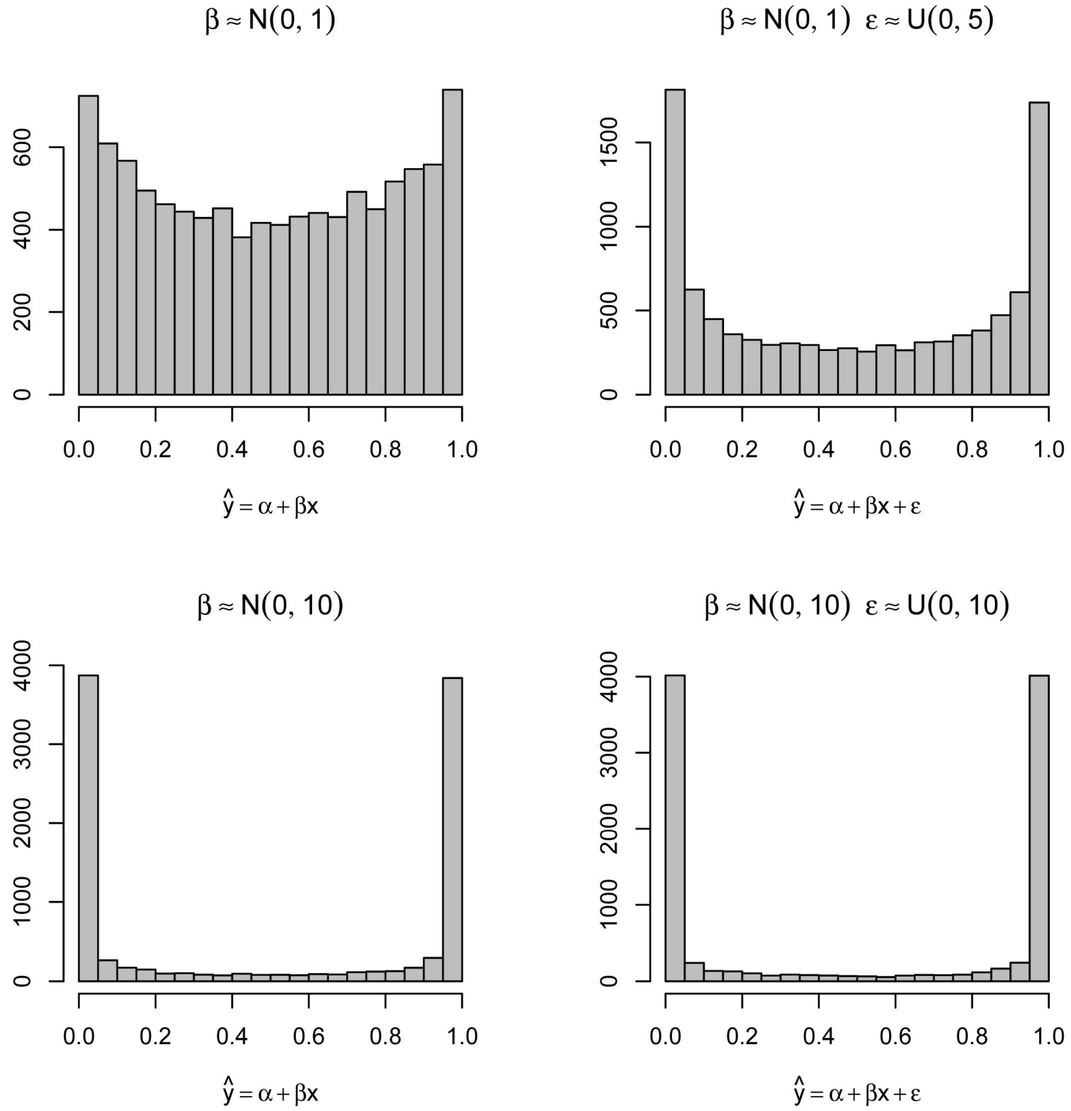
Session dates, monthly and session weighted rainfall (courtesy of Levant Island Meteorological Office), time $t_i$ since start of last session, number of individuals captured $n_i$, and the total number of marked individuals $M_{i+1}$

