

OPINION ARTICLE

Wild opportunities with dedomestication genetics of rabbits

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After domestication, wild progenitors, such as the aurochs and the wild horse, became extinct. For the European rabbit, however, ancestral, domestic, and feral populations exist. During domestication of the rabbit, very few alleles have been fixed for selective traits, and thus, the ancestral genotypes have been preserved in lowered frequencies. This facilitates investigations on genetic processes involved in domestication as well as dedomestication, that is, where domestic strains are “rewilded.” The acquired knowledge may be useful in the search for genotypic, phenotypic, and, perhaps most importantly, ecotypic equivalents that could assist in the restoration of extinct fauna and its ecosystem functions. Such efforts could provide novel evolutionary trajectories useful in nature restoration, management, and conservation.

Key words: defaunation, feral, *Oryctolagus cuniculus*, restoration, rewilding

Conceptual Implications

- The understanding of how ancestral genotypes have been preserved during domestication of the European rabbit may be useful for recreation of extinct ancestors of domesticated species such as the aurochs and wild horse.
- The potential for regeneration of genotypic, phenotypic, and ecotypic equivalents of extinct fauna provide novel evolutionary trajectories useful in nature restoration, management, and conservation.

Introduction

Dedomestication has been defined as “a process, undertaken over generations, of trying to turn domestic animals (or plants: here we are concerned with animals) into self-sustainable wild or semi-wild animals” (Gamborg et al. 2010, p. 58). Thus, dedomestication is a directed, anthropogenic effort to turn domestic animals into wild, while feralization is the process of becoming feral (Price 1984). Dedomestication and feralization as concepts relate to processes such as parallel evolution, reverse evolution, and directional selection. Parallel evolution conveys to evolutionary processes that, independently of each other, approach a similar feature. This could potentially relate to when strains of different species regain their ancestral pelt coloration, i.e. a trait coded for by the same gene complexes evolves simultaneously in different clades. Reverse evolution occurs when adaptive traits, once selected for but lost or concealed during domestication, are reverted, recovered, or restored to the ancestral state, presumably because of recurring evolutionary prerequisites. It could, as above, relate to pelt coloration, when anthropogenic forms of fur color, a very plastic feature, return to ancestral form as soon as the ancestral selection pressure is imposed again. Parallel and reverse evolutions relate to directional selection, where certain features are selected, like a cryptic fur color

that improves predation avoidance or, in the case of domestication, striking and seemingly suboptimal traits like white pelage. However, it could also be that gene complexes selected for during domestication are unstable; that is, alleles or polymorphisms selected for during domestication are not favored, or even selected against, under natural selection regimes.

The understanding of dedomestication and its potential features rely on the genetic construction and durability induced by domestication (e.g. Grant 1981; Andersson & Georges 2004; Wright 2015). If, for example, a trait is selected for, the genomic region associated with this trait undergoes a loss of genetic variation, and alternative alleles and linked loci are depleted from the genome. Thus, genetic differentiation between the domestic strains and the wild ancestor should be induced at this specific locus and neighboring, linked loci.

The European Rabbit

The European rabbit (*Oryctolagus cuniculus*) originates from southwestern Europe where it is considered a keystone species (Delibes-Mateos et al. 2008). The European rabbit is an important game species, but also considered a pest in parts of

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the nonnative distribution. The domestic rabbit, derived from the European rabbit, is an important production animal that provides meat and fur, is widely used for research and medicine, and is also a popular pet. The European rabbit has also been widely introduced by humans, and has been a successful colonizer in all continents and on over 800 islands (Flux & Fullagar 1992). The majority of introductions were performed using domestic derived animals (Thompson & King 1994; Peacock & Abbott 2013). Interestingly, depending on relative number of domestic founders and their phenotypic characteristics, feral populations may regain a wild phenotype within a relatively short time span (Lincoln et al. 1990; Johnsson et al. 2016).

