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Reducing the loss of genetic diversity associated with assisted colonization-like introductions of animals

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Abstract Translocations, especially assisted colonizations, of animals are increasingly used as a conservation management tool. In many cases, however, limited funding and other logistic challenges limit the number of individuals available for translocation. In conservation genetics, small populations are predicted to rapidly lose genetic diversity which can deteriorate population survival. Thus, how worried should we be about the loss of genetic diversity when introducing small, isolated populations? Historical species introductions provide a means to assess these issues. Here we review 13 studies of "assisted colonization-like" introductions of animals, where only a small known number of founders established an isolated population without secondary contact to the source population. We test which factors could be important in retaining genetic diversity in these cases. In many cases, loss in heterozygosity (-12.1%) was detected, and more seriously the loss in allelic richness (-27.8 %). Number of founders seemed to have an effect but it also indicated that high population growth rate could help to retain genetic diversity, i.e. future management actions could be effective even with a limited number of founders if population growth would be enhanced. On the contrary, translocated organisms with longer generation times did not seem to retain more genetic diversity. We advocate that, where possible, future studies on translocated animals should report the loss of genetic diversity (both heterozygosity and allelic richness), which is essential for meta-analyses like this one for deepening our understanding of the genetic consequences of assisted colonization, and justifying management decisions [*Current Zoology* 61 (5): 827–834, 2015].

Keywords Introduced species, Loss of genetic diversity, Number of founders, Conservation management, Population growth rate, Generation time

One "law" of conservation biology is that in small populations genetic diversity is lost rapidly due to random genetic drift, environmental stochasticity and inbreeding (e.g. Frankham and Ralls, 1998). Loss of genetic diversity may reduce fitness (reviewed by Reed and Frankham, 2003; Briskie and Mackintosh, 2004) which can in turn impede population survival due to lowered adaptation to changing conditions (Frankham, 2005; Sarre and Georges, 2009). At the same time, we know that important findings in conservation genetic research are not translated into concrete conservation actions in the arena of international policy development (Gregory et al., 2006[1]; Laikre, 2010). Thus deeper knowledge on impacts of management methods is needed. Transferring living organisms from one locality to another (translocation, IUCN 1987) is a commonly-used conservation action (Seddon et al., 2007). Assisted migration (Peters and Darling, 1985; MacLachlan et al., 2007) or assisted colonization (Hoegh-Guldberg et al., 2008) is one form of translocation. In assisted colonization, individuals are transplanted to suitable locations they could not reach themselves, for example because of human-made barriers such as areas of low habitat quality (Parmesan, 2006; Carrol and Fox, 2008). Assisted colonization has been notably applied to plant species threatened by e.g. fragmentation or global warming (Vitt et al., 2010). Given its success in plants, it is likely that this conservation tool will become increasingly attractive in animals.

One challenge, however, is the relative difficulty of introducing a large number of individuals of an animal species. This is because (1) introductions will be most attractive in species which are threatened or declining, making it unwise to taranslocate large numbers of individuals from the original population, (2) translocation of animals is likely to be shouldered by a relatively small group of engaged stakeholders forming a Non-Governmental Organization (NGO) with limited possibility tofound a population with a large number of individuals. Hence, from a practical conservation biological viewpoint, introduction of an animal population probably concerns a very small founding population. In this paper,

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we consider the issue of how concerned conservation biologists should be about genetic diversity when founding an animal population within a translocation scheme.

Conservation biologists would in first instance expect that an introduced population founded by few individuals would suffer a severe genetic bottleneck with negative consequences for population survival. However, this concern is not always shared by researchers in the field of invasion biology. This is because populations of invasive species often have managed to retain a lot of their genetic diversity (Sax et al., 2005). In fact, the "genetic paradox" of how newly founded populations can overcome expected low genetic diversity and low evolutionary potentials considered to have been partly resolved in invasion biology (e.g. Roman and Darling, 2007). Indeed, factors like high propagule pressure, multiple introductions or genetic admixture of founding populations have been found to explain the surprisingly high levels of genetic diversity of many invasive populations (e.g. presented in Allendorf and Lundqvist, 2003; Stepien et al., 2005). There are, however, also examples of invasive populations being successful despite a relatively low diversity. Nevertheless, one important potential difference between invasive species and a population introduced especially within the context of assisted migration is that colonisation in the former has occurred through the species' own dispersal capacity (although possibly aided by humans). As a consequence, a newly established population of an invasive species has the potential for secondary contact to other existing populations. In the case of a population introduced as a conservation measure (e.g. assisted migration), the dispersal capacity of the organism is – by definition – insufficient to reach the newly established population of its own accord or there may not be any other populations. Hence, what happens to genetic diversity in a small, completely isolated population, is of relevance for conservation biology but does not necessarily hold for all invasive species. Even though there are a good number of studies dealing with genetics of introduced species (Ewen et al., 2012; Groombridge et al., 2012) the exact introduction history is known only in a limited number of these reviewed cases. In this paper, we have compiled literature studies specifically on "assisted colonization-like introductions" where there is only one founding event with a small known number of individuals. Earlier reviews have handled many types of introductions where number of founders can be large, founding can happen several times and the populations are open for migration. Thus this approach of "assisted colonization –like introductions" gives a new perspective particularly targeted for conservation biology.