| Year | Month | Rainfall | Weighted Rainfall | Session | $t_i$ | $n_i$ | $M_{i+1}$ |
|---|---|---|---|---|---|---|---|
| 2007 | Apr | 12.6 | 12.6 | 1 | 0 | 53 | 53 |
| | May | 128.0 | 128.0 | 2 | 26 | 13 | 61 |
| | Jun | 2.2 | 2.2 | 3 | 36 | 60 | 114 |
| | Jul | 1.0 | 1.0 | 4 | 34 | 54 | 149 |
| | Aug | 10.2 | 10.2 | 5 | 39 | 34 | 159 |
| | Sep | 2.4 | 13.4 | 6 | 55 | 38 | 169 |
| | Oct | 24.4 | | | | | |
| | Nov | 78.6 | 53.5 | 7 | 54 | 40 | 183 |
| | Dec | 28.4 | | | | | |
| 2008 | Jan | 91.2 | 91.2 | 8 | 48 | 43 | 196 |
| | Feb | 8.0 | 38.9 | 9 | 86 | 35 | 208 |
| | Mar | 52.4 | | | | | |
| | Apr | 56.2 | | | | | |
| | May | 46.0 | 45.8 | 10 | 42 | 42 | 238 |
| | Jun | 45.6 | | | | | |
| | Jul | 1.2 | 1.2 | 11 | 43 | 106 | 321 |
| | Aug | 1.0 | 1.0 | 12 | 42 | 49 | 334 |
| | Sep | 35.4 | 46.6 | 13 | 40 | 35 | 340 |
| | Oct | 57.8 | | | | | |
| | Nov | 188.4 | 173.2 | 14 | 112 | 91 | 395 |
| | Dec | 220.4 | | | | | |
| 2009 | Jan | 110.8 | | | | | |

# ANNEXE 3.

## Influence of covariate priors on logistic models.

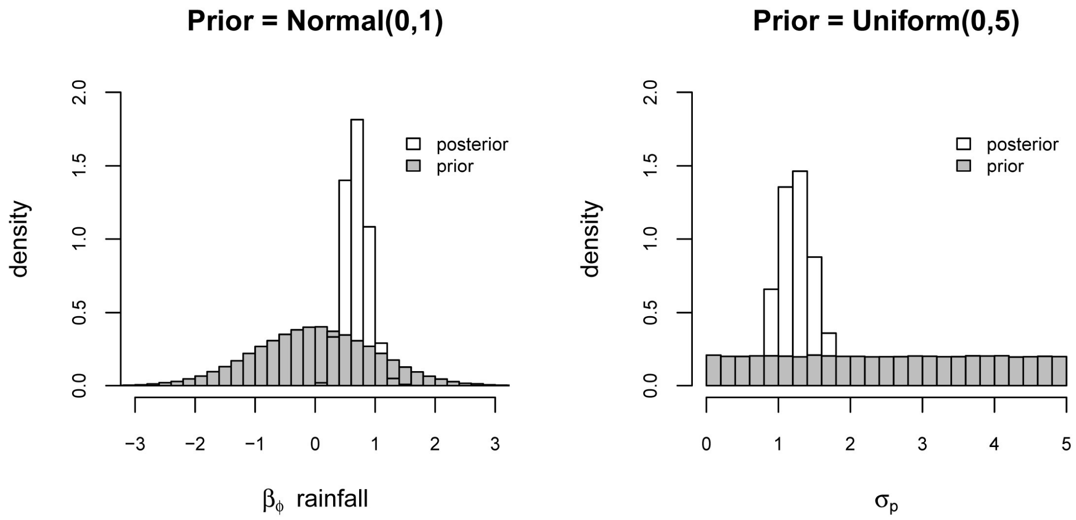
Perceivably uninformed priors on logistic model fixed and random effects can have substantial influence on the prior distribution of the modelled response variable ( $\hat{y}$ ) despite the prior on the baseline (y) being Uniform(0,1). Simulations are for $n$ = 10,000 draws on a binary predictor variable (x = 1) where $\alpha = \log\left(\frac{y}{1-y}\right)$ (see Van Dongen 2006 for further discussion).



# ANNEXE 4.

## Prior and posterior distributions for $\beta_{rainfall}$ and $\sigma_p$.

Estimated posterior distributions for the *log*(rainfall) fixed effect on survival and the random effect on capture probability.



