Molecular Ecology (2008) **17**, 464–474 doi: 10.1111/j.1365-294X.2007.03532.x

As the raven flies: using genetic data to infer the history of invasive common raven (*Corvus corax*) populations in the Mojave Desert

ROBERT C. FLEISCHER,* WILLIAM I. BOARMAN,† ELENA G. GONZALEZ,*§ ALVARO GODINEZ,*¶KEVIN E. OMLAND,‡ SARAH YOUNG,*†† LAUREN HELGEN,* GRACIA SYED* and CARL E. MCINTOSH*‡‡

**Center for Conservation and Evolutionary Genetics, National Zoological Park & National Museum of Natural History, Smithsonian Institution, Washington, DC 20008, USA; †Conservation Science Research & Consulting, 2522 Ledgeview Place, Spring Valley, CA 91977, and also Biology Department, San Diego State University, San Diego, CA 92182, USA; ‡Department of Biological Sciences, University of Maryland, Baltimore, MD 21250, USA*

Abstract

Common raven (*Corvus corax*) populations in Mojave Desert regions of southern California and Nevada have increased dramatically over the past five decades. This growth has been attributed to increased human development in the region, as ravens have a commensal relationship with humans and feed extensively at landfills and on road-killed wildlife. Ravens, as a partially subsidized predator, also represent a problem for native desert wildlife, in particular threatened desert tortoises (*Gopherus agassizii*). However, it is unclear whether the more than 15-fold population increase is due to *in situ* population growth or to immigration from adjacent regions where ravens have been historically common. Ravens were sampled for genetic analysis at several local sites within five major areas: the West Mojave Desert (California), East Mojave Desert (southern Nevada), southern coastal California, northern coastal California (Bay Area), and northern Nevada (Great Basin). Analyses of mtDNA control region sequences reveal an increased frequency of raven 'Holarctic clade' haplotypes from south to north inland, with 'California clade' haplotypes nearly fixed in the California populations. There was significant structuring among regions for mtDNA, with high F_{ST} values among sampling regions, especially between the Nevada and California samples. Analyses of eight microsatellite loci reveal a mostly similar pattern of regional population structure, with considerably smaller, but mostly significant, values. The greater mtDNA divergences may be due to lower female dispersal relative to males, lower N_e, or effects of high mutation rates on maximal values of F_{ST}. Analyses indicate recent population growth in the West Mojave Desert and a bottleneck in the northern California populations. While we cannot rule out *in situ* population growth as a factor, patterns of movement inferred from our data suggest that the increase in raven populations in the West Mojave Desert resulted from movements from southern California and the Central Valley. Ravens in the East Mojave Desert are more similar to ones from northern Nevada, indicating movement between those regions. If this interpretation of high gene flow into the Mojave Desert is correct, then efforts to manage raven numbers by local control may not be optimally effective.

Keywords: control region, *Corvus*, invasive species, microsatellites, Mojave Desert, ravens

Received 24 March 2007; revision accepted 27 July 2007

Correspondence: Robert C. Fleischer, CCEG, Science Building, NZP, PO BOX 37012, MRC 5503, Washington, DC 20008, USA. Fax: 1-202-673-0040; E-mail: fleischerr@si.edu

§Present address: Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain.

¶Present address: University of Maryland Biotechnology Institute (UMBI), 9600 Gudelsky Drive, Rockville, MD 20850, USA.

††Present address: Pennsylvania Association for Sustainable Agriculture, 650 Smithfield Street, Suite 210, Pittsburgh, PA 15222, USA.

‡‡Present address: Laboratory of Genomic Diversity, National Cancer Institute, Building 560, Room 21-23, Frederick, MD 21702-1201, USA.

Introduction

Humans have, either directly (through introduction) or indirectly, caused the range expansion of a great number of species, which can result in detrimental impacts on native organisms and their ecosystems (Cox 1999; Simberloff 2005). Usually invasive species are of exotic origin, but sometimes a species may be native to a region, and, through the actions of humans, increase drastically in population size and range. Often it is unclear whether the increase is due to *in situ* population increase, invasion of the region by individuals from peripheral populations, or some combination of the two means. Genetic methods have great potential to help unravel the history of an invasive population by enabling measurements of gene flow among populations, documenting secondary colonizations (e.g. Fonseca *et al*. 2006), estimating long- and short-term trends in population size (Wang 2005), and even unravelling the potential role of selection in invasion success (Lee 2002). Such results, in combination with traditional methods of population analysis, can help to identify the factors responsible for population change.

In the Mojave desert region of the southwestern USA, populations of common ravens have virtually exploded over the past half century, with perhaps as much as a 15-fold increase just in the past three decades (Boarman 1993; Boarman & Berry 1995; Liebezeit & George 2004). This increased abundance of ravens is a direct response to increased human impacts in the region, including subsidizations of water and food from agriculture, development, landfills and road kills, and creation of additional nesting sites (e.g. telephone poles, electric transmission towers, planted trees and bridges). Raven reproductive success is enhanced by proximity to anthropogenic subsidies (Kristan & Boarman, in press), juvenile survival is higher in nests near human habitations (Webb *et al*. 2004), and reproductive output is higher in birds with garbage contained in their castings (Kristan *et al*. 2004). The increase in raven numbers also correlates with increased predation on desert tortoises (*Gopherus agassizii*, a Federally Threatened species under the US Endangered Species Act), and undoubtedly impacts other native species upon which the common raven preys.

Clearly, humans have impacted the survival and reproductive success of common ravens in the Mojave Desert, but it is not known to what extent raven populations in these regions have been increased through immigration from surrounding areas. In spite of the apparent success in this region, preliminary demographic analyses suggest that Mojave raven populations are not sustainable without immigration from some other area (Boarman & Kristan 2006). Ravens have a prodigious capability of flight, with some birds having daily commutes to landfills of up to 65 km. Juvenile dispersal distances in the desert region were found to average 8.6 km for males and 8.8 km for females (W.I. Boarman, unpublished), but both natal and breeding dispersal events up to about 320 km have been observed in other regions (Boarman & Heinrich 1999). Recent broad-scale phylogeographic analyses (Omland *et al*. 2000, 2006) suggest that ravens may have a higher level of philopatry than would be expected based on their powers of flight and reported studies of individual movements. Our study provides genetic assessments on more local scales to help shed light on the source of population increase and long-term effectiveness of management efforts (US Fish and Wildlife Service 2007) to reverse those trends. In addition, the documented population growth in the Mojave affords comparison of census estimates of growth with trends we estimate from genetic data.