Our aim here is to assess the loss of genetic diversity following narrow introductions, for example, whether the loss of genetic diversity in these particular cases is smaller (or larger) than the losses reported in more general reviews. Moreover, based on literature studies, we test hypotheses regarding factors possibly lowering the loss of genetic diversity. First, we expect low loss of genetic diversity in translocated populations which experienced a rapid initial population growth. This is because the loss rate of genetic diversity in a population is inversely related to the effective population size (Nei, 1975). Rapid initial population growth is thus likely to be a main factor to counteract the loss of genetic diversity in a population founded by few individuals. Second, we expect that animals with a long generation time show a lower loss rate of genetic diversity. Individual-based population genetic models demonstrate that when generations overlap, loss rate is higher when generation time is shorter (Kaeuffer et al., 2007). Third, we expect that a larger number of founders could pass on more genetic diversity to the following generations especially in terms of allelic richness.

1 Material and Methods

We scanned the literature for population genetics studies on introduced populations where the number of founders was known, but where the newly founded population had no gene flow with other populations. Databases used for this purpose wereISI Web of science, EBSCO and Google Scholar. Search strings were: population genetics, small populations, introduction, re-introduction, genetic diversity, loss of genetic diversity, invasion, invasive, conservation, population of origin, source population, bottleneck, number of founders, population growth rate. These were used in the searches both individually as well as in all combinations. Based on the details given in the original publication, we further selected studies where a comparison between the genetic diversity of the founded population and the genetic diversity of the original population (or one close to it) was possible. While it is interesting to estimate the introduction history based on the genetic attributes of the current

[1] Gregory A et al., 2006. The conservation of genetic diversity: Science and policy needs in a changing world. JNCC report No 383.

population (e.g. Bonhomme et al., 2008) it does not give us a reliable picture of how the genetics are affected by very specific initial conditions. Lastly, we extracted information on the population growth of the initial years after founding the population.

To explore the possible factors affecting the amount of genetic diversity which is retained in these founding events, cases of high and low population growth rates were separated. The criteria of high and low population growth rates was determined by checking the numbers reported in the studies and moreover how the authors themselves described the population growth rate when they took into account the species and its ecology. As a result, in 8 out of 9 cases of high population growth rate the number of animals had increased from the founding within tens of years into thousands or tens of thousands and authors also considered the rate high. In one case (hihi, Brekke et al., 2011) one population of hihi was considered having a high population growth rate even though the number of animals was around 140. This was because the authors described the carrying capacity of the island for this sized population and the growth rate having been very high for hihi. The other hihi population had a low growth rate for a long time. In the study cases that were classified as having low population growth rates the number of animals had increased only to tens or maximum of few hundreds and the authors considered them low for the species. Multiple regression analyses were conducted so that population growth rate, generation time (transformed with square root) and the number or founders were included as explanatory factors and either the loss of expected heterozygosity or the loss of allelic richness as the dependent variable. All analyses weredone with program R 2.10.1 (R development Core Team, 2010). Expected (instead of observed) heterozygosity was focused on in our analysis since it is less sensitive to sample size andbest comparable across studies. In addition, allelic richness was included since it is generally predicted to be more sensitive to founder effects than is heterozygosity.

2 Results

Among the 13 published studies we compiled according to the strict criteria (with a known number of founders, without gene flow, and genetic diversity indexes reported; Table 1), the overall mean decline in expected heterozygosity was 0.085 (-12.1%) and in allelic richness 1.60 (-27.8%). The number of loci used in each study ranged from 4 to 40, being on average 13. All loci were polymorphic. In all of the studies the loci used were either developed for the species in question or carefully selected from loci developed originally for other related species but now tested to amplify efficiently and correctly for the particular study species. The same loci where used for pre- and post-bottleneck comparisons in every study. Thus the generalisations made by this review are based on reasonably good genetic data.

