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FAST-TRACK

Elevation and connectivity define genetic refugia for mountain sheep as climate warms

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Abstract

Global warming is predicted to affect the evolutionary potential of natural populations. We assessed genetic diversity of 25 populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in southeastern California, where temperatures have increased and precipitation has decreased during the 20th century. Populations in low-elevation habitats had lower genetic diversity, presumably reflecting more fluctuations in population sizes and founder effects. Higher-elevation habitats acted as reservoirs of genetic diversity. However, genetic diversity was also affected by population connectivity, which has been disrupted by human development. Restoring population connectivity may be necessary to buffer the effects of climate change on this desert-adapted ungulate.

Keywords: bighorn sheep, climate change, genetic diversity, habitat fragmentation, metapopulation, *Ovis canadensis*

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Introduction

Major climate transitions during the Earth's history are typically associated with species extinctions, as the rate of ecological change supersedes that of species adaptation. The current global climate forcing has the potential to represent such a major transition, and has already caused substantial ecological changes which have led to local population extinctions and species-range shifts upward in elevation or towards the poles (McCarty 2001; Walther *et al.* 2002; Parmesan & Yohe 2003). As ecological evidence of the effects of global climate forcing on populations and species has mounted, subsequent changes in evolutionary potential (as measured by genetic diversity) are predicted for many species (Kappelle *et al.* 1999; Davis & Shaw 2001; Jump & Penuelas 2005). Genetic diversity has been theoretically and empirically linked to fitness (e.g. Frankham 2003; Hildner *et al.* 2003; Charpentier *et al.* 2005; Hedrick 2005), and may enhance ecosystem recovery after climatic extremes (Reusch *et al.* 2005). Change in genetic diversity may be both an indicator of rapid ecological change and, in the event of loss of genetic diversity resulting from unfavourable ecological change for a given species, a potential factor in limiting the ability of that species to adapt to further ecological change.

However, the effect of rapid environmental change on genetic diversity may also be mediated by the spatial distribution of species (Jump & Penuelas 2005): those that persist in small, fragmented populations may be particularly likely to experience an accelerating loss of genetic diversity as rapid habitat changes or increased environmental stochasticity cause local extinction or population 'bottlenecks'. For this reason, species inhabiting 'sky islands' (mountains isolated by surrounding low-elevation desert habitat) may serve as indicators for the effects of climate change on species in the temperate regions of the earth (McDonald & Brown 1992). Species in such high-elevation habitats are often more isolated and more likely to become 'trapped' outside their climatic optimum (Jump & Penuelas 2005). Thus, changes in genetic diversity resulting from recent climate change may be more quickly detectable for these species, given that connectivity is low and the opportunity for behavioural responses (e.g. northward movement) is limited. However, while changes in genetic diversity (both increases and decreases) have been correlated with previous periods

