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Connectivity in fragmented landscape: Generalist and specialist gerbils show unexpected gene flow patterns

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ABSTRACT

Landscape structure can affect connectivity among populations. In a patchy landscape, specialist species that are limited to particular elements are expected to show low gene diversity, low connectivity and high differentiation among patches. Conversely, for generalist species, genetic variability and gene flow among sites are expected to be high, and differentiation is expected to be low. Here we tested this hypothesis for two rodent species: *Gerbillus gerbillus*, the psammophile specialist species abundant in sandy habitats, and *Gerbillus nanus*, the parapatric habitat generalist species, found in the more stable sands in Israel and West Africa. We found that among the psammophile specialist *G. gerbillus* populations, differentiation was low and connectivity was high. In contrast, the parapatric generalist species *G. nanus* demonstrates markedly high genetic differentiation between localities within short distances in Israel. Furthermore, our results support a division between the African and the Israeli *G. nanus* populations, suggesting two distinct species.

1. Introduction

Deserts are characterized as arid environments where annual precipitation is extremely modest. The limited water availability results in relatively low land productivity (Noy-Meir, 1973; Hadley and Szarek, 1981). Spatial variations in topography, soil type and soil moisture often lead to a patchy landscape where "productive" patches are separated by areas where harsh and stressful conditions prevail. This patchiness may have considerable consequences on gene flow between populations occupying favorable habitat patches (Wiens, 1976; Hanski, 1998; Kubisch et al., 2014).

The southern Arava Valley, part of the Syro-African rift valley in Israel, is a highly arid zone. Low average rainfall of 25 mm/year occurs almost entirely between December and March (Marcus, 1989), and average summer temperatures (May to October) exceed 30 °C (State of Israel 1998). The region is comprised of several unique landscape elements including sand dunes, salt flats, and narrow tracks of acacia tree savannas, each with its own distinguishing biological characteristics (Shanas et al., 2006). Consequently, despite the harsh climate, the Arava Valley provides a unique habitat for a rich variety of flora and fauna (Shanas et al., 2006, 2011).

Landscape structure can affect connectivity among populations (Kubisch et al., 2014). In the Arava Valley, the landscape elements form a mosaic of isolated patches of different sizes and shapes along the valley (Shanas et al., 2006). Anthropogenic impacts have affected connectivity in the last decades, promoted fragmentation and possibly further distressed connectivity. As a result, the remnant small, isolated populations may undergo processes of declining gene diversity by genetic drift and/or inbreeding depression.

Rodents of the genus *Gerbillus* (Rodentia, Gerbillinae) are adapted for life in deserts (Harrison and Bates, 1991) and are an important component of the mammalian fauna in arid zones of the Old World (Shenbrot and Krasnov 2001). In the Arava Valley, *Gerbillus* is the most abundant rodent genus (Shanas et al., 2006). Two gerbil species are common in the region, the lesser Egyptian gerbil (*Gerbillus gerbillus*) and the Baluchistan gerbil (*Gerbillus nanus*). *G. gerbillus* is a psammophile specialist species, abundant in sandy

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habitats, notably sand dunes and semi-stable sands, while the habitat generalist species, *G. nanus* replaces it in more stable sands on the edge of sand dunes and salt flats (Zahavi and Wahrman, 1957; Harrison and Bates, 1991; Yom-Tov, 1991; Shanas et al., 2006).

The distinction in habitat preference of the two gerbil species may possibly be manifested in different magnitudes of gene diversity and connectivity among populations. We hypothesize that if a certain species is limited to a particular landscape element (i.e. specialist) and the patches are relatively isolated and small, the gene diversity of that species within sites will be low, and the differentiation between populations would be high. Conversely, for generalist species, genetic variability and gene flow among sites would be high and differentiation between localities will be low.

In the current study, we analyzed gene diversity and genetic distance among local populations of the two parapatric gerbil species inhabiting different habitat patches. For genetic evaluation, we used amplified fragment length polymorphism (AFLP) markers, a commonly used molecular marker in landscape genetics (Storfer et al., 2010) allowing comparison of diversity levels between different species, and found to be further informative when population size and/or migration rates are low and genomic heterogeneity of genetic diversity between loci is high (Mariette et al., 2002), as well as sequence analysis of a fragment of the mitochondrial cytochrome *b* (cyt*b*) gene. Early genetic surveys of the genus *Gerbillus* in the Israeli desert yielded low levels of polymorphism (Ritte et al., 1976; Nevo et al., 1984; Sinai, Krasnov and Choshniak, unpublished data). To better assess the genetic characteristics and differentiation of these Israeli populations, we also considered samples of both species from West Africa (Mali and Mauritania) located more than 3500 km away from the Arava Valley. These African samples come from areas closed to the westernmost limit of the two species ranges and characterized by less habitat diversity than the ones from Israel, at the local scale. Therefore, they may represent interesting reference in terms of comparative genetic diversity relative to the Israeli samples.