In this study, we assess levels and patterns of variation in both mitochondrial DNA control region sequences and nuclear microsatellite loci. We then estimate a range of genetic and demographic parameters for the West and East Mojave Desert raven populations, including estimates of genetic variation within and among populations, rates of gene flow, and tests of population size change. We interpret our findings to determine whether the population increase in the Mojave Desert is detectable by genetic analyses, whether we can differentiate how much of the growth may be due to *in situ* population growth vs. immigration or expansion from neighbouring regions, and from which direction (i.e. coastal northern, southern or Central Valley of California, or Great Basin of Nevada) this migration may occur.

Materials and methods

Sampling

We obtained blood or tissue samples from adult ravens from collecting localities nested within five regions of California or Nevada (Fig. 1): (i) West Mojave Desert (WMoj), individual birds were trapped, banded and bled from the US Army National Training Center, Fort Irwin, San Bernardino County, California ($n = 34$) and Edwards Air Force Base, Kern County, California ($n = 32$); (ii) East Mojave Desert (EMoj), where birds were salvaged from two localities in Clark County, southern Nevada: Boulder City Landfill (35.96471°N by 114.80894°W) ($n = 29$) and Laughlin Landfill (35.18230°N by 114.63502°W) ($n = 15$); (iii) northern Nevada (Great Basin; NoNV), where we obtained salvaged tissues or feather samples from birds collected as part of raven control programmes from five counties (Washoe, Elko, Humboldt, Lander and Mineral; $n = 25$); (iv) coastal southern California (SoCA), salvaged or museum tissue samples from San Diego ($n = 6$) and Los Angeles/Riverside Counties ($n = 6$); and (v) museum tissue samples from coastal northern California (all from the San Francisco Bay area in Marin, San Mateo, Alameda, Solano and Contra Costa counties, $n = 16$; NoCA). An additional three samples

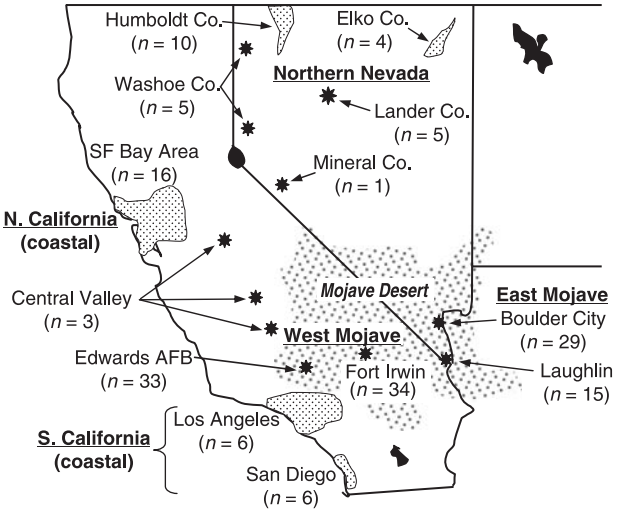

Fig. 1 Map of the southwestern USA showing the Mojave Desert and the approximate localities of common raven sampling sites in California and Nevada. The five major sampling regions are in boldface and underlined. Sample sizes are total numbers of birds analysed, but differ between mtDNA and microsatellite analyses.

were obtained from three sites in the Central Valley of California, utilizing raven control programmes and museum tissue collections, but the limited sample size precluded extensive analyses of this sample.

DNA methods

DNA was isolated from whole blood, tissue or fresh feather samples using QIAGEN DNeasy kits following the manufacturer's protocol. A 314-bp portion of the mitochondrial DNA control region was amplified and sequenced for 129 Nevada and California common ravens using primers Cor-Lgl2 and H417 and protocols described in Tarr & Fleischer (1999) and Omland *et al*. (2000). In addition, 24 sequences from California populations obtained for earlier studies (Tarr & Fleischer 1999; Omland *et al*. 2000) were incorporated into the analyses (see Fig. 2 legend for GenBank Accession nos).

A suite of eight microsatellite loci was also amplified from 163 samples from these localities and analysed for size variation on an ABI PRISM 3100 sequencer (Table 1). Primers for seven of these loci (CK1B5D, CK1B6G, CK2A5A, CK4A3G, CK4B6D, CK5A4B, and CK5A5F) were originally developed for the Marianas crow (*Corvus kubaryi*; Tarr & Fleischer 1998) and one (MJG1) was developed for the Mexican jay (*Aphelocoma ultramarina*; Li *et al*. 1997). We used laboratory conditions as described in Tarr & Fleischer (1998) and Omland *et al*. (2000) for the microsatellite amplifications, with the annealing temperatures provided in Table 1. All of the Marianas crow primers are dinucleotides (CA). The MJG1 locus normally contains a tetrameric repeat (GAAA) in the Mexican and other jays (Li *et al*. 1997; Lillandt *et al*. 2002; R.C. Fleischer, E.G. Gonzalez, S. Young, unpublished), but was found to contain a pentameric (GAAAA) repeat in the common raven. In addition, a number of MJG1 alleles were scored at an unexpected size (i.e. they were not sized 5 bp apart from the next smaller or larger allele). All individuals with unexpected allele sizes were re-amplified and rerun at least one additional time to confirm the allele size. In addition, we cloned and sequenced a subset of these, and some alleles of expected pentanucleotide motif, to confirm that the sizes called by the genotyping program matched the prediction from the actual sequence. This also allowed us to determine whether alleles of the same size have identical sequences (i.e. no evidence of size homoplasy), which was generally the case. In cases where alleles did not match the size expected from a pentanucleotide repeat, the difference was due to an increase or reduction in the size of one or more repeats (e.g. from GAAAA to GAAA or GAAAAA, etc.).