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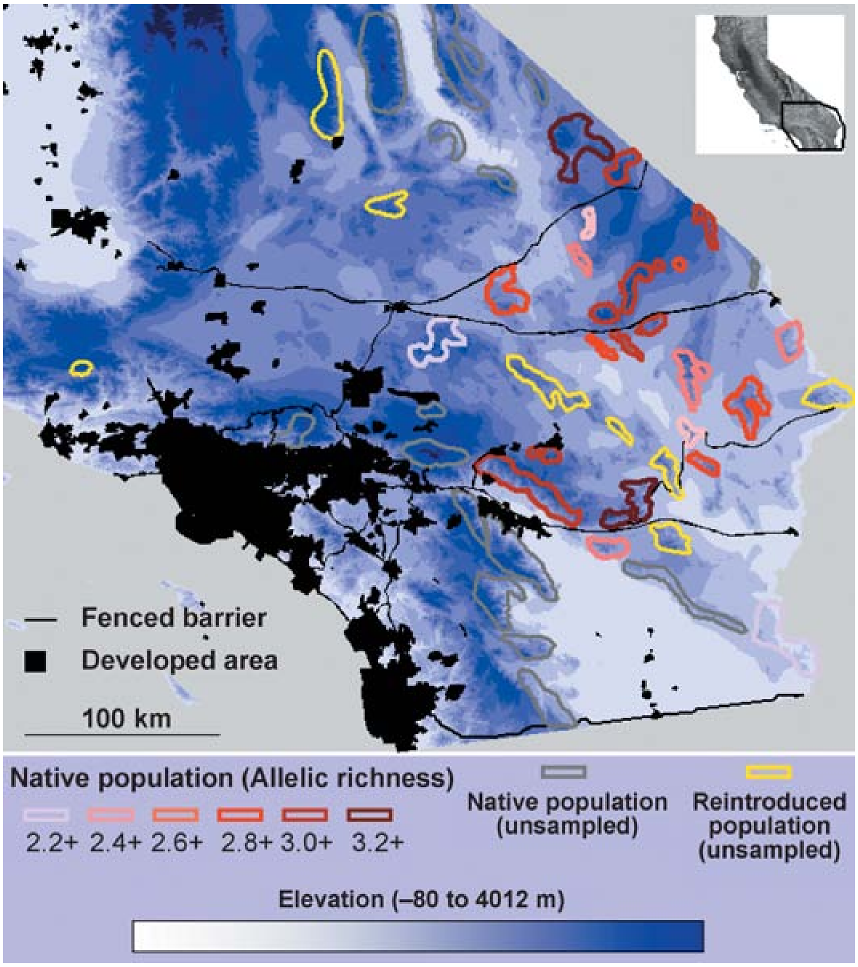

Fig. 1 Genetic diversity of 25 desert bighorn sheep populations in California, USA, with elevation and human-made barriers to dispersal (developed areas, fenced highways and canals). Unsampled populations were included when measuring isolation of sampled populations; sampling was not conducted in these locations because they were in military bases with restricted access, supported translocated sheep of known origin, or were outside the area defined for this study. Clusters of genetically diverse populations in high-elevation habitat with good connectivity may serve as genetic refugia during extended droughts and as sources of genetic diversity during more favourable climatic conditions.

of rapid climate change (e.g. Hadly *et al*. 2004), recent examples of this phenomenon (e.g. Levitan & Etges 2005) are still rare. Here, in a temperate desert region that has experienced declining precipitation and increasing temperature during the 20th century, we assess whether genetic diversity of a 'sky island' species is correlated with variation in elevation and the spatial structure of populations.

Desert-dwelling mountain sheep (*Ovis canadensis nelsoni*, hereafter referred to as desert bighorn sheep), though adapted to desert conditions (Wehausen 1984), are generally restricted to mountainous habitat that offers escape terrain and suitable forage. Moreover, there is evidence that their range has contracted during the period of recent climate warming: desert bighorn sheep were originally distributed over more than 75 mountain ranges in the desert regions of California, as of the early 20th century (Wehausen *et al*. 1987; Torres *et al*. 1994; Wehausen 1999). However, coincident with a 20% decrease in precipitation (Ball *et al*. 1998) and a 1 °C increase in average temperature during the latter half of the 20th century in the southeastern deserts of California (Lane *et al*. 1994), at least 26 populations have gone extinct (Wehausen 1999; Epps *et al*. 2005b). As expected for a species dependent on sky-island habitat, population extinction was more common in mountain ranges of lower elevation, where average annual precipitation was low, perennial springs were lacking, and temperatures were higher (Epps *et al*. 2004). Environmental stochasticity in the region is high; as a result, lamb recruitment is very variable (Wehausen 2005). Thus, desert bighorn sheep in this region appear vulnerable to any decrease in habitat quality as mediated by climate.

