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Gene flow counteracts the effect of drift in a Swiss population of snow voles fluctuating in size

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ABSTRACT

Genetic monitoring has emerged as a useful tool to better understand evolutionary processes acting within and among natural populations. Longitudinal studies allow the examination of temporal changes in neutral genetic patterns in relation to demographic data, which is particularly interesting in populations that undergo large fluctuations in size. Taking advantage of eight years (2006–2013) of genetic survey data (18 microsatellite loci) from a snow vole (*Chionomys nivalis*) population in the Swiss Alps, we explore whether and how gene flow and selection shape temporal variability in genetic diversity by counteracting the effect of genetic drift, and thereby maintain the high levels of heterozygosity observed in this population. Using simulations and empirical data, we show that effective population size is small, and that genetic drift would lead to a marked decline in genetic diversity. However, this force is counterbalanced by the restoring effect of immigration. In agreement with the predictions of neutral genetic theory, we found a strong, positive association between genetic diversity and population size, which suggests positive density-dependent dispersal. This is also supported by the observed changes in genetic composition over time. Meanwhile, selection for heterozygosity was weak, overriding the effect of drift only in one out of eight years. Altogether, our results highlight the importance of gene flow as a significant evolutionary force in shaping genetic patterns in the wild, and as a crucial process for the maintenance of genetic diversity in small populations.

1. Introduction

Genetic variability is diminished through two major genetic processes: genetic drift (i.e., inbreeding under random mating) and inbreeding due to non-random mating (Frankham et al., 2002; Briskie and Mackintosh, 2004; Bouzat, 2010). In particular the effect of drift is considered to be a major threat to the viability and persistence of small and fragmented natural populations (Frankham, 1996; Allendorf et al., 2013). Genetic monitoring, i.e., the quantification of temporal changes in population genetic metrics (Schwartz et al., 2007), makes it possible to identify the moment when a population reaches a critical threshold and demands appropriate management actions to counteract the causes and consequences of reduced genetic variation (Frankham, 2010; Allendorf et al., 2013). More in general, it constitutes a useful tool for studying ecological and microevolutionary processes (Hoban et al., 2014).

The amount of drift a population experiences is not proportional to its census size, but rather its so-called effective population size (*Ne*)

(Wright, 1978; Nei et al., 1975). Thereby, knowledge of the effective size of a population provides insight into the rate at which a population losses genetic variation. The effective population size is not only reduced by unequal sex ratios and variance in reproductive success, but also by fluctuations in population size, where years with small population sizes have disproportionally large effects (Motro and Thomson, 1982; Whitlock, 1992; Palstra and Ruzzante, 2008). However, non-stable demographic conditions disrupt the equilibrium between drift and immigration, which complicates the relationship between genetic variation and *Ne* (Vucetich and Waite, 2000).

The negative effect of genetic drift can be overcome by gene flow, even when it is rare or limited. Indeed, just a few immigrants can have a strong impact on the genetic diversity of a population (Madsen et al., 1999; Keller et al., 2001; Johnson et al., 2010; Hedrick et al., 2014). Two good examples of the positive impact of immigration on the viability of isolated populations come from wolf (*Canis lupus*) populations in Scandinavia (Vilá et al., 2003) and Isle Royale, Canada (Adams et al., 2011). In both cases, the arrival of a single immigrant led to the rescue and recovery of these bottlenecked populations (Vilá et al., 2003; Adams et al., 2011). The positive effect of immigration on genetic variability is the result of immigrants introducing novel alleles into the pool of local alleles, which can increase heterozygosity and offset the

potentially negative effects of inbreeding (Keller and Waller, 2002; Westemeier et al., 1998; Marr et al., 2002). Hence, a rapid accumulation of new alleles through immigration can contribute to the maintenance of high levels of genetic variability in fluctuating populations (Ehrich and Jorde, 2005; Rikalainen et al., 2012; Gauffre et al., 2014). Furthermore, in addition to being different, the alleles introduced by immigrants may increase in fitness by increasing heterozygosity (i.e., overdominance effect), as only more heterozygous individuals may be able to successfully disperse into a new population (e.g., Selonen and Hanski, 2010; García-Navas et al., 2014). However, immigrant individuals may exhibit lower viability and fecundity if they express genes that are not adapted to local conditions (local maladaptation or outbreeding depression; Lynch, 1991; Hansson et al., 2004).

From the above it follows that for small populations, the arrival of immigrants is crucial not only in demographic terms (Ward, 2005; Schaub et al., 2010), but also in genetic terms (Hansson et al., 2000; Ortego et al., 2007). However, it has to be emphasized that immigration and gene flow cannot necessarily be equated, as the amount of gene flow will depend on the immigrants' capacity to spread their genes at their new location (Saccheri and Brakefield, 2002). Furthermore, the effect of immigration on genetic variability may interact with density, as evidenced by studies on arvicoline rodents (e.g., Ehrich and Jorde, 2005). For example, if gene flow increases with density, and because it is the absolute rather than the relative number of migrants that shapes genetic variation (Slatkin, 1985; Yu et al., 2010), genetic variability is predicted to increase with density (Charnov and Finnerty, 1980). On the other hand, if immigration shows negative density-dependence, the effect of increased immigration in low-density years may counteract or outweigh the effect of the increased amount of genetic drift in those years, resulting in the relationship between density and genetic diversity being zero or negative (Lambin and Krebs, 1991). Both models also make different predictions in terms of temporal genetic differentiation and genetic structure; the model of Charnov and Finnerty (1980) predicts the existence of temporal instability in genetic composition due to a loss of genetic variability at low density and low immigration, whereas the model of Lambin and Krebs (1991) does not predict significant temporal differentiation.

