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Chapter 3

Genetic Diversity in Small Populations

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Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/intechopen.76923

Abstract

The chapter focuses on animal populations of low genetic diversity, among which some have low population size and are, or have been, threatened by extinction. Genetic diversity is regarded as a must for a species to be able to adapt to environmental challenges, but despite this, several species, also among advanced animal groups like birds and mammals, seem to thrive well with low genetic diversity. Some species are assumed to have done so for thousands of years. Other species have low genetic diversity resulting from heavy bottleneck events, in some cases very close to extinction, caused by human activities. Although some species live with surprisingly low genetic diversity, being prone to further loss of genetic variation, this may be retarded due to sexual selection and fitness superiority of heterozygotes. Simulations with population size N = 25 showed that a homozygote fitness of 0.75 compared to fitness = 1.0 of the heterozygote resulted in exclusion of a p = 0.10 frequency allele in <10% of 50 simulation over 50 generations, whereas fitness 1.0 of all genotypes resulted in exclusion of the p = 0.10 allele in 78% of 50 simulations.

Keywords: allele exclusion, genotypes, heterozygote fitness, population size, selection

1. Introduction

Genetic diversity is a crucial characteristic of any population or species, as genes coding for causative traits are tools by which the populations are equipped to adapt to environmental challenges [1–3]. High genetic diversity, therefore, is assumed an advantage or even a must, for species survival when environmental factors are changing, like climate change, new species appear, and among those new parasites and diseases. The development at present, with steadily decreasing number of species, often caused by human activity [4] imposes a responsibility on human society to take countermeasures. This is necessary also for our own welfare and prosperity.

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In the conservation of populations and species, the preservation of natural habitats, for example wooden areas, of sufficient size should always be the first priority, though it is not always possible, and it may already be too late. One could claim, in a conservation perspective, that the population or the species, first of all is a gene pool, and that the preservation of a population handles about preservation of the gene pool as the most inalienable. The genetic diversity should therefore be explored and described as soon as possible in any population, but primarily for those already known to be threatened. Alleles may go extinct, especially low frequency alleles in small populations, and new alleles are added by a certain mutation rate, not necessarily keeping up with the loss rate.

Several molecular biological methods are available, and the choice of method is a matter of discussion and depends on the purpose. Amplified fragment length polymorphism (AFLP) [5] randomly amplified polymorphic DNA (RAPD) [6], restriction fragment length polymorphism (RFLP) [6], microsatellite analysis (MS), also denoted simple sequence repeat (SSR) [7] and single nucleotide polymorphism (SNP) [8] are conducted on selected marker loci. The latter two are favorites, and MS loci are polymorphic, that is, one locus may exhibit several different alleles, commonly 3–15, whereas SNP loci, like RFLPs, are biallelic. MS analysis includes usually 10–20 marker loci, sometimes more, whereas SNP analysis includes several thousand loci. Microsatellite loci are noncoding and therefore neutral, though the loci may be linked to coding loci and apparently be under selection, if the linked locus is under selection. SNPs may be located in coding loci and consequently be under selection. The SNP assays have an advantage due to being easier to standardize across detection platforms and laboratories than the MS method.

To describe the genetic variation of a population and relatedness, or lack of such, between individuals and populations, the MS method is well suited due to its high variability. Allele frequencies may be compared between populations and genetic structure within groups of populations, for example, in metapopulations, may be explored. Number of alleles (allele richness, when adjusted for sample size) per analyzed locus is an important index together with the fraction of heterozygote genotypes, that is, observed (H_O) and expected (assuming Hardy Weinberg equilibrium) heterozygosity (H_E), often referred to as genetic diversity, the inbreeding (F_{IS}) and outbreeding (F_{ST}) coefficient. Estimates of effective population size N_e [9] may also be conducted based on linkage disequilibrium, heterozygote excess, and others [10, 11]. F_{ST} is one of several indices of genetic differentiation between populations. Microsatellites are well suited for that kind of studies due to the high variability.

