

CORRESPONDENCE



The origin of *Rattus rattus* on the Îles Éparses, Western Indian Ocean

ABSTRACT

Tollenaere *et al.* (*Journal of Biogeography*, 2010, 37, 398–410) present a phylogeographic analysis of *Rattus rattus* for the Western Indian Ocean, with particular emphasis on Madagascar, but do not include samples from three island groups centrally located in the Mozambique Channel. Haplotypes from these islands provide additional information on the colonization pathways of *R. rattus* in the Western Indian Ocean region. For each of the three Îles Éparses groups in the Mozambique Channel, we test the competing hypotheses that colonization by *R. rattus* was most likely: (1) from the Arabian Peninsula, (2) from East Africa, (3) from Madagascar, or (4) from independent shipping. These results are combined with historical observations of the presence of *R. rattus* on these islands to give stronger inference on the colonization pathways. Additionally, more accurate colonization dates provide guidance for contemporary conservation management.

Keywords Commensal rodent, invasive species, island colonization, mitochondrial DNA, Mozambique Channel, phylogeography.

INTRODUCTION

The Îles Éparses, literally translated the ‘scattered islands’, are a collection of five coral atolls located around the coast of Madagascar. They are a French territory, and on 21 February 2007 officially became the fifth district of the Terres Australes et Antarctiques Françaises (TAAF). They have been identified as Important Bird Areas (IBAs) because of their diverse and massive seabird colonies (Le Corre & Safford, 2001). Black rats (*Rattus rattus*) are present on all

three of the vegetated Îles Éparses in the Mozambique Channel: Europa (2223 ha), Juan de Nova (561 ha) and Grand Glorieuse (462 ha) (Fig. 1). They were eradicated in 2003 from Île du Lys (12 ha) in Les Glorieuses. Historical records indicate that black rats have probably been present on all three islands since at least the start of the 20th century (Russell & Le Corre, 2009).

Tollenaere *et al.* (2010) recently published a phylogeographic analysis of *R. rattus* in the western Indian Ocean, with particular emphasis on Madagascar, following previous work by Hingston *et al.* (2005). They found that Madagascar was probably colonized from the Arabian Peninsula, but that diverse colonization pathways existed in the Western Indian Ocean. They described three geographically distinct

clades (Groups A–C) with basal Arabian Peninsula specimens as the historical invasion origin. Apart from the Comoros (Grand Comore and Mayotte), Tollenaere *et al.* (2010) did not include samples from the major remote coral atolls lying between Madagascar and East Africa. The phylogeographic context of *R. rattus* invasion on these islands could provide important additional information on rat invasion of the Western Indian Ocean. The Îles Éparses (Europa, Juan de Nova and Grand Glorieuse) could have acted as stepping stones for the invasion of Madagascar from the Arabian Peninsula (Hypothesis 1; basal Arabian Peninsula), or could have been invaded from East Africa (Hypothesis 2; Group C), or could have been invaded as satellites from Madagascar (Hypothesis 3;