The rabbit is a suitable model for examining the genetics of dedomestication because wild-type, domestic, and feral strains still remain simultaneously. Rabbits are easy to sample because they often are considered to be a pest species (e.g., in Australia) and killed in large numbers, and although they are near threatened in their native range (Smith & Boyer 2008), hunting is still common practice. In addition, the short generation time of rabbits enables rapid return to wild forms. The rabbit is widespread; it has a restricted native area but has also been introduced to many places worldwide for hundreds of years (Flux & Fullagar 1992). For nonnative areas, the ancestry is often known, at least approximately, sometimes even the number of specimens released, their origin, and the degree of admixture of domestic strains. Particularly nonnative insular populations provide interesting experimental opportunities (Foster 1964; Sakai et al. 2001). Finally, nonpreferred wild-type alleles, that is, alleles often selected against during domestication, often remain in low frequencies in domestic breeds (Gamborg et al. 2010).

Genetics of Rabbit Domestication

In a genome-wide study of levels and patterns of genetic variation in both wild and domestic rabbits, several candidate regions with signatures of directional selection in the domesticated lineage were inferred (Carneiro et al. 2014). Although many alleles shifted their allelic frequencies in response to selection during domestication, only 20 of more than 50 million single nuclear polymorphisms were fixed for alternative alleles. Thus, although selective signals are widespread over the genome, which is consistent with a highly polygenic genetic architecture associated with domestication, very few alleles are fixed for the selective trait across the entire domestic population (cf. Gamborg et al. 2010). This result has important implications; if selection pressure, for example imposed by domestication, is relaxed or removed, there is a potential for many alleles that had their frequencies reduced during domestication to again increase their frequency in the population. This implies that feral populations may adapt to the wild by back-selection at loci that have not gone to full fixation.

Dedomestication Genetics

Recreating extinct animals is a controversial desire in fantasy-struck forms of biology (Zimov 2005). Efforts to

“recreate” extinct species by conventional animal breeding started in the early nineteenth century (Heck 1951). Modern genetics has enabled novel approaches by for example cloning (Corley-Smith & Brandhorst 1999) or using the CRISPR/Cas9 technique for genome editing (Jinek et al. 2012). There are also discussions of how to form wild eco-equivalents of currently extinct ancestors of for example horse (*Equus ferus*) and cattle (*Bos taurus*), needed to create functional future ecosystems (Seddon et al. 2014). Here we introduce the term “dedomestication genetics” as a process in which we define ancestral (remnant) allelic variation in order to reacquire wild-type features lost during domestication. This is a form of reverted domestication, where wild-type is the desired goal or evolutionary trajectory rather than production features or behavioral adaptations to anthropogenic conditions.

If wild-type alleles are preserved, we may only need a population pool of domestic breeds and removal of anthropogenic selection pressure together with natural selection to acquire phenotypes reminiscent of extinct ancestors. Although time cannot be reverted, dedomestication may generate novel, wild phenotypes that may function as an eco-equivalent to extinct ancestors and, thus, become useful tools in shaping future ecosystems and restoring functions therein.

The main inferences from comparing genetic diversity in domestic and wild rabbits may be applied to other domestication events and open a novel window towards the extinct ancestors of domestic species such as cattle and the horse. Thus, despite the long period of anthropogenic selection, ancestral “wild” alleles may be preserved within the genomes of existing domestic breeds.

Emerging Opportunities

Conservation and restoration biology have conceptual limitations in that conservation biology aims to preserve a certain condition and restoration biology aims to recreate an imprecise past. The evolutionary processes that underlie biodiversity, however, can per se only have a future trajectory. In this sense, the concept of “rewilding,” that is, boosting, reestablishing and/or recreating wildlife and their ecosystem functions, facilitates novel paths for biodiversity that fit better with evolution (Barlow 1999; Donlan et al. 2005).

The exploration of the genetics of domestication and dedomestication in rabbits enables us to follow the inheritance of the gene-complexes that code for the domestic phenotypes, and to evaluate the relative importance of different genes. Ultimately, it may provide us with genetic instruments to identify wild-type alleles in low frequencies in domestic strains useful for recreating extinct species and restoring their ecosystem function in the wild. Such opportunities have strong implications for evolutionary biology related to parallel evolution, reverse evolution, and/or directional selection that could provide novel evolutionary trajectories useful in nature restoration, management, and conservation.

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