The value of such indices depends on the markers, that is, marker set chosen, so the comparison between populations should be based on the same marker set. The same applies to SNP analysis, but SNPs are advantageous when the aim is to focus on important traits to explore selectivity and fitness among individuals and populations [12–14]. In a breeding context, for improved growth and survival of economical important species, to secure survival and fertility of populations and species, wild or domestic, the preservation of certain alleles or combination of such, can be monitored. There is a potential for selection of mates when animals are bred in captivity by conducting genetic screening of parental generation before fertilization to strengthen or weaken specific traits [15].

http://dx.doi.org/10.5772/intechopen.76923

2. A short review

2.1. Low genetic diversity, but still successful

Though genetic diversity is assumed to be a prerequisite of success, there are several known examples of viable and apparently successful species with low genetic variability, like the African Cheetah (*Acinonyx jubatus*), with expected heterozygosity $H_E < 0.0153$, showing no characters of inbreeding, like reduced fertility, survival or fluctuating asymmetry, in the wild [16]. There are problems with reproduction in captivity, that is, in zoos [17], but this may be due to management as reproduction of cheetahs in North America was improved by changed husbandry [18–20], though this could potentially be due to limited adaptability as a consequence of low genetic diversity.

Mauritius kestrel (*Falco punctatus*) of the Mauritius Islands was characterized as one of the rarest bird species in the world when only one pair was left in 1974, after deforestation and invading species. After careful breeding, by picking naturally laid eggs in nest in the wild, for hatching and breeding chics for stocking, the endemic species now counts several hundred pairs [21, 22]. The population appears viable, though the genetic variability is low with heterozygosity $H = 0.10$, as compared with historical $H = 0.20$ (from up to 170 years old museum skins) and $H = 0.59–0.70$ in continental kestrel species [21].

Another example of successful species with low genetic diversity is two species of albatross, the wandering albatross (*Diomedea exulans*) with a circumpolar distribution in the Southern Sea, breeding on six islands in numbers of tens of thousands, and the Amsterdam albatross (*Diomedea amsterdamensis*) breeding on the Amsterdam Islands in the Indian sea. The Amsterdam albatross was down in only five breeding pairs due to introduction of cattle, cats and ship rats [23]. The two species are supposed to have developed from a common root 840,000 years ago, and this time span includes repeated glaciations, and the low genetic diversity with $H \leq 0.08$ may have existed before the deviation [24]. Both seem successful in their natural environment, though, the question is what will happen if the species encounter a new environment? Nevertheless, it is questioned whether their low genetic diversity has ever been a potential problem?

In Australia, with its distinctive fauna, the duck-billed platypus (*Ornithorhynchus anatinus*), representing the primitive mammal order Monotremata, is one of the most special. If any species deserves special attention, this is one of them. The distribution is limited to South and East Australia, and the populations are small. Reserves are established and platypuses have also been stocked to establish new populations [25], the last mean of conservation action, next to breeding in captivity. Two island populations are described by Furlan et al. [25]: one natural occurring population on King Island and a stocked population on Kangaroo Island. The King Island population has low genetic diversity due to low population number, whereas the stocked population has quite high genetic diversity due to admixture of specimens from different populations. Though the genetic diversity generally is low, $H_O = 0.026–0.55$, in platypus populations, they survive.

In North America, the black-footed ferret (*Mustela nigripes*) has been present from pleistocen (> 11,700 years ago) when they immigrated from Asia over the Bering strait [26]. The species was extinct in the wild, after the close to extinction of its main prey the prairie dog (*Cynomys* sp), followed by plague, when a breeding program started in 1985, based on 18 individuals, of which seven reproduced in captivity [27]. The expected heterozygosity dropped to $H_E \leq 0.11$ in some populations after bottleneck events in the 1970s, but the populations now seem to reproduce without noticeable effects of inbreeding.

2.2. How to keep a small but diverse gene pool

The species described above, all with low genetic diversity in at least some populations, still seem viable, but a crucial question is whether the low diversity populations are sustainable. Can they meet environmental changes to come? The lower the diversity and population size N, the higher the risk of loss from genetic drift following bottleneck events, and after generations, fixation of the most frequent allele at a locus may be expected, when loss rate exceeds mutation rate. Experiments have demonstrated lower fitness of low diversity specimens of, for example an estuarine crustacean (*Americamysis bahia*) showed reduced fitness (fertility, survival) in populations with low genetic diversity compared to populations of high diversity, and this was most pronounced in stressful environments [28]. Closely related mates may lead to inbreeding depression with loss of low frequent alleles. Nevertheless, inbreeding in wild populations of moderate size is not necessarily harmful, as it may lead to exclusion of recessive harmful alleles, purging, and result in a population that is more adapted to its environment [29, 30]. The effect, or cost, of inbreeding in wild populations is difficult to observe, and unfit combinations may be excluded in all stages of life, from pre-zygotic to reproductive phase [31].

