







Expanding Population Edge Craniometrics and Genetics Provide Insights into Dispersal of Commensal Rats through Nusa Tenggara, Indonesia

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ABSTRACT. The Nusa Tenggara island chain consists of an archipelago that runs roughly east-west in eastern Indonesia. As part of Wallacea, it has never been connected to any continental landmass, and has been subject to a variety of biological invasions that have populated the islands. Here, we examine the craniometric and molecular genetic records of several species of *Rattus sensu lato* in the island chain. We use the predictions of expanding population edge phenotypic selection in an effort to understand the movement of *Rattus rattus* and *Rattus exulans* through the archipelago. We also examine the mitochondrial haplotype networks of *R. argentiventer*, *R. exulans*, and the *R. rattus* Complex (RrC) and microsatellite allele frequency clustering patterns for the RrC, to examine relationships within and between Nusa Tenggara populations, and those of Asia and the Pacific where relevant for each taxon. In the RrC LIV and RrC LII haplotype networks, 20 haplotypes with seven from Nusa Tenggara were observed for RrC LIV, and 100 haplotypes with seven from Nusa Tenggara observed for RrC LII. The top performing RrC craniometric model had a negative association between size and distance from the easternmost point of the samples from Nusa Tenggara, consistent with increasing size moving west to east. The *cytochrome b* network for the *R. exulans* sequences comprised 14 haplotypes, with three observed from mainland Southeast Asia, one shared with Nusa Tenggara and regions further east, and another haplotype observed in Nusa Tenggara and in the Pacific. The *R. exulans* craniometric model selection produced four equally well performing models, with no migration scenario preferred. Finally, the haplotype network of *R. argentiventer* comprised 10 haplotypes, with six observed in Nusa Tenggara, including a relatively early cluster from the east of the archipelago. Our results are compatible with a polyphasic and polydirectional invasion of Nusa Tenggara by *Rattus*, likely beginning with RrC from the west to the east, an expansion of *R. exulans* from Flores, seemingly in no preferred overall direction, and finally the invasion of *R. argentiventer* from the east to the west. We find some support for the Dong Son drum maritime exchange network contributing to the distribution of the latter species.

Keywords: *Rattus*; black rat; Pacific rat; ricefield rat; Dong Son drum; maritime exchange; Southeast Asia

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