# ANNEXE 5.

## WinBUGS code for Bagaud Island model.

```
model {

# James Russell (jrussell@berkeley.edu)

# nsess = 14, nind = 395, nstate = 3

# data are X[ij], A[ij], H[ij], S[i],

#    rain.weight[j], first[i], btw[j]



# priors for time dependent p and phi

for (j in 1:(nsess-2)) {

  p[j]~dbeta(1,1)

  lp[j]<-log(p[j]/(1-p[j]))

  phi.month[j]~dbeta(1,1)



  # build in monthly (weighted) rainfall model

  logit(phi.month.model[j]) <- logit(phi.month[j]) +

                                 b.rain*log(rain.weight[j])



  phi[j] <- pow(phi.month.model[j],btw[j]/30)

  lphi[j] <- log(phi[j]/(1-phi[j]))

}

p[nsess-1] ~ dbeta(1,1)

lp[nsess-1] <- log(p[nsess-1]/(1-p[nsess-1]))
```

```
lphi[nsess-1] <- 0

for (i in 1:2) { # 1 = p, 2 = phi
  b.sex[i] ~ dnorm(0,1)
  b.age[i] ~ dnorm(0,1)
  # fixed effect for each habitat (relative to habitat two)
  b.hab[i,1] ~ dnorm(0,1)
  b.hab[i,2] <- 0
  b.hab[i,3] ~ dnorm(0,1)
}
  b.rain ~ dnorm(0,1)

# random effect
  sigma ~ dunif(0,5)
  tau <- 1/(sigma*sigma)

# transition matrix priors (rows sum to one)
for (i in 1:3) {
  alpha[i] <- 1
  psi[i,1:3] ~ ddirch(alpha[1:3])
}

# determine missing values for habitat
for (i in 1:nind) {
```

```
  for (j in (first[i]+1):nsess) {

    # habitat matrix

    H[i,j] ~ dcat(psi[H[i,j-1],1:nstate])

  }

}



# survival model

for (i in 1:nind) {

  z[i,first[i]] ~ dbern(1)

  # reparamaterise random effect for better mixing

  eta[i] ~ dnorm(0,1)

  for (j in (first[i]+1):nsess) {

    logit(P[i,j-1]) <- lp[j-1] + 1/sqrt(tau)*eta[i] + b.sex[1]*S[i]

                       + b.age[1]*A[i,j-1] + b.hab[1,H[i,j-1]]

    logit(PHI[i,j-1]) <- lphi[j-1] + b.sex[2]*S[i]

                       + b.age[2]*A[i,j-1] + b.hab[2,H[i,j-1]]



    mu2[i,j]<-PHI[i,j-1]*z[i,j-1]

    z[i,j]~dbern(mu2[i,j])

    mu1[i,j]<-P[i,j-1]*z[i,j]

    x[i,j]~dbern(mu1[i,j])

  }

}
```

```
# forcing rest of matrix to stochastic prior

for (i in 1:nind) {

  for (j in 1:(first[i]-1)) {

    z[i,j] ~ dbern(0)

  }

}


# calculate average phi with error propagation

for (k in 1:(nsess-2)) {

  phi.weight[k] <- phi.month.model[k]*btw[k]/30

  n.weight[k] <- btw[k]/30

  }

phi.mean <- sum(phi.weight[1:nsess-2])/sum(n.weight[1:nsess-2])

}
```

# Ecologie, dynamique de population, comportement et impact d’un rongeur introduit, *Rattus rattus*, sur les îles de Méditerranée