Salmonid fishes are commonly bred in fish farms for food production and for stocking in rivers and lakes to improve fishery. Major economic interests are involved, and considerable effort is spent on research. Lehnert et al. [32, 33] found that sperm competition and cryptic female choice (CFC) help to maintain allele richness in Chinook salmon (*Oncorhynchus tshawytscha*). An assessment of genetic variation within metapopulations of steelhead trout (*Oncorhynchus mykiss*) related to climate and landscape showed that climate variation induced genetic variation [34], and the genetics of river living salmonids is affected by dams as obstacles to migration [35]. Several studies have showed genetic differentiation between wild and hatchery stocks, though of common origin, indicating serious effects of breeding based on forced, artificial mating, avoiding natural sexual selection [36, 37].

Human interventions of different kinds affect populations and their genetic diversity and structure, and the effect within a given time span is impossible to predict. Nevertheless, the loss or exclusion of alleles from a population is in any circumstances worrisome when it is due to human action. Conservation of metapopulations, consisting of small and moderately sized (effective population size $N_e < 50$) populations with some possibility of admixing, is one way to secure allele preservation. To explore this, natural metapopulations may be studied. Linløkken et al. [38] found in a study of brown trout (*Salmo trutta*) in nine tributaries to Lake Mjøsa in central Norway, that effective population size was positively related to habitat length (size). A bit unexpected, the heterozygosity based on MSs, was not correlated with

effective population size (mostly < 90) and was the highest in the middle-sized habitats. There was significant inbreeding coefficient F_{IS} in some of them, and the observed heterozygosity was in most cases lower than the expected. The low observed heterozygosity indicated inbreeding, which may lead to allele loss, but the lack of correlation between heterozygosity and N_e may suggest that other mechanisms worked. It could be due to increased fitness of heterozygotes, compared with the homozygotes, acting as a mechanism to slow down allele exclusion in populations. A conflicting interpretation of observed heterozygote excess is that heterozygote excess may indicate a recent bottleneck event [39].

Experiments with fruit flies (*Drosophila melanogaster*) demonstrated excessive heterozygosity, and this was explained by associative overdominance, that is, though the markers are noncoding loci, they are linked to causative loci that are under selection. Higher fitness of heterozygotes compared with homozygotes at the linked loci will retain the allele exclusion [40]. Noncoding or neutral markers may also be linked to (hitchhiking with) causative loci where coding alleles are removed by selection, called purging, excluding harmful recessive alleles. The reduction of hitchhiking non-coding alleles is called background selection [40].

3. On population size and heterozygosity of brown trout

3.1. Heterozygote excess in small populations of brown trout

A small tributary to the Lake Savalen in Central Norway serves as spawning area for brown trout of the lake. The number of breeders (effective population size of one cohort, N_b), based on linkage disequilibrium in 10 MS loci, was estimated to $N_b = 38$ for young of the year (0+) in autumn, and $N_b = 35$ for 1-year (1+) old fish in June the subsequent year (i.e., of the same cohort) [41]. The observed heterozygosity based on the same MSs, was $H_O = 0.69$ for 0+, and increased to $H_O = 0.78$ for 1+, and both were significantly higher than the expected heterozygosity ($H_E = 0.67–0.72$). This corresponded to $H_O = 0.333$ for both 0+ and 1+ and $H_E = 0.323$ and 0.325, respectively, based on SNPs. For both marker types, the deviation from Hardy–Weinberg equilibrium was significant, and this excess of heterozygotes is interesting. When comparing wild 0+ and 1+ and a group of hatchery brown trout, all of the same cohort, Linløkken et al. [41] found that allele frequencies were changed from October to June in the subsequent year and was even more differentiated in the hatchery group.