In this study, we assess whether genetic diversity in 25 of the remaining populations of desert bighorn sheep in California (Fig. 1) is correlated with mountain-range elevation. Elevation encapsulates much of the variation in precipitation, temperature and the presence of perennial springs in this region (Epps *et al*. 2004). If the late 20th century-trend of hotter and drier climate in this area has reduced population size or has caused stronger fluctuations in population size in low-elevation habitat, we expect genetic diversity to be reduced in these areas. Additionally, we evaluate whether genetic diversity is correlated with population area or current census population size (and ascertain that these measures are not correlated with elevation) and examine the correlation of genetic estimates of effective population size (N_e) with genetic diversity, isolation, elevation and other relevant variables.

We also assess whether spatial structuring of these populations has mediated the effects of climate change on the genetic diversity of fragmented populations. The size and relative connectivity of populations can affect levels of genetic diversity both within and across populations: if the rates of population turnover (extinction and colonization) are relatively high, genetic diversity typically declines at both levels (Whitlock & Barton 1997; Pannell & Charlesworth 1999; Pannell & Charlesworth 2000; Haag *et al*. 2005). Clusters of desert bighorn populations in California appear to behave as metapopulations (Schwartz *et al*. 1986; Bleich *et al*. 1990; Bleich *et al*. 1996) *sensu* Levins (1969), where populations in each mountain range are largely demographically independent and extinction and re-colonization are common (Wehausen 1999; Epps *et al*. 2005b; Epps *et al*. 2005c). The nonuniform distribution of these populations causes considerable variation in gene flow and genetic diversity: both are strongly negatively correlated with population isolation, previously found to be a function of the distance to neighbouring populations, as well as with the presence of fenced interstate highways, canals and urban areas which hinder dispersal among populations (Epps *et al*. 2005a). Consequently, these populations present an opportunity to evaluate how variation in connectivity and climate conditions may simultaneously affect species with highly fragmented distributions.

Materials and methods

We genotyped 361 desert bighorn sheep, at 14 microsatellite loci, in 25 naturally established populations in desert habitat in southeastern California (Fig. 1). The target loci, PCR conditions and extraction techniques are described in Wehausen *et al*. (2004) and Epps *et al*. (2005a). We employed mainly DNA extracted from faecal samples collected at waterholes during the summers of 2000–2003, as well as DNA extracted from blood and tissue samples obtained from the California Department of Fish and Game. Each sample was amplified a minimum of four times at each locus (with at least two successful amplifications) to detect and correct the increased numbers of genotyping errors that commonly result from the use of faecal DNA. The average rate of allelic dropout per locus per replicate for the faecal samples was estimated at 3.7%, and the rate of occurrence of false alleles was estimated at 0.062%, resulting in a final estimate of 0.022 genotypic errors per individual, given a minimum of two successful replicates. Given an error rate of 0.022, in a sample set of ~400 individuals typed at 14 loci, the expectation is approximately 10 single-locus errors across all consensus genotypes. Because this estimated error rate assumes that every sample is heterozygous at all loci, and that there were only two replicate PCR amplifications at each locus, this estimate of the genotype error-rate is likely to be higher than the actual rate (most samples were successfully amplified 3–4 times) and is unlikely to bias our findings. Complete details of collection of genetic data, estimation of error rates and identifying unique genotypes (making it possible to eliminate duplicate samples) are described in Epps *et al*. (2005a).

We evaluated allelic richness (A = average number of alleles per locus, corrected for sample size) and expected heterozygosity (H_e). A is expected to decline more rapidly than H_e when the effective population size is small and therefore is a sensitive indicator of population bottlenecks (Leberg 2002). Our sample sizes varied widely (mean $n = 14.5$, range 4–29, 22 of 25 populations had at least 10 samples, see Table S1), in part because some populations are so small (< 10–15 individuals) that obtaining samples sizes > 10 via faecal DNA required a great deal of effort. We used FSTAT version 2.9.3 (Goudet 1995) to estimate A, corrected by the smallest population sample-size, for all populations. We used GENEPOP (Raymond & Rousset 1995) to estimate H_e for each population.

