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Understanding hybridization and competition processes between hare species: Implications for conservation and management on the basis of a mathematical model

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ABSTRACT

Hybridization and introgression frequently occur in animal communities, both in nature or caused by human actions. In the genus *Lepus* (Mammals, Lagomorphs) genetic mixing has been widely documented and it probably affected the population dynamics of species, particularly during climatic oscillations. We thus propose and investigate a mathematical model, with the aim to describe and predict the outcome of interspecific interactions in a three-population system including European (*Lepus europaeus*), mountain (*Lepus timidus*) and hybrid hares.

Our results show that the three-population system can survive at a stable level, but equilibria involving only parental species could also be feasible. This implies that, depending on initial conditions, the mountain hare could suffer from the competition with European and hybrid hares and its population could disappear in the near future. Under climate change scenarios, the conditions for coexistence will become even more restrictive, mountain hare populations could be depressed and finally collapse.

Thus, at present the hybridization phenomenon does not necessarily represent a threat to the conservation of the unique genomes of the parental species, but climate change and human intervention, namely the introduction of European hares in the range of the Alpine mountain species, could result in an increase in the contact zones between populations, finally promoting hybridization and biotic homogenization.

1. Introduction

The biological processes of hybridization, i.e. the interbreeding of individuals from genetically distinct populations, and introgression (gene flow between populations achieved when hybrids backcross to one or both parental populations) have been the focus of much research. Botanists often recognized the creative role of both these processes, while in zoology hybridization has been mainly regarded as a negative determinant of the loss of distinct gene pools (Rhymer and Simberloff, 1996). In wildlife conservation, the concerns related to these phenomena increased with the awareness of the threats posed by animal translocations (AA VV, 2007) and by Invasive Alien Species (Quilodrán et al., 2015).

Simultaneously, advancements of molecular genetic analyses made the documentation of the extent of hybridization and introgression available for a larger and larger number of *taxa* (Haig, 1998; Allendorf et al., 2001).

Coupling this information with the results of studies on inter-specific competition provided a clear evidence of the effects of combined competition and introgressive hybridization. When these occur between widely distributed generalist species and more narrowly distributed or endemic ones, the population abundance of the latter may be largely affected and the risk of extinction by hybridization may be actualized (Rhymer and Simberloff, 1996; Allendorf et al., 2001).

On the other hand, under certain conditions, introgressive hybridization may represent an important mechanism for species rescue, since it has the potential to generate the diversity required for rapid evolution in response to environmental shifts (Baskett and Gomulkiewicz, 2011).

Thus, the outcome of inter-specific interactions involving introgressive hybridization can only be determined by a careful evaluation of the system under study and the species involved in it. In this respect, the Lagomorphs may represent an interesting model. In the genus *Lepus* in particular, genetic mixing (Rhymer and Simberloff, 1996) via introgressive hybridization has been widely

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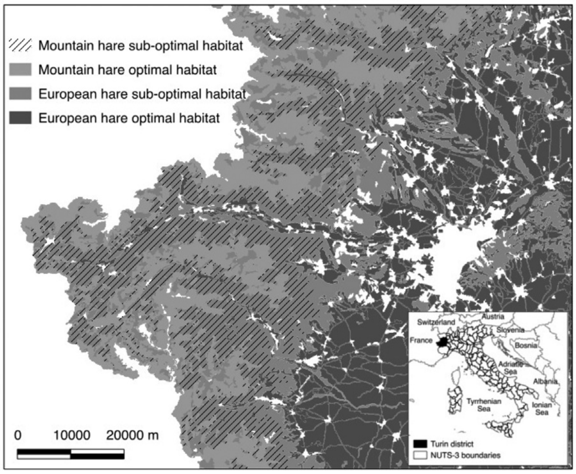

Fig. 1. Suitable habitats for the mountain and European hares in the Western Italian Alps. The map shows part of the Turin district, NUTS-3 (located in the North-West of Italy, in the Piedmont Region), where the optimal habitat for the European hare is mainly located in lowlands and valley bottoms (dark grey areas). On the contrary, the optimal habitat for the mountain hare is located at the highest altitudes (light grey areas). In-between, the medium grey, dashed areas actually identifies the zones where sub-optimal habitats of the two species overlap (and where hybrids presumably thrive). The habitat suitability map is based on Boitani et al. (2002).

documented worldwide and mainly related to climatic oscillations during the glaciations (Alves et al., 2008).