By analyzing biallelic markers, that is, with two possible homozygotes and one heterozygote, like in SNPs, this is simpler to explore than in cases of the poly-allelic microsatellites. Outlier F_{ST} analysis of 3871 SNP loci detected 421 (10.8%) loci as candidates of selection, and among those, 34 loci showed significant mean length differences between genotypes in the 1+ wild fish group. In 30 of these loci, the largest genotype was significantly more frequent in the 1+ than in the 0+ group, indicating positive selection of large specimens, and 19 (63%) of these large genotypes were heterozygotes. This indicated that the differentiation between fry and the yearlings was in part due to size selective mortality, disfavoring the smallest specimens of fry through increased autumn to spring mortality. At five loci, only one of the homozygotes was recorded in the 0+ group (**Figure 1**). The heterozygote was significantly more frequent in

the 1+ than in the 0+ group (Fisher exact test, $P < 0.05$) and was larger than the homozygote, different from in the 0+ group (**Figure 2**) (t-test, $P < 0.05$).

3.2. Simulating the fate of a low frequency allele at biallelic loci

The low allele frequency of **Figure 1** (p = approximately 0.10) was used to simulate allele exclusion by means of the Allele Simulator software (available on the web: http://popgen-simulator.pitt.edu/graphs/allele), choosing population size N = 25, 50, and 100, and performing 50 replicates of 50 simulations over 50 generations (corresponding to 150–250 years with maturation at 3–5 years of age). To explore the effect of allele frequency on exclusion rate, 50 simulations with N = 25 and allele frequency p = 0.01, 0.05, 0.10, 0.25, and 0.50 were conducted. Fitness was set to 1.00 for all genotypes, and the proportion of exclusion showed a curved decrease by increasing p and resulted in 97% exclusion with p = 0.01, being reduced to 90% with p = 0.05, further to 78% with p = 0.10 and to 23% with p = 0.50 (**Figure 3**). This suggests that with N = 25, the probability of retaining a p = 0.01 allele in 50 generations, without any heterozygote superiority, is close to null.