2. Material and methods

2.1. Sampled populations

Ninety *G. gerbillus* and 68 *G. nanus* samples from 2 to 3 sites in the Arava Desert, Israel and additional samples from numerous localities in Mali and Mauritania, West Africa, were analyzed genetically (Fig. 1, Table 1). In the Arava Desert, gerbils were sampled as described in Shanas et al. (2006). The sampling areas are presented in Fig. 1. In West Africa, samples were collected in a series of localities from Northern Mali and Northwestern Mauritania, (Fig. 1; for details see Granjon and Duplantier, 2009).

2.1.1. G. gerbillus

In Israel, specimens were caught in two sites that are separated by a 7 km wide, non-hospitable salt flat: Grofit Sands (North) and Samar Sands (Samar) (Fig. 1). In West Africa, samples were collected along over a nearly 2000 km wide area (Fig. 1) from various sites in Mali (seven localities) and from three localities in Mauritania. The minimal distance between the Israel and Mali sampling sites exceeds 3500 km.

2.1.2. G. nanus

In Israel, samples were collected in the margins of the two *G. gerbillus* collecting sites (North and Samar) and at the edge of Evrona salt flat (Fig. 1), 12 km south of Samar. In West Africa, *G. nanus* samples were collected in eight localities in Mali and three localities in Mauritania, over an area generally parapatric to the *G. gerbillus* collection sites.

2.2. Genetic analysis

The genetic study included AFLP fingerprint analysis, and sequencing of a segment of a 552 bp of the mitochondrial cytochrome *b* (cyt*b*) gene. The AFLP technique generates a large number of genetic markers (loci) and considered as sensitive methods for tracking genetic differences between populations (Campbell et al., 2003). The mitochondrial genome shows high sensitivity to bottlenecks and founder effects (Roderick, 1996), and is thus used in phylogenetic analyses (Bensch and Akesson, 2005). In *Gerbillus* molecular taxonomy, the cyt*b* gene found to be most informative (Abiadh et al., 2010; Ndiaye et al., 2012, 2013). DNA was extracted using a standard phenol/chloroform procedure.

2.2.1. AFLP analysis

The AFLP method was carried out essentially as described by Vos et al. (1995). High quality genomic DNA (~200 ng) was digested with a pair of restriction enzymes (*Eco*RI/*Mse*I) at 37 °C for 4 h, then ligated to double stranded *Eco*RI (E−) and *Mse*I (M−) adaptors. The resulting fragments were amplified with nonselective primers, where the ligated adaptors served as target sites for primer annealing. Two selective primer combinations (selected to yield ca 60 loci/primers pair to avoid homoplasy) were used for AFLP amplification: E-ACA/M-CAC and E-ACG/M-CTT (E− and M-representing the restriction site and its ligated adaptor sequence). The selective *Eco*RI (E−) primers were labeled with florescent dye (6-Fam and Ned, respectively). PCRs were carried out in a total volume of 13 μl. PCR amplification cycles started at an annealing temperature of 65 °C, after which the annealing temperature was lowered by 0.7 °C per cycle for 12 cycles (a touch-down phase of 13 cycles), followed by 23 cycles at an annealing temperature of 56 °C. Amplification products were visualized under a Florescence-Reader (Applied Biosystems). Fragment analyses and genotyping were determined directly from the chromatographs using Genotyper software (Applied Biosystems). DNA of several samples (~10%) were amplified and run in duplicate to validate integrity of amplifications. The similarities between duplicated fingerprints were higher than 98%.

2.2.2. Cytb analysis

A fragment of the mitochondrial cyt*b* gene (~600 bp) was amplified by PCR. Primers were designed according to *Gerbillus* spp. published sequences in the GenBank (primer F − 5′-TCCTTCTGAGGGGCCACAGTCA-3′; primer R − 5′-ATAAATGGGTGTTCTACTGGTTG-3′). PCRs were carried out in a total volume of 13 μl, and the PCR cycling scheme included 35 cycles with annealing temperature of 55 °C, following by 60 min extension at 72 °C. The singular PCR products were tested on agarose gels, and then purified with QIAquick columns (Qiagen, GmbH), followed by direct sequencing using an ABI 3130xl Florescence-Reader (Applied Biosystems).

2.3. Data analysis

2.3.1. AFLP analysis

Amplification products were scored as discrete character states (present/absent) and transformed into band frequencies. Samples that exhibited unclear band formations (~10% of all amplification products), suggesting partial digestion and/or contamination, were excluded from the analysis. For each species we considered diversity parameters for each region, i.e. Israel, Mali and Mauritania. Within each region, we separately analyzed the Israeli sampling sites, and from West Africa localities that had at least five sampled individuals. To overcome the possibility of dependency between sample size and the estimation of genetic variability, in the larger sample size of the Israeli-Samar population of *G. gerbillus*, we also