Analyses of genetic structure

We constructed a minimum-spanning haplotype network from 129 mtDNA control region sequences (58 from Nevada and 71 from California) using the program TCS 1.21 (Clement *et al*. 2000). We analysed levels and patterns of variation in mtDNA control region sequences using ARLEQUIN version 3.0 (Excoffier *et al*. 2005). We computed nucleotide diversity (π) and haplotype diversity (H) within regions, and Tajima's D, Fu's F and mismatch distributions to assess population size trends locally and across all regions. We conducted AMOVAS in ARLEQUIN to assess genetic differentiation among sampling sites nested within the two regions (i.e. California and Nevada) and between the two regions, as well as F_{ST} directly among sampling areas and regions. We also computed these values and tests for only the California clade (n = 32 for Nevada and 69 for California), and for the Holarctic clade (n = 25 for Nevada and 2 for California). More extensive phylogeographic analyses suggest that Holarctic clade haplotypes might have entered the southwestern USA more recently, and that the California clade haplotypes were in residence for a much longer period of time (Omland *et al*. 2000). As noted above, for some analyses, we combined the sampling sites into only two regions (i.e. Nevada and California) when there were no significant differences between sampling sites within regions and we wanted increased power to estimate parameters.

We estimated long-term effective population sizes from estimates of θ from mtDNA control region sequence data using MIGRATE 2.1 (Beerli & Felsenstein 1999, 2001). Because of concerns raised by Abdo *et al*. (2004), Slatkin (2005), and other authors about overestimation of the N_m in MIGRATE, especially with small values of θ and low sample sizes,

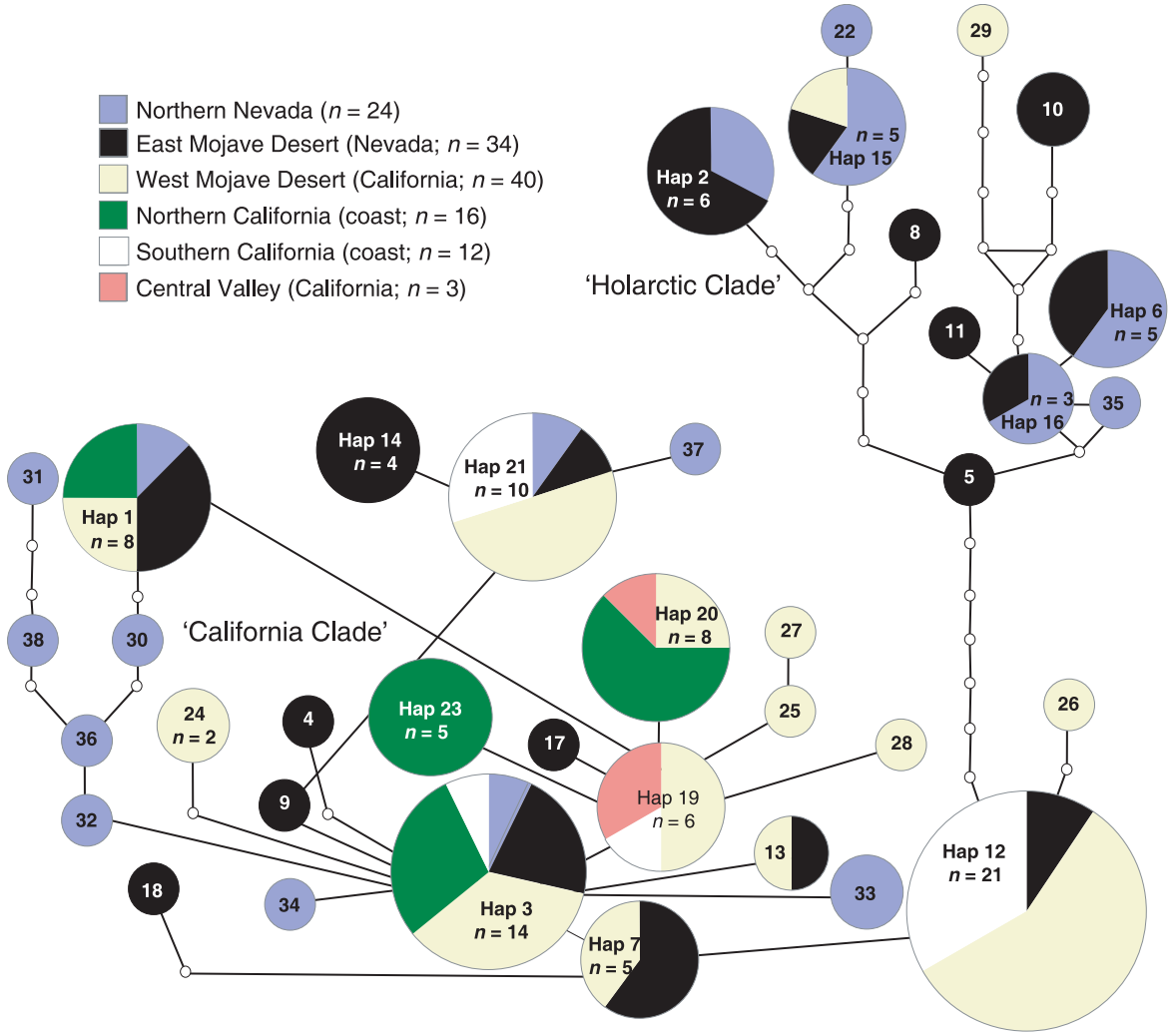

Fig. 2 Common raven mitochondrial DNA control region haplotype network constructed with the program TCS 1.21 (Clement *et al*. 2000). Sequences divide into two major clades (Holarctic and California), expected based on previous work (Tarr & Fleischer 1999; Omland *et al*. 2000; Omland *et al*. 2006). The area of each coloured pie diagram reflects the number of individuals of each haplotype (also given as 'n') and coloured segments represent the proportion of the number of haplotypes that occur from each sampling region. Note only two Holarctic clade haplotypes and individuals were found in California sampling areas. Haplotype GenBank Accession nos are listed by haplotype number (underlined are novel haplotypes discovered in this study): 1 AF115304, 2 AY710371, 3 AY005894, 4 *EU031791*, 5 *EU031792*, 6 AY710416, 7 AY005872, 8 AY005919, 9 *EU031793*, 10 *EU031794*, 11 *EU031795*, 12 AY005883, 13 AY005882, 14 *AY005888*, 15 AY710374, 16 AY710428, 17 EU031796, 18 *EU031797*, 19 AF115300, 20 AY005880, 21 AY005871, 22 *EU031798*, 23 *EU031799*, 24 AF115298, 25 AF115301, 26 AF115302, 27 EU031800, 28 AY005876, 29 AY005897, 30 AF115304, 31 *EU031801*, 32 *EU031802*, 33 *EU031803*, 34 AY005893, 35 AY710412, 36 AY005886, 37 *EU031804*, 38 *EU031805*.

we did not use the program to estimate asymmetries in migration among populations. We ran analyses using a DNA sequence mutation model and Bayesian inference. For the Bayesian analysis, we ran five independent replicate analyses of three long chains each; each long chain was run for 100 000 trees, with the first 10 000 trees discarded as unreliable 'burn-in'. We retained default parameters and starting estimates based on F_{ST} estimates.