We employed multiple linear regression models to evaluate whether genetic diversity (A and H_e) was correlated with maximum elevation of the mountain range inhabited by each population ($\log_e$ transformed, as suggested by the relationship of elevation with variance in diet quality for bighorn sheep described by Epps (2004)). We also evaluated the correlation of genetic diversity with population isolation, the area of each mountain range inhabited by each population, latitude and the current local population size (Table S1). The local population size-estimates were derived from the mid-point of population size-classes reported in Epps *et al*. (2005b); population size-classes in turn were compiled from a heterogeneous body of data that included minimum counts, aerial surveys and observations at waterholes (as a result, these data are likely to be inaccurate).

We also estimated effective population size (N_e) from the genetic data using NeEstimator (Peel *et al*. 2004), to help interpret how different factors may have affected genetic diversity. We used the linkage-disequilibrium method, which measures the breeding effective population-size and does not assume random mating (Leberg 2005), but applied the heterozygote-excess method for populations where sample size or data structure precluded determining a point estimate of N_e using the former method. We again employed multiple linear regression models to investigate whether factors that affected genetic diversity were also correlated with N_e ($\log_e$ transformed in all analyses to improve linearity), and whether genetic diversity itself was correlated with N_e. We did not include N_e in models explaining variation in genetic diversity, because N_e is a dependent rather than an explanatory variable.

We estimated population isolation as $\log_{10}$ of the harmonic mean of the distance to the nearest three populations, with a 40 km 'barrier-effect' distance added to any interpopulation distance that included a fenced highway, canal or urban area. This model of isolation was developed by Epps *et al.* (2005a) from analyses of genetic distances, geographical distances and barriers between a subset of the populations included in the dataset for this study.

We selected the best regression models using variants of Akaike's Information Criterion (AIC_c and QAIC_c, as appropriate) (Burnham & Anderson 1998). Although we had no a priori reason to suspect overdispersion, we tested for it by estimating the variance inflation factor (c) as described by Lindsey (1999) and used this to calculate QAIC_c.

Results

Linear regression models demonstrated that genetic diversity, as measured by allelic richness (A), was positively correlated with elevation and negatively correlated with population isolation as a function of distance between populations and the presence of human-made barriers to dispersal (Table 1; Fig. 2). Allelic richness was most strongly correlated with elevation for these populations, although the model containing both elevation and isolation had the highest weight

Table 1 Regression models of genetic diversity in 25 desert bighorn sheep populations tested using Akaike's Information Criterion AIC_c and QAIC_c. 'Isolation' was defined as the log of the harmonic mean of the distance to the nearest three populations, with 40 km added to any interpopulation distance with an intervening interstate highway, canal or urban area (Epps *et al.* 2005a). Models within two $\Delta(\text{Q})\text{AIC}_c$ units of the best model are considered equally explanatory (indicated by *); if $c = 1$, $\text{QAIC}_c = \text{AIC}_c$. $(\text{Q})\text{AIC}_c$ weights (w_i) are the likelihood that the given model is the best of the candidate models (Burnham & Anderson 1998). A, allelic richness; H_e, observed heterozygosity; N_e, effective population size; P, significance of model F-statistic; R^2, model fit; k, number of predictor variables +2; c, estimated overdispersion; *, see above; †, $\log_e$ transformed