In spite of the availability of genetic data documenting this phenomenon (Thulin and Tegelström, 2002; Melo-Ferreira et al., 2005; Alves et al., 2006; , 2008), and even if current climatic changes are likely to further affect the phylogeography of this *taxon*, until now no attempt has been made to model the population dynamics of spatially (and genetically) interacting Lagomorphs. This lack of attention can be attributed to the satisfactory conservation *status* of most hare populations inhabiting high latitudes, but this may not be the case for the endemic populations of mountain hare (*Lepus timidus*) of some European regions. Hybridization with the European brown hare (*Lepus europaeus*) has been recognized as a major threat for the conservation of the endemic Irish hare (*Lepus timidus hibernicus*) (Smith and Johnston, 2008), it was pointed out as a factor potentially influencing the long-term decrease of mountain hare in Sweden (Thulin and Tegelström, 2002), and it could also negatively affect the population dynamics of the endemic Alpine mountain hare (*Lepus timidus varronis*), whose populations seems to be declining (Mitchell-Jones et al., 1999).

In this paper we will thus propose and investigate a mathematical model, with the aim to understand under which parameter conditions stability can occur for a three-population system including European, mountain and hybrid hares. To illustrate the model, we will particularly refer to the Alpine situation. Here, because of niche differentiations, the European brown hare mainly inhabits low and intermediate altitudes, while the mountain hare is restricted to the mountain peaks (see Fig. 1 for an example of the expected hare distribution in North-Western Italy). Since recent investigations confirmed the ongoing process of hybridization among the two species (Scandura et al., 2008; Tosatto, 2011) in the Alps, a hybrid swarm is likely to be located at least at intermediate altitudes, where the range of the parental species partly overlaps.

The paper is organized as follows. The next Section describes the methods, in particular the model, Section 2.1, and its parameters, Section 2.2. Section 3 reports the simuations results under two possible scenarios: (i) a "current scenario", Section 3.1, based on the parameterization of the model using values presented in Section 2.2; (ii) a "climate change scenario", Section 3.2, where the future evolution of the system is analyzed under the hypothesis of a change in the values of the model parameters, specifically changes in the rate of competition for resources and/or change in the carrying capacities. A final discussion, Section 4, concludes the paper.

2. Methods

This section is divided into two parts. Section 2.1 describes the equations of the proposed mathematical model and discuss it in broad ecological terms. Section 2.2 presents a possible model parameterization, taking into account and describing the demographic traits of European and mountain hares.

2.1. The model

The ecosystem considers three hare "populations", the European brown hare E, *L. europaeus* (Pallas, 1778), the mountain hare M, *L. timidus* (Linnaeus, 1758), and the hybrid hare H populations. The latter can reproduce among themselves, as well as by coupling with both confining populations E and M. The proposed dynamical system is

$$\begin{aligned} \frac{dE}{dt} &= rE\left(1-\frac{E}{K}\right) - \tilde{a}\sqrt{E}\sqrt{M} - b\sqrt{E}H, \\ \frac{dM}{dt} &= sM\left(1-\frac{M}{L}\right) - \tilde{c}\sqrt{E}\sqrt{M} - e\sqrt{M}H, \\ \frac{dH}{dt} &= qH - nH^2 + \left[q_M\sqrt{M} + q_E\sqrt{E}\right. \\ &\quad \left. -(g\sqrt{E}+f\sqrt{M})\right] H + \tilde{w}\sqrt{E}\sqrt{M} \end{aligned} \tag{1}$$

In the first equation, the dynamics of the European hare (E) is shown. The latter grows logistically with net reproduction rate r and carrying capacity K, and competes for resources with the mountain hare population at rate $\tilde{a}$. Since the environments in which these populations live are only in part overlapping, the interactions are considered as if they were occurring only for the animals living on the border of each environment. This is modeled via the use of the square roots of these populations, as recently proposed in models for prey herd behavior (Ajraldi et al., 2011). The population E further competes with the hybrid population at rate b. Note that again not the whole population E is involved in the interspecific competition, but only the portion of the population that resides on the boundary, which is expressed once more by the square root term (Ajraldi et al., 2011). Note also that the root does not involve the hybrid population, because this population lives at the intersection of the territories where M and E live, and this boundary zone can be thought of as a thin and possibly long stripe.

This statement does not mean that the stripe has a linear behavior, like for instance it would be found in Sweden, where the mountain chain that borders it with Norway lies along a straight line, but it could also be a curve, like indeed the Alps that crown Northern Italy and border it from the confining nations. Therefore the model assumptions hold also in this particular case, as this stripe resembles a one dimensional manifold, so that it essentially coincides with its boundary. Hence the population H is already living in a strip of land, thus the whole of it is subject to these interactions.

For the mountain hare (M), modeled in the second equation, again we have logistic behavior, with net reproduction rate s and carrying capacity L. Competition in this case occurs on the neighboring territories where the European hare thrives, at rate $\tilde{c}$. Once more, the interaction involves only the part of the M and E populations that are close to the population boundaries. This is again expressed by the square root terms. The interaction with the hybrid hare occurs again on the border, giving rise once more to the square