For microsatellites, we used GENEPOP version 1.2 (Raymond & Rousset 1995) and ARLEQUIN version 3.0 (Excoffier *et al*. 2005) to estimate expected and observed heterozygosities and to test for deviations from expectations of Hardy–Weinberg equilibrium. GENEPOP was also used to test for linkage disequilibrium among loci. Differentiation of allele frequencies across populations was tested with a Markov chain–Fisher Exact Test in GENEPOP. The inbreeding coefficients F_{ST} and R_{ST} were estimated from allele frequencies under infinite alleles and stepwise mutation assumptions, respectively, in ARLEQUIN, and tested using permutations for significant difference from zero. However, we present

Table 1 Microsatellite loci used in the study (Li *et al*. 1997; Tarr & Fleischer 1998), number of alleles, observed heterozygosity (calculated in GENEPOP version 1.2; Raymond & Rousset 1995) and annealing temperature during polymerase chain reaction. Mean and standard error on bottom line

Locus	No. of alleles	H_O	Annealing temp (°C)
CK1B5D	8	0.827	60
CK1B6G	4	0.578	55
CK2A5A	8	0.631	55
CK4A3G	4	0.654	55
CK4B6D	6	0.490	55
CK5A4B	11	0.765	62
CK5A5F	7	0.662	55
MJG1	44	0.900	55
Mean	11.5 ± 4.7	0.688 ± 0.048	

only F_{ST} because of concerns of accuracy of R_{ST} estimates given our sample sizes (Gaggiotti *et al*. 1999). We assessed the deviation in observed heterozygosity from that expected under mutation–drift equilibrium using the coalescent program BOTTLENECK 1.2.02 (Piry *et al*. 1999); this program assesses the likelihood of a recent ($t = 2N_e$) population bottleneck. We used a two-phased mutation model (TPM) set at 90% stepwise and 10% infinite allele mutation, and tested the deviation using a nonparametric Wilcoxon test. The Bayesian analysis program STRUCTURE 2.1 (Pritchard *et al*. 2000) was used to determine the number of distinct populations to which individuals could be assigned based on their multilocus genotype. We ran analyses without prior information on population identity, with both independent and correlated allele frequencies, and used four replicates of 10 000 runs for 'burn-in' and sampling from 100 000 replicates to assess likelihoods for k from one to five populations. We also analysed the microsatellite data set with the program MIGRATE 2.1 (Beerli & Felsenstein 1999, 2001) as we did for mtDNA; we used the stepwise-mutation model and 100 000 trees per chain (with a burn-in of 10 000). We obtained Bayesian estimates of θ within each sampling area.

Results

Mitochondrial DNA analyses

We obtained up to 314 bp (range 286–314 bp) of mtDNA control region sequence for each of 129 ravens from California and Nevada (Figs 1 and 2). In total, there were 38 distinct haplotypes and 51 variable sites. The sequences, as expected from previous work (Tarr & Fleischer 1999; Omland *et al*. 2000), separated into two divergent clades: 11 haplotypes (27 individuals) in the Holarctic clade and 27 haplotypes (102 individuals) in the California clade. TCS 1.21 (Clement *et al*. 2000) produced a haplotype network (Fig. 2) with only one ambiguous connection in the Holarctic clade, but a sizeable number of ambiguous connections in the California clade. All but two of the 71 raven sequences from California fell into the California clade (i.e. two birds from Fort Irwin were in the Holarctic clade), whereas a little more than half of the 58 Nevada raven sequences fell into the California clade (50.0% of the northern Nevada ravens and 61.8% of the southern Nevada ravens; Fig. 2). Control region sequences recovered included 23 haplotypes that had been found in prior studies and their GenBank Accession nos are listed in the legend to Fig. 2; GenBank Accession nos for 15 novel sequences are underlined.

We found that mtDNA sequence variability differs among sampling sites, states and clades (Table 2). Sampling sites within Nevada have more haplotypes and higher values of haplotype diversity (H), nucleotide diversity (π) and θ. These differences are caused, in part, by the equal occurrence of haplotypes of both clades in Nevada, while the California populations contain haplotypes primarily (Fort Irwin) or only from a single clade. However, when considering the California clade alone, there are 11 haplotypes among 12 individuals from northern Nevada populations ($H = 0.985$ and $\pi = 0.012 \pm 0.007$), 11 haplotypes among 22 individuals in the East Mojave Desert sampling area ($H = 0.924$ and $\pi = 0.009 \pm 0.006$), and only 14 haplotypes among 66 individuals from California populations ($H = 0.865$ and $\pi = 0.009 \pm 0.005$), suggesting that the differences in diversity between the states are not due only to the equal proportions of haplotypes from the two divergent clades in Nevada.