Response variable	Predictor variables	P	R^2	k	ΔAIC_c	w_i (AIC_c)	ΔQAIC_c	w_i (QAIC_c)
A $c = 1.60$	*isolation, elevation†	0.0005	0.50	4	0	0.73	0	0.55
	*elevation†	0.0009	0.38	3	2.47	0.21	1.23	0.30
	isolation	0.0058	0.29	3	6.14	0.03	3.53	0.09
	population size	0.6101	0.01	3	14.30	<0.01	8.64	0.01
	population area	0.7116	0.01	3	14.44	<0.01	8.73	0.01
	latitude	0.1837	0.08	1	12.48	<0.01	7.50	0.01
	elevation†, isolation, population size, population area, latitude	0.0070	0.56	5	7.37	0.02	6.33	0.02
H_e $c = 3.21$	*isolation	0.0367	0.18	3	0	0.34	0	0.37
	*elevation†	0.0373	0.18	3	0.03	0.34	0.01	0.37
	*isolation, elevation†	0.0355	0.26	4	0.12	0.32	0.63	0.27
N_e† $c = 1$	*isolation, elevation†, population size	0.0031	0.48	3	0.90	0.35	—	—
	*isolation, population size	0.0022	0.43	2	0	0.55	—	—
	population size	0.0144	0.23	1	4.41	0.06	—	—
	isolation, elevation†	0.0613	0.22	2	7.58	0.01	—	—
	isolation	0.0444	0.16	1	6.68	0.02	—	—
	elevation†	0.0697	0.14	1	7.41	0.01	—	—

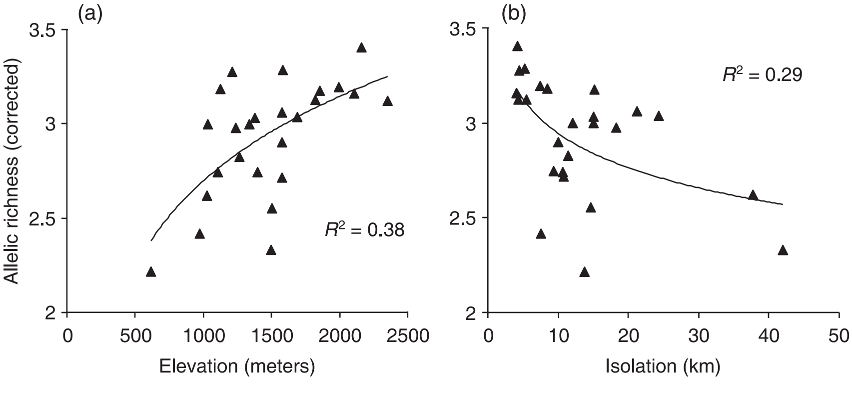

Fig. 2 Observed allelic richness (A, corrected for sample size) regressed against (a) elevation ($\log_e$ fit) of mountain range inhabited by each population and (b) isolation (log fit) of each population, calculated as the harmonic mean of the distance to the nearest three populations with 40 km added to any comparison crossing a human-made barrier (Epps *et al.* 2005a).

(using $\mathrm{QAIC_c}$ as a selection criterion, the model of elevation alone was competitive with the model containing both elevation and isolation). An alternate measure of genetic diversity, heterozygosity (H_e), was also positively correlated with elevation and negatively correlated with isolation, although the overall fit of this model was relatively poor as indicated by the low R^2 and high estimated overdispersion (Table 1). Although all three models considered (elevation, isolation and both) were correlated with H_e, no model was clearly favoured. Models including current (census) population size, latitude or area explained no additional variation in A or H_e (Table 1), nor was elevation correlated with estimated current population size or area (Pearson pair-wise correlation; population size, $r = 0.01$, $P = 0.98$; area, $r = -0.13$, $P = 0.52$). Elevation was not correlated with isolation (Pearson pair-wise correlation; $r = -0.33$, $P = 0.09$); however, this statistically nonsignificant trend of greater isolation at lower elevation may have made it more difficult to differentiate the effects of isolation and elevation on genetic diversity.

Two models, one including isolation and estimated current population size, the other including elevation, isolation and estimated current population size, were competitive as explanatory models for effective population size (N_e) (Table 1). However, of the univariate models examined, only isolation and current population size (not elevation) explained a significant amount of variation in N_e (Table 1). Genetic diversity measures (A and H_e) were correlated with N_e ($R^2 = 0.30$, $P = 0.0049$; $R^2 = 0.17$, $P = 0.0438$, respectively).