When results of these studies were analysed with multiple regression models (Table 2), the directions of the effects of explanatory variables were similar for both genetic diversity indices. Given the low number of studies available, it was encouraging that the direction of the effects of number of founders and population growth rate made biological sense: with more founders less diversity was lost and also high population growth rate helped to retain more diversity. However, with more overlapping generations more diversity was lost which is not biologically expected when considering the general predictions of the genetic theory. An increased number of founders lowered the reduction in allelic richness significantly (Table 2), and the reduction in allelic richness tended to be lower (one-tailed significance; Table 2) in population with a high population growth rate.

3 Discussion

How worried should we be about the loss of genetic diversity when founding a small, isolated population as a conservation management action? We here explore this question using published information of genetic diversity of translocated animal populations which have been founded by a limited number of individuals and which have not had a secondary contact to the source population. We searched the literature for such examples, because they provide a reasonable case study of what an assisted migrationor other conservation targeted translocation event in conservation would look like. Expected heterozygosity in these studies declined by 12.1% and allelic richness by 27.8%. We expected that high population growth rate would be one factor to ameliorate the loss of genetic diversity. The results from literature cases did not give clear support to this hypothesis but the direction was clear andwe found some evidence ($P < 0.1$) of a lower loss in allelic richness when the initial population growth rate was high. In addition, a striking aspect is that all translocations where the loss of expected heterozygosity was less than 10% were populations with a high population growth rate. A higher number of founders reduced loss of genetic diversity ($P = 0.049$). In contrast to what we pre-

Table 1 Compilation of literature on "assisted colonization-like introductions" reporting loss of genetic diversity

Species	Location	Generation time (years)	N of f	N of gen	Pgr	Number of loci	Change in genetic diversity indices			Reference
							H_E	H_O	A_R	
European rabbit *Oryctolagus cuniculus*	Australia 1859	1	13	~143	high	7	0.64-0.79 → 0.67	0.44-0.66 → 0.66	NR→NR	1
Bennett's wallaby *Macropus rufogrisens r.*	New Zealand 1874	5	3	~25	high	4	0.60-0.87 → 0.59	0.45-0.60 → 0.57	NR→NR	2
Bighorn sheep *Ovis Canadensis*	Montana USA 1922	5.7	12	14–15	low	9 *	NR →NR	0.59 → 0.44	NR →NR	3
Mouflon *Ovis aries*	Kerguelen Island 1957	~2	2	~23	low	25 *	NR →NR	0.45 → 0.48	NR →NR	4
Moose *Alces alces*	Newfoundland 1878 and 1904	6.9–10.7	6	17–11	high	5 *	NR →NR	0.41 → 0.22-0.35	NR →NR	5
Marsh frog *Rana ridibunda*	Britain 1935	3	12	~23	high	5	0.52 → 0.48	0.35 → 0.36	3.2 → 2.2	6
Hihi *Notiomystis cincta*	New Zealand 2004-07	2.5	30 (1983) 37 (1994)	9.1 4.9	low high	19 19	0.68 → 0.58 0.68 → 0.64	0.66 → 0.61 0.66 → 0.66	5.19 → 3.88 5.19 → 4.71	7
Alpine ibex *Capra ibex ibex*	Alps 1921-1984 several populations	8	9–137	11.5–3.6	high	40 *	0.45 → 0.35–0.47	0.42 → 0.34–0.49	2.81 → 2.12–2.76	8
Elk *Cervus elaphus roosevelti*	Alaska 1929	4	8	20	high	15 *	0.53 → 0.42	0.53 → 0.41	3.67 → 2.67	9
Bison *Bison bison*	Texas. USA 1997/1880's	4	36/5	1-31	low	15 *	0.57 → NR	0.63 → 0.38	4.74/4.15 → 2.54	10
Pronghorn antelope *Antilocapra Americana*	Oregon. USA 1969	3	17	~13	low	5	0.75 → 0.66	0.73 → 0.71	8.6 → 5.6	11
Brown bear *Ursus arctos*	Austria 1972 1 male 1989- 93. 2 females, 1 male	10	4	~4	low	8	0.73 → 0.59	NR → 0.70	NR → 2.88	12
White-tailed deer *Odocoileus virginianus*	Finland 1938	3	4	~24	high	14	0.74 → 0.69	NR	9.07 → 5.36	13

1. Zenger et al. 2003. 2. Le Page et al. 2000, 3. Hogg et al. 2006, 4. Kaeuffer et al. 2007, 5. Broders et al. 1999, 6. Zeisset and Beebee 2003, 7. Brekke et al. 2011, 8. Biebach and Keller 2008, 9. Hundertmark and van Daele 2010, 10. Halbert et al. 2004,11. Stephen et al. 2005, 12. Kruckenhauser et al. 2009, 13. Kekkonen et al. 2012.