To assess the possibility of population change or selection, we also calculated Tajima's D, Fu's Fs, and goodness-of-fit statistics to mismatch distributions from the sequences within each sampling site and state (Table 2). Only the WMoj sampling area had a significant difference from zero for Tajima's D (–1.52, $P < 0.05$), suggesting either recent population expansion or purifying selection in this population. In addition, the mismatch distribution for WMoj is not significantly different from predictions of a sudden expansion model ($P = 0.08$). The mismatch distribution for NoCA strongly indicated a bottleneck, with highly significant deviations from the expansion model. D was significantly negative for all California sampling areas combined (Table 2), possibly because the West Mojave Desert sample overwhelmed the smaller samples from coastal California. Nonsignificant, positive D's for the two Nevada sampling areas suggest no change in population size or selection in this region. However, when the analysis is conducted on California clade haplotypes alone, both Fs and D are

Table 2 Statistics of variation in mtDNA sequences from the five sampling areas and divided by state (see Fig. 1)

	N	No. of haplotypes (private)	*H*	π (SD)	D_{Taj} (*p*)	Fu's *F* (*p*)
NoNV	24	17 (10)	0.967	0.033 (0.018)	0.861 (ns)	–1.99 (ns)
EMoj	34	19 (9)	0.957	0.029 (0.016)	0.464 (ns)	2.45 (ns)
NV all	57	29 (22)	0.965	0.031 (0.016)	0.393 (ns)	–4.81 (ns)
WMoj	40	15 (6)	0.881	0.012 (0.007)	–1.524 (= 0.05)	–3.33 (ns)
NoCA	16	4 (1)	0.775	0.005 (0.003)	0.894 (ns)	0.76 (ns)
SoCA	12	4 (0)	0.636	0.005 (0.004)	0.627 (ns)	0.35 (ns)
CA all	68	16 (9)	0.873	0.011 (0.006)	–1.422 (< 0.05)	–2.93 (ns)

N, sample size; *H*, haplotype diversity; π, the nucleotide diversity; D_{Taj}, Tajima's *D* statistic

negative in both NoNV and EMoj, significantly so for *Fs* in both cases (*Fs* = –5.0, *P* = 0.008 and –3.9, *P* = 0.018, respectively). As before, for the three California sampling areas, Tajima's *D* and Fu's *Fs* are significantly negative only in WMoj, but not for either SoCA or NoCA (Table 1). When conducted on the Holarctic clade haplotypes alone for the NoNV and the EMoj sampling areas, neither Tajima's *D* nor Fu's *Fs* were significantly different from zero, and mismatch distributions were significantly different from an expanding population model (*P* = 0.03 and 0.05, respectively). Thus, analysis of the California clade provides evidence of population expansion in both regions, but the Holarctic clade shows evidence of population stasis in Nevada.

The minimum-spanning network produced by TCS (Fig. 2) shows no evidence of reciprocal monophyly among sampling sites or regions, nor fixed differences in haplotype frequencies. Nonetheless, the populations showed a relatively high level of haplotypic frequency differentiation as assessed by F_{ST} and AMOVA. When all samples were grouped into either a California or a Nevada sample, F_{ST} was 0.214 (*P* < 0.0000), indicating a relatively low rate of gene flow between the states (N_m = 1.84 migrants per generation). When the five sampling areas were grouped hierarchically by state (NV = NoNV and EMoj; CA = WMoj, NoCA and SoCA) and analysed by AMOVA, we recovered a relatively high and significant Φ_{ST} value among sampling areas (Φ_{ST} = 0.246, *P* < 0.0001), and this was further divided into a Φ_{SC} among sample regions within states of 0.073 (*P* = 0.014), and higher component of the variation Φ_{CT} between states of 0.186 (*P* < 0.0001). Pairwise F_{ST} values calculated among sampling regions are shown in Table 3, along with estimates of N_m from ARLEQUIN. When the two Mojave sampling regions are combined into a group, Φ_{SC} increases to 0.172, suggesting that the two Mojave Desert sites are not a natural group. In addition, when assessing the structure of the haplotype network (Fig. 2) or tree (not shown), haplotypes from Nevada and California often occur in separate 'subclades' and are more often connected to members of their own region than might be expected by chance. The difference between the regions is not due only to the higher presence of Holarctic clade haplotypes in Nevada: Φ_{ST} across the sampling areas for just the California clade is 0.229 (*P* < 0.0001); and for just the Holarctic clade is 0.107 (*P* = 0.26). F_{ST} for Holarctic clade haplotypes between the northern Nevada and East Mojave Desert sampling areas is only 0.008 (*P* = 0.29), indicating high mtDNA similarity of the two populations and reflecting a rate of gene flow, N_m, of 65.2 individuals per generation.

Microsatellite analyses

We analysed variation in eight microsatellite loci (Table 1) for 163 individuals (mean recovery of 158.4 individuals per locus). The microsatellite loci varied in level of polymorphism, averaging 11.5 alleles per locus (range from 4 to 43 alleles) and 68.8% observed heterozygosity. Mean heterozgosity for microsatellites was highest in the Mojave Desert sampling areas and lowest in NoCA (EMoj = 0.720; WMoj = 0.683; NoNV = 0.626; SoCA = 0.622; NoCA = 0.557), but did not differ significantly among sampling areas. As for mtDNA, we combined the five sampling sites in northern Nevada into one sampling region (*n* = 23); there were no significant differences among the sites in allele frequencies. We conducted preliminary analyses on this and seven other locality samples (NoNV, Laughlin, Boulder City, Fort Irwin, Edwards AFB, NoCA, SoCA and the Central Valley;

Table 3 Population pairwise F_{ST} values below the diagonal, and migration (N_m, number of migrants per generation) values above the diagonal, for the five sampling areas in Nevada and California calculated from mtDNA control region haplotype frequencies. F_{ST} values significantly different from zero are indicated by asterisks (**P < 0.01, and ***P < 0.001)

	NoNV	EMoj	WMoj	NoCA	SoCA
NoNV	—	58.40	1.41	0.94	1.40
EMoj	0.008	—	3.03	1.29	3.05
WMoj	0.261***	0.141***	—	1.61	17.96
NoCA	0.348***	0.279***	0.238***	—	0.35
SoCA	0.263***	0.141**	0.027	0.585	—

Fig. 1). Because of their proximity, and a lack of significant differences in allele frequencies between them, we combined the Laughlin and Boulder City as the EMoj sampling region ($n = 44$), and the Fort Irwin ($n = 32$) and Edwards AFB ($n = 34$) samples as the WMoj region ($n = 66$). We divided our other California samples into NoCA ($n = 16$) and SoCA ($n = 11$), and Central Valley ($n = 3$) samples. There was no significant difference in allele frequencies between San Diego and Los Angeles area samples ($P = 0.35$).

