

Brevia

Biogeography of telomere dynamics in a vertebrate

Daniele Canestrelli, Roberta Bisconti, Anita Liparoto, Frederic Angelier, Cécile Ribout, Claudio Carere and David Costantini

D. Canestrelli (<https://orcid.org/0000-0001-9351-4972>), R. Bisconti (<https://orcid.org/0000-0002-0600-7436>) ✉ (bisconti@unitus.it), A. Liparoto and C. Carere (<https://orcid.org/0000-0003-1644-2113>), Dept of Ecological and Biological Science, Tuscia Univ., Viterbo, Italy. – F. Angelier (<https://orcid.org/0000-0003-2619-167X>) and C. Ribout, Centre d'Etudes Biologiques de Chizé, CNRS-ULR, UMR 7372, Villiers en Bois, France. – D. Costantini (<https://orcid.org/0000-0002-8140-8790>) and AL, Unité Physiologie Moléculaire et Adaptation (PhyMA), Muséum National d'Histoire Naturelle, CNRS, CP32, Paris, France.

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Telomere length variation has been implicated in processes of ecological and evolutionary importance in a wide range of organisms. However, while the temporal component of this variation has been the subject of much research, we do not know yet whether a spatial component exists within species in telomere dynamics. Here, we investigated for the first time whether the biogeographic history of populations, a key driver of eco-evolutionary processes, can influence telomere dynamics. Based on a one-year longitudinal common-garden experiment in a tree frog species we found that co-specific populations can show striking differences in telomere dynamics, not explained by distinct environmental conditions experienced by individuals through time. Indeed, the populations did not differ in telomere length at the beginning of the study, yet they did after one year under standard conditions. We observed stability of telomere length over time within historically stable populations, but remarkable elongation (31.2% on average) within populations arisen during a recent range expansion. Our results suggest the intriguing scenario that non-equilibrium processes, such as range expansions, might promote plasticity in the molecular machinery regulating telomere dynamics.

Telomeres are nucleoprotein structures located at the terminal ends of chromosomes that play a major role in maintaining genome stability and in avoiding loss of genetic material (O'Sullivan and Karlseder 2010). In recent times, there has been a burgeoning interest in understanding the fitness consequences of variation in telomere length and dynamics (Monaghan et al. 2018). A core idea is that telomere length might integrate the individual history, thus representing a valuable metric of individual phenotypic quality (Angelier et al. 2019 and references therein). For example, the telomere dynamics may be affected by habitat quality, intraspecific competition, immune function, inbreeding, and have been associated with personality traits and the expression of sexual weapons. This emerging integrative view of telomere biology,



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raises immediate questions about its potential implications in eco-evolutionary processes that are prototypical of the integrative phenotype, such as dispersal.

Dispersal is a key process in ecology and evolution, which can influence – and be influenced by – the evolution of virtually all the features of an organism, including behaviour, morphology, physiology and genetics (Clobert et al. 2012, Canestrelli et al. 2016). Here, we ask for the first time whether dispersal-driven processes of historical biogeographic relevance, such as range expansions, can affect telomere dynamics. We hypothesize that, if individual variation in telomere dynamics translates into heritable variation in the capacity to cope with the new demographic and/or environmental conditions encountered during a range expansion, a spatial structure in telomere dynamics might emerge along the range of a recently expanded population. We explore this hypothesis using the Tyrrhenian tree frog *Hyla sarda* as study species. This is a small, cryptically coloured amphibian endemic to the Tyrrhenian islands, which colonized the Corsica island (i.e. the northern portion of its current range) from the Sardinia island, during a Late Pleistocene range expansion (Bisconti et al. 2011a, b, Fig. 1A). Using a long-term longitudinal common garden experiment (12 months) during which animals have been housed under identical conditions, we compared telomere length and its change over time between individuals sampled in the source area in Sardinia and individuals sampled in the expansion range in Corsica (Supporting information).

We found significant effects of geographic area ($F = 10.25$, $p = 0.002$), sampling time ($F = 21.59$, $p < 0.001$) and of their interaction ($F = 6.60$, $p = 0.014$). Post-hoc analyses showed that tree frogs from both Corsica and Sardinia had similar telomere length at the beginning of the experiment

($p = 0.549$), while tree frogs from Corsica had longer telomeres than those from Sardinia at the end of the experiment (coeff. estimate \pm SE: 0.218 ± 0.057 , $p = 0.002$) (Fig. 1). Telomere length did not change significantly over the experiment in Sardinia tree frogs ($p = 0.229$), while it increased significantly from the beginning to the end of the experiment in Corsica tree frogs (-0.215 ± 0.050 , $p = 0.0006$; 31.2% elongation on average) (Fig. 1B). Results do not change if four females out of 47 frogs are removed from the models (data not shown). Individual telomere length measured from samples taken at the beginning and at the end of the experiment was significantly repeatable (coefficient of 0.42 with an associated variance of 0.03), meaning that 42% of variance in telomere length during an individual's life could be explained by within-individual consistency. All frogs included in this study survived until the end of the experiment, indicating that there was no selective bias owing to individuals with shorter telomeres having lower chances of survival.

In recent years, telomere dynamics have been studied in a wide range of species (Monaghan et al. 2018). The species, however, might not be the appropriate unit of analysis. Indeed, our study showed, for the first time, that different co-specific populations can show striking differences in telomere dynamics, and that these differences can hardly be explained by distinct environmental conditions experienced by individuals through time (Supporting information). We also did not observe any differences between populations in telomere length at the beginning of the study; rather, these differences emerged along a longitudinal common-garden experiment, indicating that point estimates (e.g. as routinely used when comparing sexes or developmental stages) might provide blurred pictures of interindividual variation in telomere dynamics.