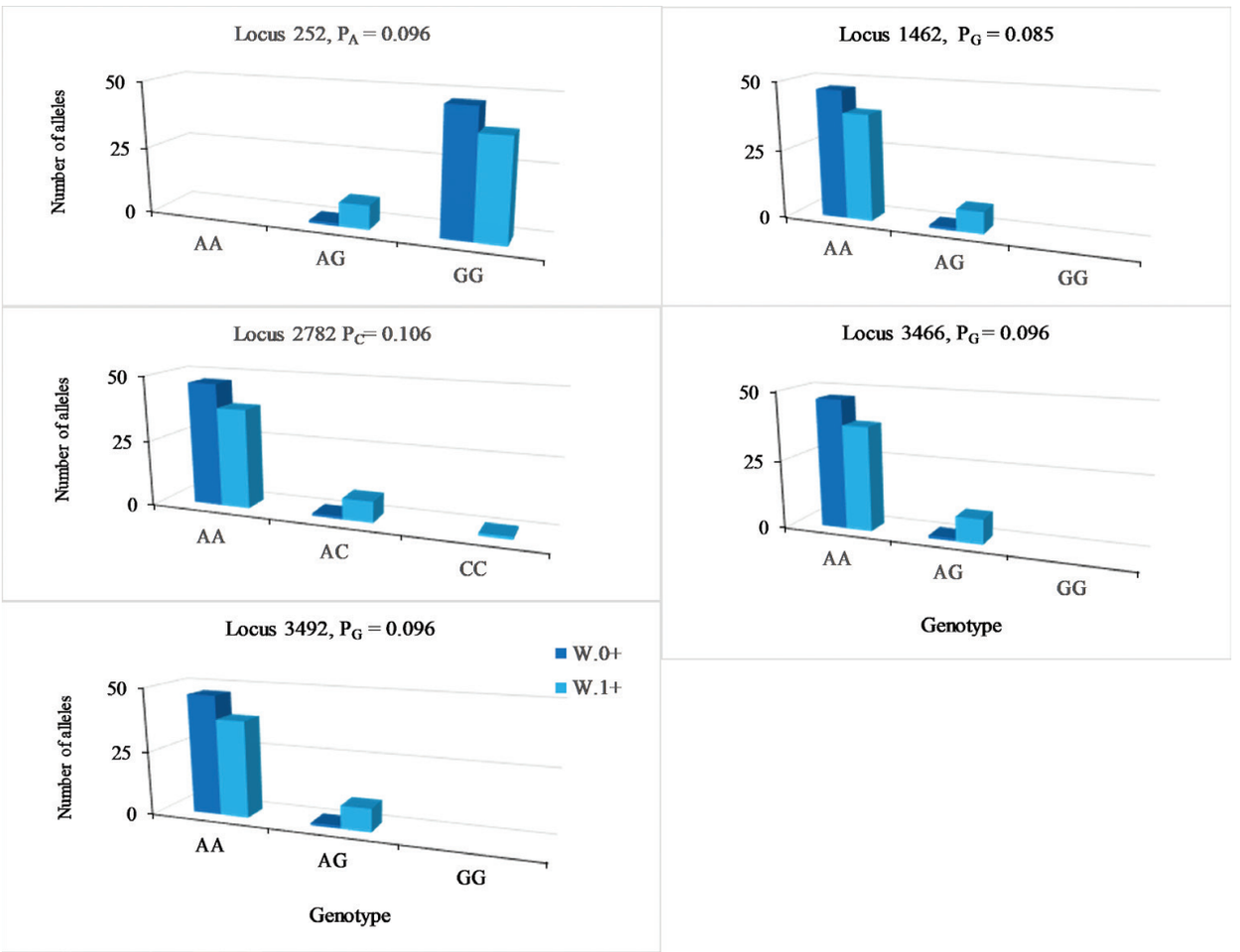

Figure 1. The distribution of genotypes of five SNP loci (numbers refer to Linløkken et al. [36]) in young of the year (W.0+, N = 48) and 1-year-old (W.1+, N = 47) brown trout of the same cohort and population. P denotes the observed frequency of the low frequency allele at the five loci.

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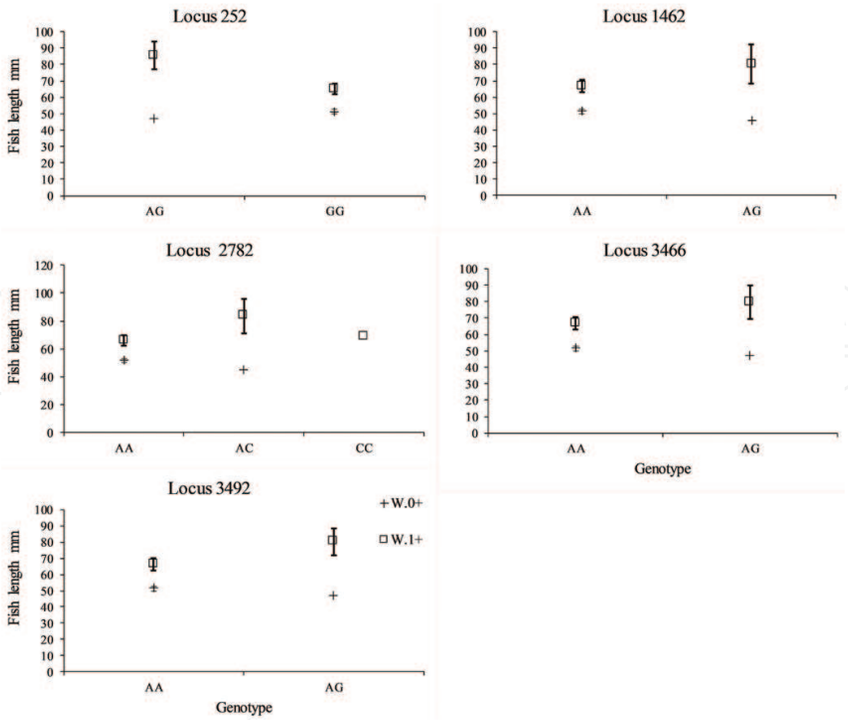

Figure 2. Mean lengths of young of the year (+) and 1-year-old brown trout (□) of different genotypes at loci at which mean length of heterozygotes were larger than that of homozygotes, and heterozygotes were more frequent in the 1-year-old group (W.1+) than in the young of the year group (W.0+) (**Figure 1**). Vertical lines show 95% confidence limits.