Discussion

The distribution of genetic diversity in this natural metapopulation was strongly correlated both with elevation and with population isolation. As expected given the general trend of warming and drying in this region during the latter half of the 20th century, higher-elevation populations retained more alleles and maintained higher heterozygosity (H_e). However, this relationship was also affected by population isolation (or conversely, connectivity), as defined by the distance to the nearest neighbouring populations and the presence of intervening human-made barriers, such as interstate highways and canals. Populations less isolated by distance or barriers retained more alleles and maintained higher H_e. Allelic richness (A) was more strongly correlated with both elevation and isolation than was H_e; as A is expected to decrease more quickly than H_e in the event of a population bottleneck (Leberg 2002), this may indicate that the loss of genetic diversity in low-elevation habitat has been fairly recent.

Genetic diversity is a function of N_e, which in turn is influenced by a number of factors. The correlation of population connectivity (isolation) with genetic diversity was presumably the result of the relationship between connectivity and N_e: populations with higher connectivity have higher N_e because they receive migrants at high frequency from nearby populations, thereby replacing genetic diversity lost via genetic drift. This interpretation is supported by our finding that N_e was positively correlated both with isolation and with genetic diversity (Table 1). However, because N_e (from linkage disequilibrium) was not correlated with elevation, but A and H_e were, we conclude that the correlation of elevation with genetic diversity results primarily from fluctuations in the number of breeding individuals (reflecting climate-related stochasticity in habitat conditions). We propose that the marginal, low-elevation populations have been affected to a greater extent by the increasingly severe climate conditions as precipitation decreased and the mean temperatures increased in the desert regions of California during the latter half of the 20th century (Lane *et al.* 1994; Ball *et al.* 1998). The high degree of environmental stochasticity results in many years of good habitat conditions but, as those trends of greater aridity and warmer temperatures developed, low-elevation populations may have experienced more years of poor habitat conditions and were thus subject to more frequent changes in N_e due to bottlenecks and founder events. Although the number of generations (6–7, given ~7 years/generation) elapsed during this time period is small, the very small N_e of these populations (see Table S1) causes genetic drift to occur at a very rapid pace in these populations (Epps *et al.* 2005a).

The mechanisms underlying fluctuations in population size resulting from climate conditions are well established for desert bighorn sheep. Bender & Weisenberger (2005) found that desert bighorn population dynamics in one population in New Mexico were strongly correlated with precipitation but not correlated with population density. Studies of bighorn sheep in the Mojave Desert of California showed that low winter rainfall reduces the quality of the forage in the spring diet which, in turn, causes low lamb recruitment; rainfall and thus recruitment are highly variable between years (Wehausen 2005). Higher spring and summer temperatures also reduce diet quality for bighorn sheep (Epps 2004). Extended droughts and drying of water holes may cause 'die-offs' of adult animals or cause local population extinction altogether (Allen 1980). Much of the variation in severity of regional climate trends for bighorn sheep likely is captured by the elevation of each mountain range: low-elevation populations have poorer spring-diet quality (Epps 2004), are subject to higher temperatures and lower precipitation and have fewer dependable water holes compared to populations at higher elevations (Epps *et al.* 2004).

This apparent history of stronger fluctuations in population size in low-elevation habitats implies that these populations have been, and will be, in greater danger of extinction due to demographical or environmental stochasticity as the climate warms. Moreover, loss of genetic diversity itself can result in the decline of reproductive fitness and survival (Hogg *et al*. 2006), increase the risk of population extinction (Saccheri *et al*. 1998) and decrease evolutionary potential (Frankham 1996; Fraser & Bernatchez 2001) through drift and increased loss of alleles. Genetic diversity is needed to maintain evolutionary potential, for instance when the habitat changes rapidly due to global climate change or other causes (e.g. Reusch *et al*. 2005). While these populations are small enough for extinction due to demographical stochasticity to appear more likely than loss of genetic diversity (as argued in the general case by Lande 1988), small populations have often persisted in this system because of its metapopulation structure. Thus, loss of genetic diversity may have implications for long-term health of these populations, especially if whole clusters of populations suffer erosion of genetic diversity as habitat quality declines. Given the strong role of connectivity in maintaining genetic diversity in this system, loss of genetic diversity in remaining populations could also be accelerated if nearby populations go extinct as a consequence of a hotter and drier climate.