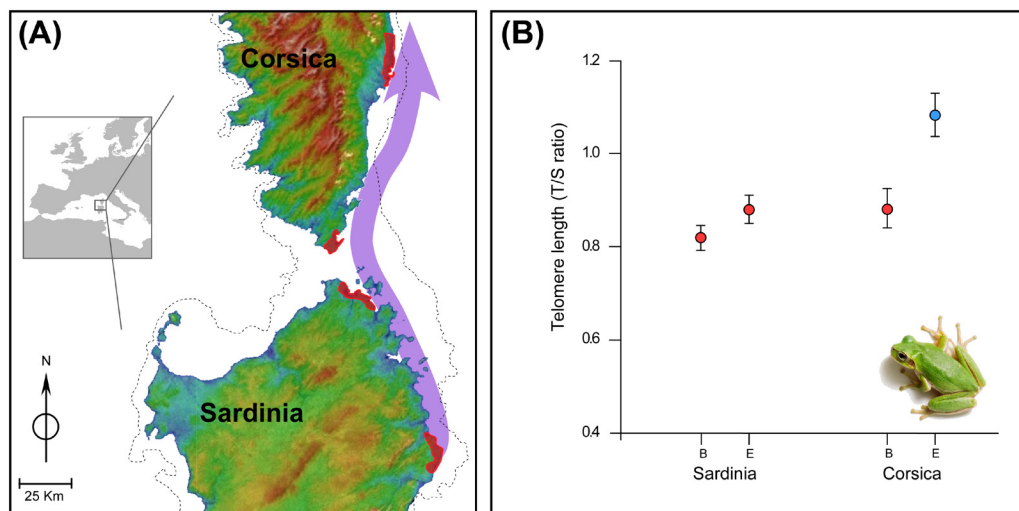


Figure 1. (A) Study area. Red shapes represent the four geographic areas where Tyrrhenian tree frog individuals were collected within Sardinia and Corsica islands. Purple arrow indicates the approximate route of late-Pleistocene range expansion of the Tyrrhenian tree frog, as inferred by previous population genetics, phylogeographic and species distribution modelling investigations (Bisconti et al. 2011a, b). Dashed line shows the coastline during the last glacial maximum (21 000 yr ago). (B) Values of telomere length in tree frogs sampled twice over a common garden experiment of 12 months. Groups sharing the same colour do not differ significantly from each other. Least square means \pm standard errors are shown. B: beginning of the experiment; E: end of the experiment.

Telomeres shorten with age in most organisms studied to date (Tricola et al. 2018), but not in the Tyrrhenian tree frog, as in some other species (Hoelzl et al. 2016, Spurgin et al. 2017). Our longitudinal data covered a non-negligible portion of the expected lifespan of an individual tree frog (one out of approximately three years), so that telomere attrition was a plausible expectation. Instead, we observed no differences between time points in the Sardinia population, and substantial lengthening of telomeres in the Corsica population. Since Corsica population was founded during a recent range expansion from Sardinia (Bisconti et al. 2011a, b), the evolution of the observed differences in telomere dynamics between the two populations should have occurred during the expansion process or later. Previous data showed that levels of both genetic diversity and bioclimatic suitability did not differ appreciably between the studied populations (Bisconti et al. 2011a, b; see also Supporting information). Accordingly, founder events, genetic drift and environmental adaptation following the expansion, appear unlikely as drivers of the observed divergence in telomere dynamics. Hence, we suggest that adaptive processes occurred during the range expansion event have promoted the evolution of this geographic pattern in telomere dynamics.

In vertebrates, telomere length is maintained and restored by the enzyme telomerase (Monaghan and Haussmann 2006). Telomerase activity appears to be particularly relevant for the regulation of telomere dynamics in ectotherms (Olsson et al. 2018). Telomere elongation in Corsica but not Sardinia under common garden conditions suggests differential expression (i.e. re-activation or upregulation) of the telomerase in Corsica in response to these novel conditions. This might imply that the range expansion event promoted plasticity in telomere dynamics, adding perspective to the burgeoning focus on the role of plasticity in evolution (Schwander and Leimar 2011). Since telomere attrition may also be linked to behavioural phenotype (Bateson et al. 2015), it might also be that frogs with a specific behavioural type, related to exploration or boldness, are more common in the sink population (i.e. Corsica; Canestrelli et al. 2016). Whether such increased plasticity is an adaptation to the unpredictability of the novel environments, variation in developmental conditions across populations, life-history/behavioural strategies, or to the non-equilibrium demographic dynamics encountered during the expansion process, is a further intriguing subject for future research.

Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.vdncjsxst>> (Canestrelli et al. 2020).

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Author contributions

Frederic Angelier: Original draft (supporting); Methodology (equal); Investigation (equal). **Roberta Bisconti:** Conceptualization (supporting); Review and editing (equal); Investigation (equal). **Daniele Canestrelli:** Conceptualization (lead); Original draft (lead); Methodology (equal); Funding acquisition (lead). **Claudio Carere:** Conceptualization (supporting); Review and editing (equal). **David Costantini:** Conceptualization (lead); Original draft (supporting); Formal analysis (lead); Methodology (equal). **Anita Liparoto:** Review and editing (equal); Formal analysis (supporting); Investigation (equal). **Cécile Ribout:** Review and editing (equal); Investigation (equal).

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