Observed heterozygosity at all eight loci in each of the eight locality samples did not significantly deviate from expectations of Hardy–Weinberg equilibrium with the exception of locus CK2A5 A in NoNV ($P = 0.007$) and CK1B6G in NoCA ($P = 0.026$). These loci were in Hardy–Weinberg equilibrium in the other populations and this deviation may reflect the broad geographic sampling across NoNV, or just be a chance deviation. There was no evidence for linkage disequilibrium in the microsatellite data set; only a single test out of 224 disequilibrium tests (eight loci in eight populations) was significant (CK4B6D and CK5A5F in NoNV, $P = 0.034$). In addition, it is very unlikely that birds from a sampling site were more related to each other than random: we analysed microsatellite genotypes using the program KINSHIP 1.3.1 (Goodnight & Queller 1999) within each larger locality sample in Nevada and California, and found only a small fraction of pairwise comparisons of individuals had values of R indicative of first-order relationship (1.7% for Boulder City; 1.9% for Laughlin; 3.0% for Fort Irwin, and 4.1% for Edwards AFB). For samples in northern Nevada and southern and northern California, samples were not taken at a single time or site, so incidental sampling of close relatives is very unlikely.

Only the NoCA sample showed a significant excess heterozygosity in comparison to that expected under mutation–drift equilibrium and a two-phase mutation model (Wilcoxon test, $P = 0.0098$; Piry *et al*. 1999). This significant result suggests that the northern California population may have undergone a recent bottleneck. This test does have low power with small sample sizes of individuals ($n = 16$ for this sample) and loci (only eight), but the mtDNA data also suggested a bottleneck in NoCA, as does the lower mean heterozygosity in the NoCA sample.

All loci except CK5A4B showed significant variation in allele frequencies across five sampling regions ($P < 0.0014$). An AMOVA, grouping the populations into Nevada and California, revealed low divergence among groups within states ($F_{SC} = 0.019$) or among states ($F_{CT} = 0.005$). Pairwise F_{ST} values were considerably lower than those calculated for mtDNA, a pattern that may be caused by the very high mutation rates in these markers (Hedrick 1999; Epperson 2005; see discussion). F_{ST} ranged from 0.003 to 0.042 across the eight loci (Table 4), but most values were significantly different from zero based on permutation tests in ARLEQUIN version 3.0. F_{ST} values indicate that genetic divergence is highest between the NoNV and other sample areas (mean $F_{ST} = 0.032 \pm 0.005$), and was very low between SoCA and the West Mojave Desert ($F_{ST} = 0.003$). In spite of the significant F_{ST} values, Bayesian analysis of genetic structure using STRUCTURE 2.1 (Pritchard *et al*. 2000) with no prior population identification did not support differentiation into more than one population (i.e. $k = 1$), nor show any clustering of individuals geographically (data not shown).

Table 4 Population pairwise F_{ST} values below the diagonal, and migration (N_m; number of migrants per generation) values above the diagonal, for the five sampling areas in Nevada and California, calculated from microsatellite allele frequencies. F_{ST} values significantly different from zero are indicated by asterisks (*$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$)

	NoNV	EMoj	WMoj	NoCA	SoCA
NoNV	—	7.8	6.2	15.8	5.7
EMoj	0.032***	—	10.5	18.0	18.6
WMoj	0.039***	0.023***	—	8.1	72.6
NoCA	0.016*	0.014**	0.029***	—	11.3
SoCA	0.042**	0.013	0.003	0.021*	—

Estimating gene flow and N_e

Gene flow estimates were calculated in ARLEQUIN using Slatkin's (1995) method (Table 3). These values are very high between NoNV and EMoj and SoCA and the WMoj, but are small between the EMoj and WMoj samples, and between NoCA and WMoj. Gene flow estimates from microsatellite data were on average higher and showed a mostly similar pattern to those from mtDNA (Table 4). Gene flow was very high between SoCA and the WMoj, but not as high between NoNV and the EMoj, and perhaps greater than expected for other comparisons in relation to the rates obtained from the mtDNA analyses. Whitlock & McCauley 1999), among others, have pointed out the problems of untested assumptions and sampling error in estimating gene flow rates from F_{ST} and its analogues, so we provide these as relative estimates only.

Values of θ estimated from mtDNA control region sequences using MIGRATE 2.1.3 were generally higher in the Nevada populations (NoNV = 0.0234; Emoj = 0.0417) relative to the California ones (Wmoj = 0.0243; SoCA = 0.0038; NoCA = 0.0026). Estimates of θ from microsatellites were also calculated using a Bayesian approach in MIGRATE 2.1.3, and were also higher inland (NoNV = 0.6107; EMoj = 1.1051; WMoj = 2.0103) than along coastal California (SoCA = 0.6555; NoCA = 0.3572). If we assume a mean mutation rate of 10^{-7} for mtDNA CR (e.g. Omland *et al*. 2006), the

long-term effective population size (N_e) estimates based on $\theta = 2N_e\mu$ are relatively small in coastal California (NoCA = 13 000; SoCA = 19 000) and considerably larger in the desert regions (WMoj = 121 500; EMoj = 208 500; NoNV = 117 000). For microsatellites, if we assume a mean mutation rate of 10^{-4} (range of 10^{-2}–10^{-4}; Epperson 2005), the long-term effective population size (N_e) estimates based on $\theta = 4N_e\mu$ mostly match in pattern, but are considerably smaller in magnitude (NoCA = 1786; SoCA = 3277; WMoj = 10 065; EMoj = 5525; and NoNV = 3054 individuals). These order of magnitude differences in effective population size estimates between markers could be a result of an incorrect mutation rate for either marker, that is if the microsatellite mutation rate is 10^{-5} or the mtDNA mutation rate is 10^{-6}, these estimates would converge. Alternatively, the differences may be caused by a very different mutational timeframe for the two marker classes (mtDNA measuring a considerably longer period in the past than microsatellites), or there just could be considerable measurement error in one or both data sets.