We provide the common and scientific species name (Species) as well as the location of the introduction, the generation time and type of founding event (introduction = I. re-introduction = RE). For each study, we provide the N of founders (N of f), and the approximate number of generations since founding the population when the genetic diversity was measured (N of gen) as well as the population growth rate (pgr) qualitatively categorised as high or low based on the original report. All of the studies had microsatellite loci. Asterisk (*) next to the number of loci indicates that the loci used in the study were homologous. The absolute change in genetic diversity (measured statistic reported, comparison between original -> founded population) for expected heterozygosity (H_E), observed heterozygosity (H_0) and allelic richness (A_R). All the studies have used microsatellites. NR = not reported.

Table 2 Results for multiple regression models on loss of expected heterozygosity and allelic richness

	Coefficients for loss of expected heterozygosity				Coefficients for loss of allelic richness			
	Estimate	Std. Error	*T*-value	*P*-value	Estimate	Std. Error	*T*-value	*P*-value
Intercept	4.76	5.20	0.9	0.395	18.65	16.77	1.1	0.328
Number of founders	-0.17	0.097	-1.3	0.242	-0.66	0.24	-2.8	0.049
Population growth rate	3.99	3.28	1.2	0.269	14.85	6.57	2.3	0.087
sqrt(generation time)	4.02	2.49	1.6	0.158	10.27	9.57	1.1	0.344

sumed, however, animals with long generation time did not experience a lower loss in genetic diversity. Overall, however, it should be noted that the number of studies is relatively low so the results need to be interpreted with caution. Nevertheless, these analyses raise important issues which should be considered in conservation biology.

Our focus was different from previous reviews dealing with introduction genetics because it included only introductions wherea known small number of individuals were introduced by humans to new isolated areas and from which the population growth patterns were also available. In a review of 29 studies where genetic diversities of introduced animal populations could be compared to populations of origin, Wares et al. (2005) found that diversity loss was typically rather small, on average 17% for heterozygosity with most values being even much smaller. When comparing allelic diversities they found that founder effects may have a slightly larger impact on the loss of rare alleles (average loss 18.7%). Also a review studying the role of multiple introductions to invasion success including 80 plant and animal species (Dlugosch and Parker, 2008) revealed the average loss of expected heterozygosity to be 18.7% and the reduction of allelic richness 15.5% (however, note that a paired comparison showed that proportional losses of allelic richness were on average 5.1% more severe than losses of heterozygosity). However, many of these case studies do not meet the criteria for "assisted colonization-like introductions" which we are interested in. Hence, the lack of loss of variability in these studies can be often be explained by propagule pressure, admixture or multiple introductions. Indeed, in a meta-analysis Uller and Leimu (2011) showed that multiple founding events and number of founders positively correlated to establishing a population, but that the loss or gain of genetic variation was not correlated with invasiveness. This suggested that even with considerable loss there is a possibility to become invasive. Our review of the literature shows that the average rate of loss for "assisted colonization-like introductions" was less in terms of heterozygosity than the above mentioned examples i.e. 12.1% vs. 17% and 18.5% reported by Wares et al. (2005) and Dlugosch and Parker (2008), respectively. On the other hand, loss of allelic richness in these "assisted colonization-like" introductions was larger, 27.8% vs. 18.7% and 15.5% reported by Wares et al. (2005) and Dlugosch and Parker (2008), respectively. The strong reduction in allelic richness is not surprising since allelic richness is clearly determined by the number of individuals used to found an introduced population and the number of founders is likely much smaller in "assisted colonization-like introductions" compared to introductions in general. The number of studies where allelic richness was reported was fewer than cases reporting heterozygosities. In theory this could mean that the reductions in allelic richness would be on the large side by chance. However, the trend itself is clear and also the choice and testing of loci were executed well in all of the studies increasing the reliability of our results and the comparability of the studies to each other. On the other hand, a potential problem measuring the loss of genetic diversity could rise from employment of homologous loci (i.e. loci originally developed for related species). Homologous loci are known to be less polymorphic in the recipient species (e.g. Forbes et al., 1995) potentially deflating also the loss of diversity. However, in this review, seven out of thirteen studies had loci specifically designed for the study species. The remaining six studies may have suffered from reduced diversity due to the use of homologous loci (indicated in Table 1). Overall, this could imply that the results of our analyses are a potential under-estimate of the expected loss in genetic diversity after assisted colonization.