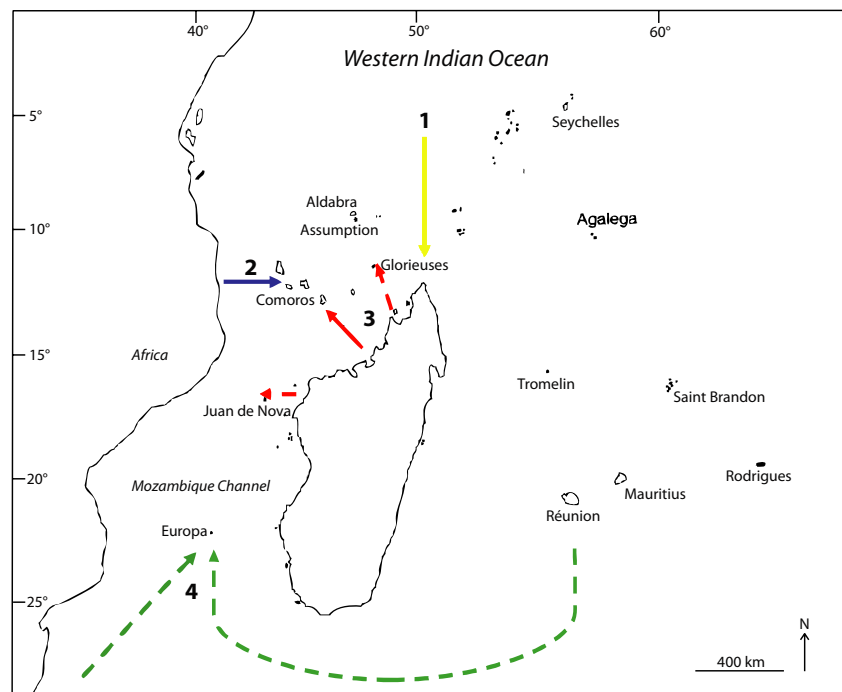


Figure 1 Map of the Western Indian Ocean islands, showing the four hypotheses of colonization pathways by *Rattus rattus*: Hypothesis 1 – from the Arabian Peninsula; Hypothesis 2 – from East Africa; Hypothesis 3 – from Madagascar; Hypothesis 4 – independent shipping. Filled arrows: results presented in Tollenaere *et al.* (2010); dashed arrows: results presented here.

Group B), or could even have been invaded entirely independently, given the frequent historical use of the Mozambique Channel as a shipping lane by Arabians, Africans and more recently Europeans (Hypothesis 4; Group A). European settlement also occurred on all three islands from the late 19th century (Russell & Le Corre, 2009). We sequenced introduced black rats from all three islands following the methods of Tollenaere *et al.* (2010) and interpret the results within the context of the work by Tollenaere *et al.* (2010) and Hingston *et al.* (2005).

MATERIALS AND METHODS

Samples from three black rats per island (Europa, Juan de Nova and Grand Glorieuse) were obtained in the winter of 2008 from two trapping grids on the north of each island. One centimetre tail samples were stored in 70% ethanol at room temperature prior to analysis. DNA from ethanol-preserved tissue was extracted using the DNeasy Tissue Kit (Qiagen, Hilden, Germany) and the complete cytochrome *b* (*cyt b*), two tRNA (*tRNA-Thr* and *tRNA-Pro*) and partial D-loop gene regions were amplified and sequenced following Tollenaere *et al.* (2010). The polymerase chain reaction (PCR) products obtained were purified using a Purelink™ PCR Purification Kit (Invitrogen, Auckland, New Zealand), following the manufacturer's instructions. Sequences were analysed on an Applied Biosystems 3100-Avant Genetic Analyzer using DNA SEQUENCING ANALYSIS SOFTWARE v. 5.1 (Applied Biosystems, Mulgrave, Australia). Sequences from our nine specimens and the 40 previously published *R. rattus* sequences of Tollenaere *et al.* (GenBank accession numbers GQ891569–GQ891608), as well as sequences from *Rattus tanezumi*, *Rattus exulans* (GenBank NC_011638 and NC_012389) and *Rattus norvegicus* (GenBank X14848), were aligned using CLUSTALW (Chenna *et al.*, 2003). The posterior probability (PP) consensus tree was constructed using MRBAYES v. 3.1.2 (Ronquist & Huelsenbeck, 2003) following Tollenaere *et al.* (2010).

RESULTS

Using the 1754 bp comprising *cyt b*, tRNA and D-loop, four new haplotypes (Hap 41–44 GenBank accession numbers JF178276–9) and one previously identified widespread haplotype (Hap 20) were found on the Îles Éparses. The phylogenetic tree (Fig. 2) esti-