Discussion

Genetic structure

Our mitochondrial DNA control region analyses revealed a surprising degree of genetic structure in common raven populations in the southwestern USA, and less gene flow among the Great Basin deserts of Nevada, the Mojave Desert and coastal regions of California than might be expected based on the flight capabilities of ravens and availability of habitat. The high AMOVA F_{ST} value among sampling areas (= 0.246) for mtDNA control region sequences indicates a fairly low level of overall maternal gene flow, as does the high percentage of private haplotypes (41.9% overall, with the highest values in the two Nevada sample regions). The pattern of pairwise F_{ST} values (Table 3) and shared haplotypes among sampling areas (Fig. 2) indicates high gene flow between the West Mojave Desert and coastal southern California sampling areas ($F_{ST} = 0.027$, ns), and between the East Mojave Desert and northern Nevada ($F_{ST} = 0.008$, ns), but not between the East and West Mojave Desert sampling areas ($F_{ST} = 0.141$, $P < 0.001$). The northern California sampling area is as divergent from all the other regions as the Nevada sample (Table 3).

The microsatellite data, on the other hand, did not reveal as many private alleles within sampling regions (9.8%), and produced F_{ST} values that were considerably smaller in value (mean of 0.022, $P < 0.0001$) than those calculated from mtDNA sequences. They showed low and nonsignificant differentiation between the West Mojave Desert and southern California sampling areas ($F_{ST} = 0.003$), but significant divergence between the West Mojave Desert and the other three sampling areas. In general, the analyses of gene flow based on microsatellites and mtDNA provide a roughly similar pattern of gene flow among sampling areas (with the exception of relatively low gene flow between northern Nevada and East Mojave Desert ravens), but very different magnitudes. Similar discrepancies in the values of F_{ST} between mtDNA and nuclear microsatellite data sets have been found for other avian and vertebrate taxa (e.g. Gibbs *et al*. 2000; Haavie *et al*. 2000; Chappell *et al*. 2004; Tiedemann *et al*. 2004). Milot *et al*. (2000) estimated an F_{ST} of 0.53 for mtDNA control region sequences across the range of the yellow warbler (*Dendroica petechia*), while the F_{ST} calculated from microsatellites for the same population samples was only 0.014 (Gibbs *et al*. 2000) and Tiedemann *et al*. (2004) found an F_{ST} of about 0.502 for mtDNA control region and only 0.053 for microsatellites among colonies of eider ducks (*Somateria mollissima*).

This discrepancy in divergence levels based on *F*-statistics between mtDNA and microsatellites could indicate that nuclear alleles are moving more between regions than the maternally inherited mtDNA haplotypes (high female philopatry). Alternatively, because coalescence or sorting of nuclear alleles occurs at a slower rate than for mtDNA haplotypes, the lower differentiation may reflect an earlier stage of divergence. Hedrick (1999) notes that F_{ST} values calculated using highly mutable and variable markers should underestimate F_{ST}, and provides a method (equation 2a) to calculate the maximum F_{ST} value expected for rapidly evolving markers such as microsatellites. For our raven sample, this is 0.288. Thus, the highest F_{ST} we obtain of 0.042 actually represents 14.6% of the maximum theoretical value. Epperson (2005) has recently quantified the divergence underestimates for genetic markers with very high mutation rates (such as microsatellites) relative to those with slower rates (such as mtDNA). Some, if not all, of our microsatellites may fall into this hypermutable category (especially MJG1, Table 1). Alternatively, if the hypothesis of reduced mtDNA gene flow is correct, it means that female ravens are dispersing much less than males, and this is unexpected from existing demographic data for both ravens and other songbirds, in which females usually disperse more often and further (Clarke *et al*. 1997; W.I. Boarman, unpublished). But if males are dispersing at high rates, we should still see less mtDNA divergence because they carry their mtDNA with them when they move.

Population size changes and gene flow

Calculations of Tajima's *D* and Fu's *Fs* from our mtDNA sequence data provide evidence of raven population growth in the Mojave Desert but population stasis in the Great Basin in Nevada and southern California. When this was dissected by clade, there was evidence of expansion for the California clade in both California and Nevada, but

evidence of stasis for Holarctic clade samples in Nevada. This suggests that birds from the California clade may have been expanding into the Great Basin, where Holarctic clade members existed, although results from our structure analyses do not completely confirm this. Our bottleneck analysis of microsatellite variation reveals evidence of a bottleneck only for the NoCA sample. The evidence for Mojave Desert population growth matches expectations based on historical data on population trends for this region (Boarman 1993; Boarman & Berry 1995; Liebezeit & George 2004). Ravens were rare in most parts of the Mojave Desert up until the past 50 years. Once humans began to provide excess food and nesting sites with their garbage, road-killed animals and power lines, raven reproductive success and population size increased dramatically (Boarman 1993; Knight & Kawashima 1993; Webb *et al*. 2004). The great increase in numbers of ravens in the Mojave Desert may be due to *in situ* increases from such subsidies, or to invasion of ravens from adjacent regions (or some combination of the two). Anthropogenic resources facilitate survival of ravens in the Mojave Desert, but modelling enigmatically suggests that the populations are not self-sustaining, and can only be maintained or increased via immigration (Boarman & Kristan 2006). This result may be a partial artefact of the high level of mortality caused by illegal poisoning of mostly juveniles by dairy farmers in the area where the above study took place (W.I.B., personal observation).

Our assessment of genetic structure was able to shed only limited light on whether the West Mojave Desert common raven population increase was due to *in situ* population growth, immigration, or both factors combined. Our results did indicate that if an invasion was the cause of the massive population increase in the West Mojave Desert rather than *in situ* growth, it likely did not occur from Nevada and the Great Basin or Northern California. The WMoj ravens are genetically very similar to those in SoCA and there is a high level of gene flow between them, thus SoCA would seem to be the likely invasion source. However, we cannot rule out the inverse: that the WMoj ravens were the source of movement into southern California. In support of this idea is the finding that genetic variation in mtDNA (Table 2) and microsatellites are much lower in SoCA than WMoj (although so is sample size). But this would also be expected if SoCA is not the only source population for WMoj, and we cannot rule out an expansion from the Central Valley into the WMoj. Indeed, the three individual samples from the Central Valley all share haplotypes with the WMoj sample. The higher variation in the WMoj could reflect the mixed nature of the population arising from movement from SoCA and the Central Valley. Another finding of our genetic structure analyses is that there appears to be relatively limited gene flow between the EMoj and WMoj sampling areas.