The initial allele frequency was then set to p = 0.10, and 50 simulations were run with fitness = 1.00 of all genotypes and N = 25, 50, 100, 200, and 400. The proportion of exclusion decreased exponentially by increasing N, and less than 50% of the simulations ended in exclusion when N > 77, and 62% of the simulations ended with exclusion with N = 50 (calculated from the regression, **Figure 4**). With N = 400, only 4% of the simulations resulted in exclusion.

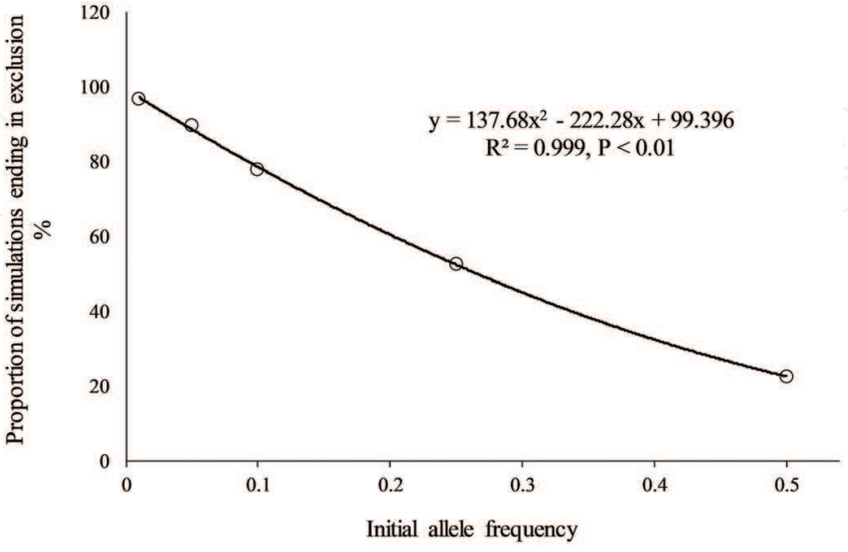

Figure 3. The proportion of 50 simulations that led to extinction during 50 generations in a population of N = 25 as a function of the initial frequency of the allele.

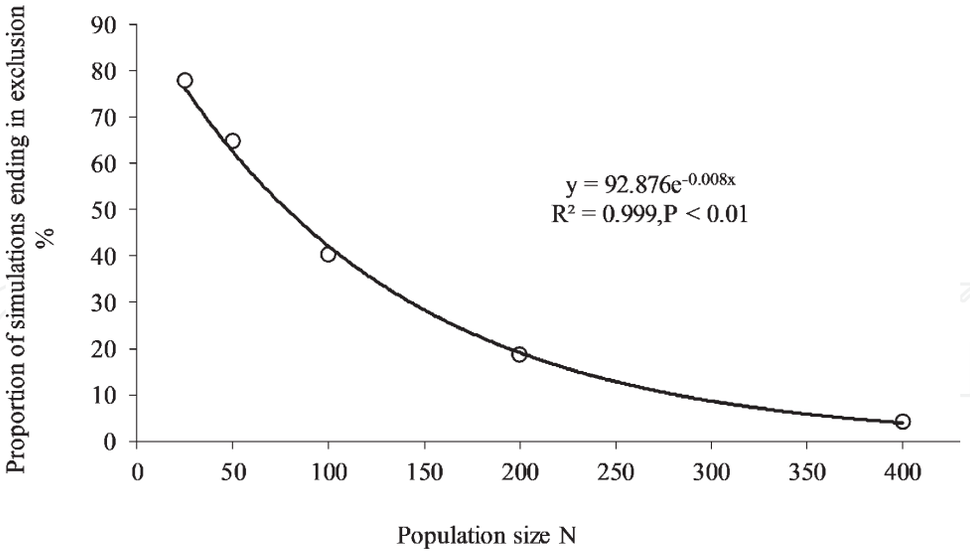

Figure 4. The proportion of 50 simulations that led to extinction during 50 generations of an allele with initial frequency p = 0.10 as a function of population size N = 25, 50, 100, 200, and 400.