## Résumé

Les rats introduits du genre *Rattus* spp. sont reconnus à l’heure actuelle comme un facteur majeur de raréfaction d’espèces d’oiseaux marins et de risque d’extinction de pétrels et de puffins. Cependant, le fonctionnement des populations insulaires de rats ainsi que les facteurs favorisant leurs impacts sur les écosystèmes insulaires restent encore mal connus. Des interrogations persistent sur les mécanismes réels et l’intensité d’impact du rat sur des oiseaux aux mœurs aussi discrètes que certains oiseaux marins. L’idée générale de ce travail de thèse s’inscrit dans la nécessité d’une meilleure compréhension de l’écologie, de la dynamique de population des rongeurs introduits, des mécanismes d’impact du rat sur les oiseaux marins, mais aussi de persistance d’espèces, afin de contribuer à la construction de bases scientifiques solides en vue d’une meilleure évaluation du degré de vulnérabilité des espèces et de la mise en place de stratégies de conservation pertinentes et efficaces. Dans le cadre d’un premier axe de recherche, nous nous sommes intéressés à la dimension temporelle des invasions biologiques. L’analyse d’une base de données concernant *ca*. 300 îles et îlots du bassin méditerranéen occidental a permis de souligner que la persistance sur le long terme des pétrels et puffins de Méditerranée, malgré une présence ancienne des rats noirs sur ces îles, a pu être facilitée par la diversité de contextes insulaires aux caractéristiques biogéograqhiques variées. Dans un second temps, une étude plus fine des mécanismes d’interactions et d’impact a révélé, de manière contre-intuitive, des interactions limitées entre rats noirs et puffins yelkouan au niveau des sites de reproduction des puffins de l’île de Port-Cros (Var), ainsi que des capacités de prédation limitées des rats noirs sur des œufs d’oiseaux marins, même de petite taille. En outre, une synthèse bibliographique des méthodologies employées depuis les 30 dernières années pour évaluer l’impact des rats sur les oiseaux marins appuient l’existence de lacunes dans nos outils, illustrant ainsi la forte nécessité de combiner les sources d’information variées afin d’éviter certains biais méthodologiques qui pourraient contribuer à une mauvaise évaluation de l’impact des rats, et par conséquent du degré de vulnérabilité des espèces. Enfin, l’étude de l’écologie trophique d’une population de rats noirs, combinée à un suivi sur deux années de leurs dynamiques de populations et patrons de déplacements sur une petite île de Méditerranée, présentant une hétérogénéité spatio-temporelle marquée dans la disponibilité des ressources, a permis de souligner la faible plasticité écologique et alimentaire des individus, comparativement à celle de la population entière, ainsi que l’importance des effets des apports hydriques et des ressources d’origine allochtone sur le fonctionnement des populations de rats. Des pistes d’investigations nouvelles sont suggérées qui permettraient de mieux appréhender les processus impliqués dans l’impact des rats sur la faune insulaire, dans les extinctions d’espèces mais aussi dans leur coexistence durable parfois observée.

**Mots clés :** Dynamique de population, écologie trophique, espèces invasives, extinctions, îles méditerranéennes, impact, oiseaux marins, prédation, *Rattus* spp.

# Ecology, population dynamics, behaviour and impact of an invasive rodent, *Rattus rattus*, on Mediterranean islands.

## Abstract

Rats *Rattus* spp. are considered as a main driver of seabird rarefactions and a leading cause of petrel and shearwater extinction risk. However, the functioning of insular rat populations and the factors likely to affect their impacts on island ecosystems are still poorly understood. Indeed, questionings have been recently raised on the real mechanisms and the magnitude of rat impact on some seabirds with so cryptic nesting behaviours. The general idea of this PhD work lies on the necessity to better understand the ecology, the population dynamics of invasive rodents, the mechanisms of rat impact on seabirds but also of species persistence, in order to provide a robust scientific knowledge for a better evaluation of the degree of species vulnerability and designing accurate and efficient conservation strategies. As a first research axis, we were interested in the temporal dimension of biological invasions. The analysis of a database of *ca*. 300 islands and islets from the western Mediterranean basin allowed to underline that the long-term persistence of petrels and shearwaters, despite the longstanding introduction of black rats on these islands, may have been facilitated by various biogeographical contexts. Secondly, the study of the mechanisms of interactions between rats and shearwaters, and more particularly the mechanisms of impact, revealed unexpected limited interactions between black rats and yelkouan shearwaters in shearwater breeding sites on Port-Cros Island (SE France), along with limited predation capacities on seabird eggs, even of small sizes. Moreover, a literature review of the methods used during the last 30 years in studies on rat impact on seabirds stressed the existence of deficiencies in our research, which illustrate the strong necessity to combine multiple sources of corroborative evidence in order to avoid some methodological bias which may contribute to under- or over-estimate the impact of rats, and consequently the degree of vulnerability of species. Finally, the study of the trophic ecology of black rats, combined with a long-term survey of the population dynamics and movement paterns on a small Mediterranean island, with a marked spatio-temporal variation in the availability of resources, allowed to underline the low individual diet plasticity of black rats compared to the population level, and the importance of the effects of fresh water inputs and those of allochthonous resources on the functioning of insular rat populations. Future research perspectives should focus on better understanding the processes involved in the impacts of rats on insular biotas, in species extinctions but also in their long-term coexistence.

**Keywords**: extinctions, invasive species, Mediterranean islands, population dynamics, predation, *Rattus* spp., seabirds, trophic ecology.