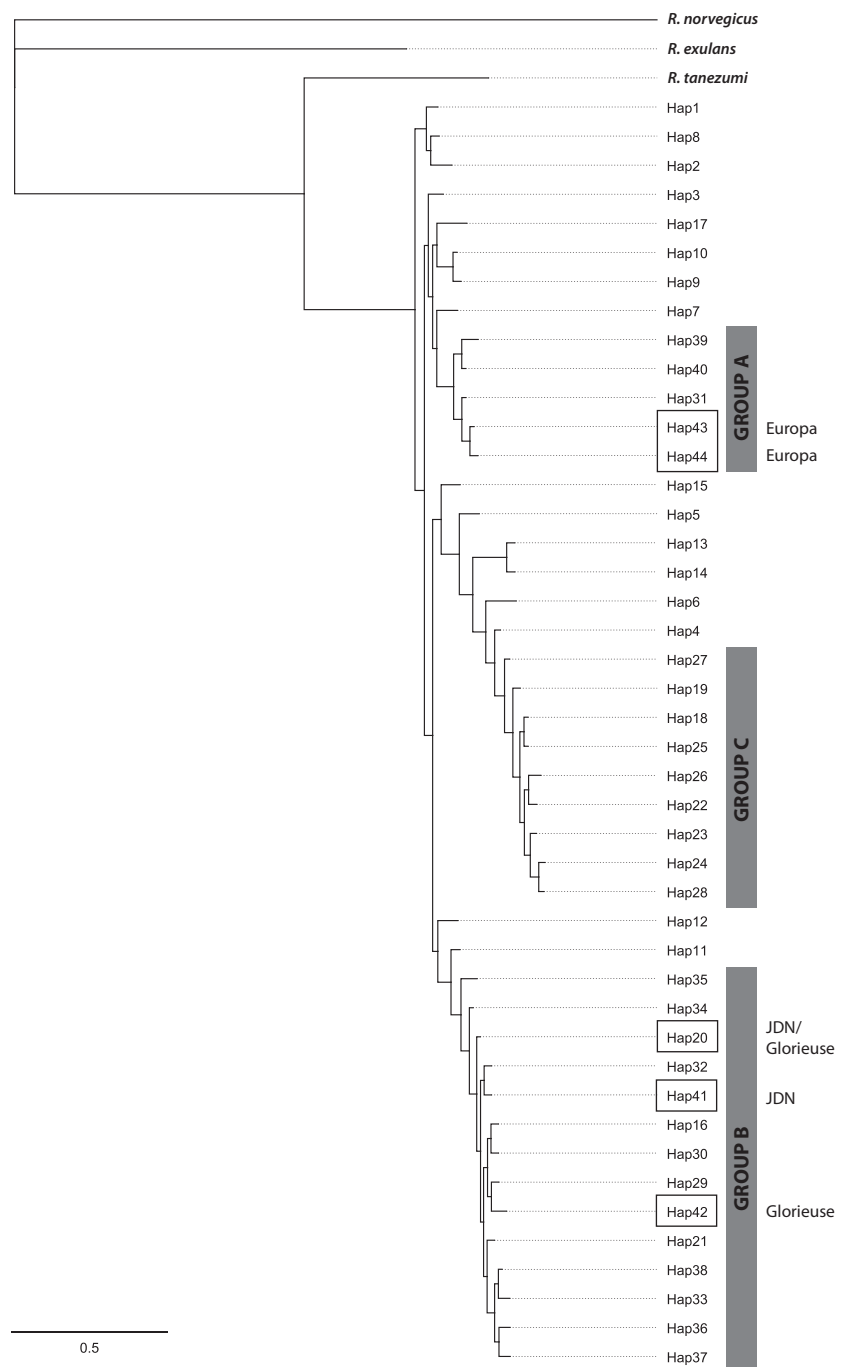


Figure 2 Bayesian tree of the 44 *Rattus rattus* mitochondrial DNA haplotypes and the closely related species *R. tanezumi*, *R. exulans* and *R. norvegicus*. Haplotypes found on the Îles Éparses are indicated in boxes. The scale bar is the number of substitutions per site.

mates the coalescence for the 44 haplotypes, rooted by *R. tanezumi*, *R. exulans* and *R. norvegicus*. This tree supports the three same monophyletic clades identified by Tollenaere *et al.* (Groups A–C), with Arabian Peninsula rats basal to each clade. *Rattus rattus* from Juan de Nova and Glorieuse shared the same haplotype (Hap 20) with rats from the monophyletic Group B

(Madagascar and East Africa; PP = 0.66) and within this group included new haplotypes on Juan de Nova and Glorieuse (Hap 41 & 42). The new haplotype from Glorieuse Island was most closely aligned with rats from neighbouring Mayotte Island (Hap 29 & 30). *Rattus rattus* from Europa nested within the monophyletic Group A (Réunion, South Africa and Madagascar;

PP = 0.70) expressed through two sister haplotypes (Hap 43 & 44).