Most translocation attempts fail or succeed only partially, and we presently do not have a clear understanding on why this is the case (Seddon et al., 2007; Chauvenet et al., 2013). The role of the loss of genetic diversity in causing failure of translocation hence remains unclear. Because our compilation of published studies necessarily focuses on those translocations which succeeded, it does not inform us of the importance of loss of genetic diversity for translocation in general. On the

other hand, the literature estimates we here present reveal that successful establishment of a translocated population is possible even when 20%–25% of expected heterozygosity and up to 40% of allelic richness is lost. Furthermore, one striking finding is that genetic diversity may not be lost as easily as intuitively would be predicted when looking at just the number of founders. There are several successful translocations based on less than 10 individuals where the loss of heterozygosity was minimal. Our analyses show that the number of founders is one determining factor but it is not the only one. We find weak evidence that high population growth rate could be another importantfactor in lowering the loss of genetic diversity after translocation. For example, in bighorn sheep (Hogg et al., 2006), birds introduced in New Zealand islands (Jamieson, 2010; Brekke et al., 2011) and bison (Halbert et al., 2004) population growth has been very limited and there has been a clear decrease in diversity (note that in bighorn sheep a genetic rescue done after bottleneck increased then the genetic diversity). In the European rabbit (Zenger et al., 2003) and the marsh frog (Zeisset and Beebee, 2003) the number of founding individuals has been low but diversity has not been lost much which could be a result of the strong growth of populations. However, there are case studies that do not fall into this dichotomy. For example, an island mouflon population founded by only two individuals where population growth rate has been small, much of the genetic diversity has been retained (Kaueffer et al., 2007). This low loss rate was argued to be due to positive selection on the genetic diversity itself (heterosis; Kaeuffer et al., 2007), a process which is particularly likely to occur after a bottleneck (Hansson and Westerberg, 2002). One study which directly implicated high population growth rate as the rescue of genetic diversity is the introduction of the hihi, where a similar number of individuals were introduced to two islands but the populations experienced very different population growth rates (Brekke et al., 2011). Contrary to our expectation, we found that animals with long generation time did not experience a lower loss in genetic diversity. Kaeuffer et al. (2007) used an individual-based population genetic model to demonstrate that lower loss of genetic diversity was expected when generation time was assumed to be longer in their study species. Across species, however, long generation time is associated with low productivity of offspring which may hamper the capacity of the population to reach large effective population sizes after introduction. In particular, loss of genetic diversity would be expected ifthe long-lived species had strong assortative mating, thereby further lowering effective population size.

The amount of case studies here is limited and thus more targeted research would be highly useful. The fact that only this many cases were found is in itself noteworthy because it flags out the lack of studies in this important topic. We expect there are a number of populations resulting of a known translocation events of animals where information is available on when and what number of founders were released as well as on the dynamics of the population. By carrying out genetic studies on such populations, we could expand our knowledge of the relative roles of founders, population growth rate and generation time in determining genetic diversity of translocated populations. Based on this data set, the effect of number of founders is evident (especially in terms of allelic richness) but if indeed e.g. the role of population growth rate has been underestimated in conservation introductions, more resources should be also allocated to it in management. Our compilation also reveals that many studies do not report all relevant measures: Future studies should improve reporting basic measures of both heterozygosity, as well as allelic richness. Heterozygosity can be used as a measure of a population's capacity to respond to selection immediately after a bottleneck. Allelic diversity, on the other hand, determines a population's ability to respond to long-term selection over many generations, and ultimately the survival of the population (Allendorf, 1986). Moreover, marker choice should be carefully considered. In all of the study cases found in this literature search the markers used for genetic analysis are microsatellites. This can raise criticism about how well these neutral markers indicate the changes in loci under natural selection responsible for additive genetic variance. However, as Wares et al. (2005) pointed out there are few studies where information on quantitative genetic loci is available. More importantly, neutral markers most accurately reflect a population demographic history (Avise, 2000). Clearly, population genetics employing high-throughput sequencing will in the future allow rapid and more in-depth exploration of these issues.

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