In addition to the role of gene flow in counteracting the negative effect of genetic drift on genetic variation, selection can play a significant role in shaping population genetic patterns as well. If heterozygotes have a higher fitness than homozygotes due to the negative effects of homozygosity at (linked) genome-wide distributed functional loci (i.e., inbreeding depression; Kempenaers, 2007), selection favouring heterozygotes may affect population genetic diversity. One of the most common effects of reduced genetic diversity is a decreased probability of survival, either during early-life stages or later in life (e.g., Kruuk et al., 2002; Mainguy et al., 2009). The selection against relatively homozygous individuals this generates may contribute to the maintenance or increase of heterozygosity over time (Bensch et al., 2006; Kaeuffer et al., 2007; Nietlisbach et al., 2015). However, although there is a growing literature showing evidence for a positive association between heterozygosity measured at putatively neutral microsatellite markers and fitness-related traits (e.g., Da Silva et al., 2009; reviewed in Chapman et al., 2009), the magnitude and direction of heterozygosity-fitness correlations may depend on the environmental conditions (Fox and Reed, 2011). In this vein, recent studies highlight that inbreeding depression may be accentuated under stressful and unpredictable conditions (Da Silva et al., 2005; Lesbarrères et al., 2005; Brouwer et al., 2007; Auld and Relyea, 2010), and accordingly, the strength of selection for heterozygosity may vary across years (Forcada and Hoffman, 2014).

Here, we study temporal changes in genetic variability in a small and relatively isolated population of European snow voles (*Chionomys nivalis*) over a period of eight years (2006–2013), which represents one of the few long-term individual-based study populations of rodents.

This time interval comprises a decrease in population size by around 40%, and a subsequent recovery period. Thereby this population provides a good model to investigate the relationship between genetic variability and demography. Specifically, we quantify the importance of the three evolutionary forces that have the potential to influence genetic variation over relatively short time periods (drift, gene flow and selection) in shaping temporal changes in genetic variability. Furthermore, we test whether these changes are density-dependent, and whether they show a pattern of genetic differentiation over time. Thereby, we provide insight into the mechanisms contributing to the maintenance of high genetic diversity in populations with erratic (i.e., non-cyclic) density fluctuations.

2. Methods

2.1. Study species

The European snow vole is a relatively large-sized (up to ~13 cm) microtine rodent whose distribution is restricted to mountainous regions of southern and eastern Europe (Pyrenees, Alps, Apennines, Carpathians) and south-western Asia, and which for this reason is considered a glacial relict species (Amori, 1999; Yannic et al., 2012). It inhabits high-mountain biotopes (mostly above the tree line; >1000 m), showing an overwhelming preference for rocky environments (scree and boulder-covered slopes) (Luque-Larena et al., 2002). This habitat preference leads to highly isolated populations and a naturally fragmented distribution (Castiglia et al., 2009). The snow vole has a promiscuous mating system in which both males and females mate with multiple partners (Luque-Larena et al., 2004). Females show territorial behaviour but tolerate the presence of relatives; daughters usually remain in their natal area, resulting in matrilineal female clusters. Males have overlapping home ranges, which can encompass the territories of several females (Luque-Larena et al., 2004). The reproductive period is from May to August, during which they produce one or two litters of one to five pups each (Janeau and Aulagnier, 1997). The average snow vole lifespan is 12–13 months, which means that most individuals do not survive the first winter (Janeau and Aulagnier, 1997; Pérez-Aranda, 2009). Unlike other microtine species, snow voles do not show strong population cycles (Yoccoz and Ims, 1999).

2.2. Study area

The study was carried out in the Swiss Alps, near the Churer Joch (Churwalden, canton of Graubünden; 46°48′ N, 9°34′ E; 2.030 m.a.s.l.). The study area (approx. 5 ha in size) consists of a west-exposed scree slope with sparse vegetation (high altitude shrubs) surrounded by meadows to the south and to the north, bedrock to the east and a coniferous forest to the west (see Supporting information for more details). Based on this, and the fact that our study site comprises most of the suitable habitat that can be found in this area, we assume this population to be ecologically fairly isolated. Nevertheless, there is another suitable habitat in close proximity (app. 400 m), which is inhabited by snow voles and which may act as a source of immigrants.

2.3. Live trapping

For eight consecutive years (2006–2013), snow voles have been live-trapped between mid-June and early October in a standardised manner. To this end, the study area is overlaid with a 10×10 m grid consisting of a total of 559 cells. A catch-and-release trap (Longworth model, Penlon Ltd, Oxford, UK) filled with hay and baited with apple, hamster food and peanut butter is placed in each cell. Animals captured for the first time are ear-clipped (2 mm diameter, thumb type punch, Harvard Apparatus, Massachusetts, USA) and individually marked by implanting a PIT tag (ISO transponder, Tierchip Dasmann, Tecklenburg, Germany) under the skin of the neck. Ear biopsy samples were