DISCUSSION

Including the three Îles Éparses lying between Africa and Madagascar provides additional information on the colonization history of the entire region by *R. rattus*. *Rattus rattus* from Juan de Nova and Grand Glorieuse align with *R. rattus* from Madagascar and Mayotte, the other north-western island off Madagascar, and all three islands are nested within a monophyletic clade of *R. rattus* from Mozambique, Ethiopia and Madagascar. We agree with Tollenaere *et al.* (2010) that the *R. rattus* colonization of these islands probably occurred from Madagascar, in accordance with our Hypothesis 3: Madagascar satellite colonization (Fig. 1). The presence of both unique and shared haplotypes on both Juan de Nova and Grande Glorieuse suggest that rat introduction occurred quite some time ago. Conversely, the nearby Grand Comore, which has substantial haplotype diversity, instead supports an independent colonization, possibly from East Africa, and so unsampled neighbouring islands Anjouan and Moheli warrant sampling for comparison.

Rattus rattus from Europa align with *R. rattus* from a monophyletic clade that includes South Africa and Réunion, both strongly European-influenced nations. European settlement was attempted twice on Europa in 1860 and 1910, although black rats were already present on the island (Russell & Le Corre, 2009). The presence of entirely unique haplotypes on Europa suggests an introduction independent of other locations in the region. Colonization of Europa by *R. rattus* most likely occurred with more recent shipping activity, in accordance with our Hypothesis 4: independent shipping colonization (Fig. 1).

Phylogeographic studies require sampling widely, both within sites to avoid relatedness, and among sites to maximize coverage. Although other islands are present within the Western Indian Ocean that neither we nor Tollenaere *et al.* (2010) sampled (e.g. the Seychelles, particularly Aldabra), we believe the addition of the Mozambique Channel Îles Éparses gives a more complete picture of the phylogeography of the Western Indian Ocean, and the role of Madagascar, as emphasized by previous authors (Hingston *et al.*, 2005; Tollenaere *et al.*, 2010). In addition, combining phylogeographic methods (Tollenaere *et al.*, 2010) with independent historical records of col-

onization times and observations on vulnerable fauna (Russell & Le Corre, 2009) together gives stronger confidence in the pathways of colonization by introduced species. This also allows revision where data are lacking; for example for Juan de Nova the presence of *R. rattus* has only been recorded since 1980, but colonization probably occurred earlier given the absence of rat-vulnerable species and the genetic results presented here. Phylogeographic results can also have important consequences for contemporary conservation; for example if Europa was colonized more recently by *R. rattus*, as indicated in the results presented here, this may partially explain the ongoing persistence of rat-vulnerable fauna such as tropicbirds (*Phaethon* spp.), and provide greater urgency for immediate conservation intervention.

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Subjecting the theory of the small-island effect to Ockham's razor

ABSTRACT

Species–area curves from islands and other isolates often differ in shape from sample–area curves generated from mainlands or sections of isolates (or islands), especially at finer scales. We examine two explanations for this difference: (1) the small-island effect (SIE), which assumes the species–area curve is composed of two distinctly different curve patterns; and (2) a sigmoid or depressed isolate species–area curve with no break-points (in arithmetic space). We argue that the application of Ockham's razor – the principle that the simplest, most economical explanation for a hypothesis should be accepted over less parsimonious alternatives – leads to the conclusion that the latter explanation is preferable. We hold that there is no reason to assume the ecological factors or patterns that affect the shapes of isolate (or island) curves cause two distinctly different patterns. This assumption is not required for the alternative, namely that these factors cause a single (though depressed) isolate species–area curve with no break-points. We conclude that the theory of the small-island effect, despite its present standing as an accepted general pattern in nature, should be abandoned.