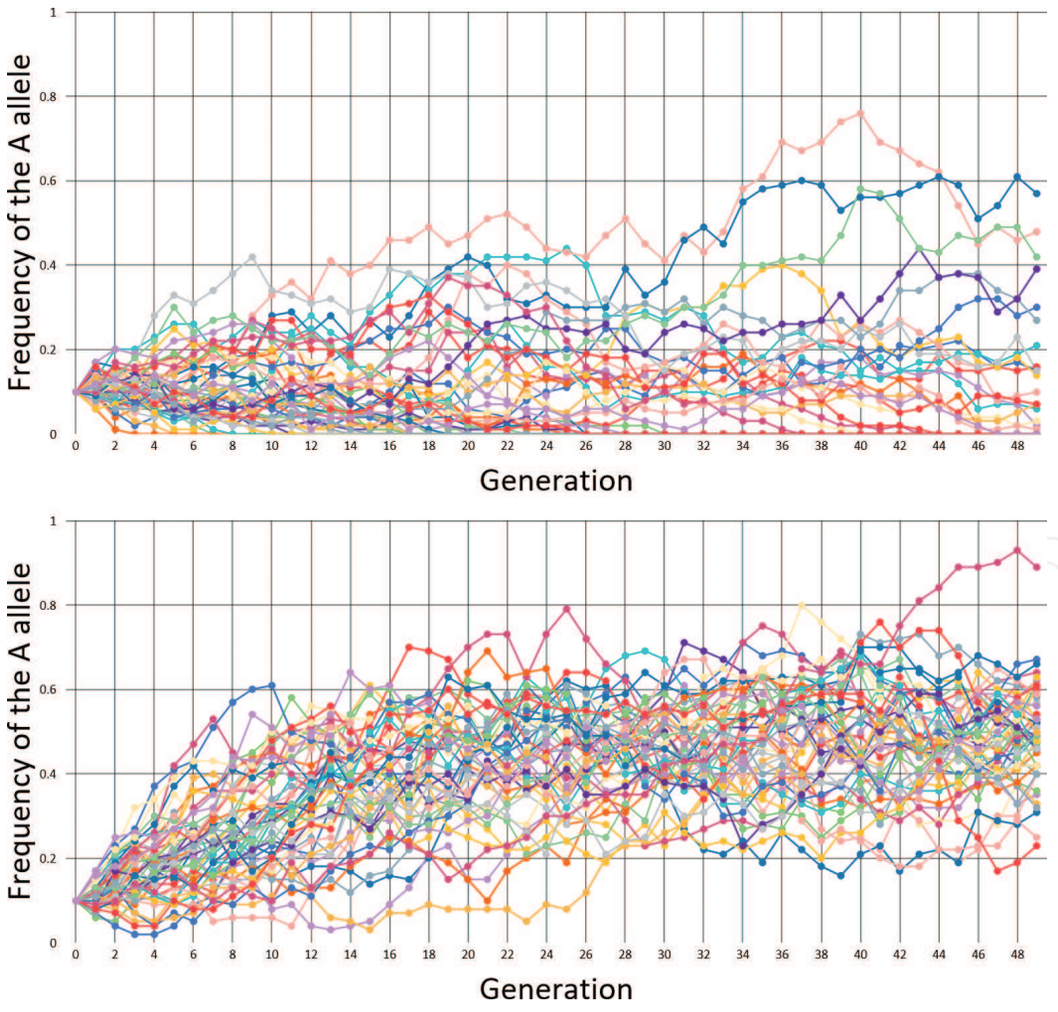

Figure 5. Proportion of 50 simulations of the frequency of an allele with initially p = 0.10 during 50 generations, population size N = 50 with fitness = 1 for all genotypes (upper panel), and with fitness = 1.0 of the heterozygote and fitness = 0.80 for both the homozygote (lower panel).