Although current population size was correlated with N_e (Table 1), neither current population size nor population area was correlated with measures of genetic diversity. These negative findings are important because these population attributes are typically considered as indices of 'extinction risk' of small populations (Berger 1990; Hanski 1999). Berger (1990) argues that desert bighorn sheep populations of less than 50 individuals are doomed to extinction. However, habitat quality in this system appears to be primarily a function of climate conditions (as represented here by elevation) and other factors rather than merely population area. Moreover, perhaps due to the high degree of environmental stochasticity in this region, current census population sizes are unlikely to reflect the long-term patterns of population size and occupancy (as reflected by levels of genetic diversity), and therefore may not be as strong an indicator of extinction risk of these populations.

While it is difficult to conclude on the basis of a correlative analysis of a single data set whether the observed patterns of genetic diversity for desert bighorn sheep are the result of climate change or merely reflect long-term variation in habitat quality, both population extinction rates (Epps *et al*. 2004) and now genetic diversity of the remaining desert bighorn sheep populations were found to vary with elevation in the manner expected under scenarios of increasing temperature and aridity. Even if the coinciding trend of increased temperature and aridity in the deserts of southeastern California (Lane *et al*. 1994; Ball *et al*. 1998) cannot be directly implicated in this decline, we believe that the link between climate conditions, genetic diversity and population persistence of desert bighorn sheep is well-supported by these multiple lines of evidence. For this reason, we conclude that further temperature increases and decreases in precipitation will result in even more loss of genetic diversity and the eventual extinction of more populations in low-elevation habitat.

Populations generally maintained the highest genetic diversity when isolation was low (that is, connectivity with other populations remained) and suitable habitat conditions persisted (i.e. elevation was high). Therefore, maintaining connectivity between populations in more favourable habitats is particularly important. These areas seem to serve as refugia for genetic diversity in the event of long drought periods or increased aridity as climate changes, and will therefore act as source populations in periods of more favourable climate. Because the size of desert bighorn sheep populations in both high- and low-quality habitat appears to be very variable (Epps *et al*. 2005b), and current estimated population sizes are not correlated with genetic diversity (Epps *et al*. 2005a), the role of these areas as genetic refugia was not obvious from population census data alone. However, it should also be recognized that desert bighorn sheep may experience different habitat conditions in some of the high-elevation mountain ranges in the southwestern United States that are not considered desert habitat. Dense tree cover or heavy snow in ranges such as the San Gabriel Mountains of California may in fact decrease habitat quality for desert bighorn because of increased risk of predation and poorer forage in wooded areas.

Although habitat conditions affected by climate are not amenable to manipulation (with the possible exception of maintaining perennial waterholes), connectivity could be improved. Epps *et al*. (2005a) demonstrated that fenced interstate highways and other human-made barriers are reducing genetic diversity in this metapopulation by limiting migration. Thus, loss of genetic diversity due to climate variation is exacerbated by human disruption of population connectivity for desert bighorn sheep. However, the reduction of genetic diversity as the climate changes might be offset, at least in the short term, by finding solutions to restore connectivity. Possible solutions include widening and improving accessibility to culverts under interstate highways, creating overpasses, translocating desert bighorn sheep between populations, and ensuring that any additional highways are designed to permit movement of wildlife. Maintaining and restoring connectivity between fragmented populations should be a conservation priority, particularly in habitats vulnerable to the effects of rapid climate change.

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Supplementary material

The supplementary material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC3103/MEC3103sm.htm

Table S1 Sample sizes, expected heterozygosity, allelic richness, total number of alleles over 14 loci, isolation (as a function of distance and barriers), elevation, area, estimated population size and effective population size for the 25 populations of desert bighorn sheep used in this study.

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