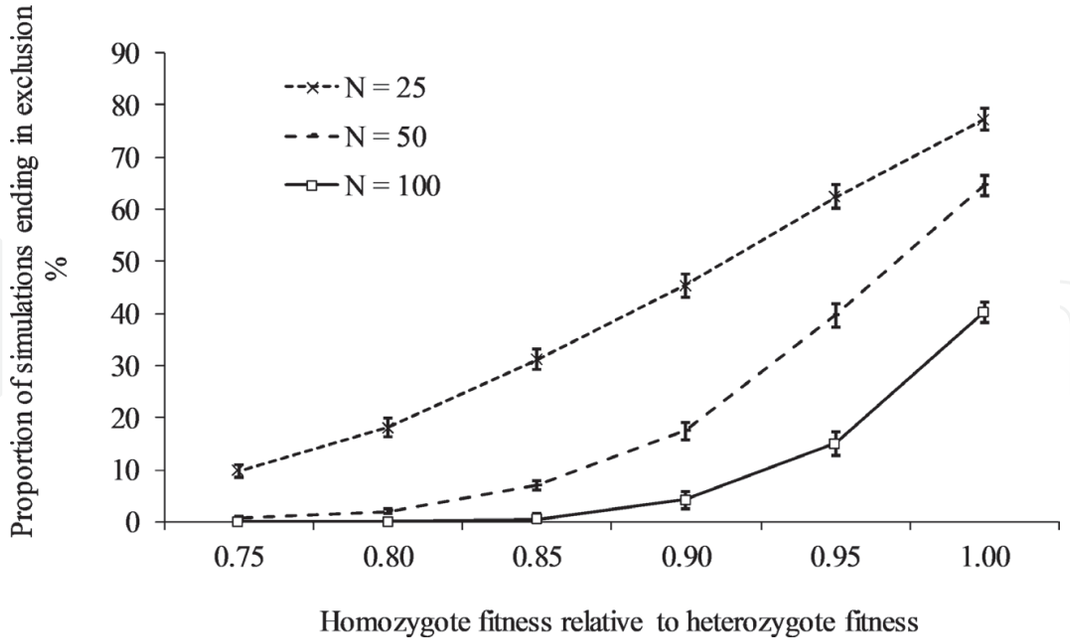

Figure 6. Proportion of 50 simulations of the frequency of an allele with initial frequency p = 1.0 that led to extinction within 50 generation with fitness = 1 of the heterozygote and fitness 0.75–1.0 of the two homozygotes and population size N = 25, 50, and 100.

To explore the effects of relative heterozygote fitness, the fitness of the heterozygote was set to 1.0, whereas the fitness of the two homozygotes was set equal, varying from 0.75 to 1.0, that is, the heterozygote fitness was similar or higher than that of the homozygotes. The simulations (**Figure 5**) showed that when fitness was equal for all genotypes, exclusion of the p = 0.10 allele decreased from 78% with N = 25 to 65% of the simulations with N = 50 and further to 40% with N = 100 (**Figure 6**). With fitness 0.90 of the homozygotes, less than 50% of the simulations ended with exclusion with N = 25, corresponding to less than 20% with N = 50, and less than 5% ended in exclusion with N = 100. Less than 10% of the simulations led to exclusion with homozygote fitness = 0.75 and N = 25, less than 1% led to exclusion with N = 50, and null simulations ended with exclusion with N = 100.

4. Conclusion

Many animal species, among them representatives of advanced groups like birds and mammals, thrive well despite low genetic diversity, that is, apparently with a limited toolbox for evolutionary adaptation to new environments. Nevertheless, when genetic diversity is low, it is important to retain the alleles that still exist to avoid fixation at all loci. In small populations, like N = 25, the exclusion rate is quite high for alleles of frequency p = 0.10, and it increased inversely with the allele frequency and population size, according to the simulation experiments. This will, to some extent, be compensated for by mutations and introgression from migrants. The exclusion rate was reduced when heterozygote fitness exceeded that of the homozygotes, as was expected, and the increased heterozygote fitness helps effectively to retard the exclusion rate of alleles. As an example, young of the year and 1-year-old brown trout suggested positive selection of heterozygotes during the first winter, possibly due to faster growth and increased survival of large specimens.

Acknowledgements

This work was funded by the Inland Norway University of Applied Sciences, as a part of the author's work as associated professor at this institution.

Conflict of interest

There is no conflict of interest.

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