There is a good deal of what is considered high quality raven habitat between the western Mojave Desert, the Central Valley and coastal California (W.I.B., personal observation). Hence, there should be high connectivity and opportunity for movement among these regions (i.e, from the Los Angeles basin or southern Central Valley into the Mojave Desert). However, much of the East Mojave Desert region, between the Great Basin and the West Mojave Desert, is extremely arid, has much lower use by humans, and consists of suboptimal habitat for common ravens, and would likely represent an obstacle to dispersal for ravens. Human habitations (isolated homesteads, small communities, roadside rests) that provide important resources for ravens, may serve as stepping-stones for dispersal and wanderings of ravens through the desert (W.I. Boarman and W.B. Kristan, in preparation). Furthermore, ravens nesting farther from anthropogenic resources tend to have more seeds and insect in their diets and have lower reproductive success (Kristan *et al*. 2004). While there has been considerable anthropogenic development on the edge of the eastern Mojave Desert in southern Nevada (i.e. Las Vegas/Clark County), there is very little human development in the region between there and the western Mojave. As development occurs in this region, in particular along interstate highways leading to Las Vegas, it may open up a corridor or conduit for raven nesting and dispersal that would lead to increased movement of ravens between the eastern and western Mojave.

Management and policy implications

Our results have implications for management of raven populations in the Mojave Desert and other parts of its expansive range. The US Fish and Wildlife Service (USFWS) is currently developing plans to reduce raven predation on tortoises through lethal and nonlethal means. It is important for them to know if limiting reproductive and feeding opportunities in the Mojave Desert will reduce raven population size and density, or whether immigration will nullify such management actions. Clearly, our genetic data show the possibility of large-scale movements with reproduction (i.e. gene flow). This evidence of large-scale, region-wide movements supports the need for regional-scale management efforts rather than just local ones. Current gaps in anthropogenic habitat are probably the only factor maintaining the genetic structure we identified. Developments and other actions that subsidize essential resources for ravens provide more hospitable habitat thereby facilitating the incursion of ravens farther into the desert. The presence of more ravens increases their predation pressure on desert tortoises and other species of concern (Kristan & Boarman 2003).

We were able to use genetic analysis of contemporary populations to gain some understanding of the dynamics

of population growth and colonization in an invasive species. Genetic analysis has been used to assess the origins, demography and consequences of biological invasions for plant (e.g. Meekins *et al*. 2000; Novak 2004), invertebrate (e.g. Ingram & Gordon 2003), lower vertebrate (e.g. Estoup *et al*. 2004; Kolbe *et al*. 2004) and bird species (e.g. Clegg *et al*. 2002; Hawley *et al*. 2006). But common ravens in the West Mojave Desert of California also represent an unusual case in that they are a native species in the region, but also apparently an invasive one, that acts as a pest, and as a potentially limiting factor on threatened populations of desert tortoises. We used genetic markers to detect signals of population growth within this region, and to exclude some potential regions as the likely source populations (Great Basin, Northern California), but not others (i.e. Southern California, Central Valley). These results illustrate the utility of population genetic analyses to help uncover or elucidate past demographic events in populations affected by human activities.

Acknowledgements

We thank M. Pavelka, K. Brock, M. Vermeys, P. Coater, J. Peter, B. Miller, D. Rowley, D. Capelli, M. Holmgren (UC Santa Barbara), K. Burns (San Diego State University), K. Garrett (LACO), J. Dumbacher (CAS), A. Engilis (UC Davis), and C. Cicero (MVZ) for assistance with collecting, or providing, tissue samples. Mark Hagan and Edwards Air Force Base provided funding and logistical support for a portion of the work. Thanks also to M. Haynie and F. Hailer for advice on data analysis. E.G.G. was sponsored by a predoctoral fellowship of the Ministerio de Educación y Ciencia from Spain.

References

Abdo Z, Crandall KA, Joyce P (2004) Evaluating the performance of likelihood methods for detecting population structure and migration. *Molecular Ecology*, **13**, 837–851.

Beerli P, Felsenstein J (1999) Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics*, **152**, 763–773.

Beerli P, Felsenstein J (2001) Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Proceedings of the National Academy of Sciences, USA*, **98**, 4563–4568.

Boarman WI (1993) When a native predator becomes a pest: a case study. In: *Conservation and Resource Management* (eds Majumdar SK, Miller EW, Miller DE, Brown EK, Pratt JR, Schmalz RF), pp. 191–206. Pennsylvania Academy of Science, Philadelphia, Pennsylvania.

Boarman WI, Berry KH (1995) Common ravens in the southwestern United States, 1968–92. In: *Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems* (ed. Laroe ET), pp. 73–75. National Biological Service, Washington, DC.

Boarman WI, Heinrich B (1999) Common raven (*Corvus corax*). In: *The Birds of North America, No. 476* (eds Poole A, Gill F). The Birds of North America, Inc., Philadelphia, Pennsylvania.

Boarman WI, Kristan WB (2006) Trends in common raven populations in the Mojave and Sonoran Deserts: 1968–2004. Report to U.S. Fish and Wildlife Service, Ventura, California.

Chappell DE, Van Den Bussche RA, Krizan J, Patterson B (2004) Contrasting levels of genetic differentiation among populations of wolverines (*Gulo gulo*) from northern Canada revealed by nuclear and mitochondrial loci. *Conservation Genetics*, **5**, 759–767.

Clarke AL, Saether B-E, Roskaft E (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**, 429–438.

Clegg SM, Degnan SM, Kikkawa J, Moritz C, Estoup A, Owens IPF (2002) Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences, USA*, **99**, 8127–8132.

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1659.

Cox GW (1999) *Alien Species in North America and Hawaii: Impacts on Natural Ecosystems*. Island Press, Washington, DC.

Epperson BK (2005) Mutation at high rates reduces spatial structure within populations. *Molecular Ecology*, **14**, 703–710.

Estoup A, Beaumont M, Sennedot F, Moritz C, Cornuet J-M (2004) Genetic analysis of complex demographic scenarious: spatially expanding populations of the cane toad *Bufo marinus*. *Evolution*, **58**, 2021–2036.

Excoffier L, Laval G, Schneider S (2005) ARLEQUIN ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Fonseca DM, Smith JL, Wilkerson RC, Fleischer RC (2006) Pathways of expansion and multiple introductions illustrated by large genetic differentiation among worldwide populations of the southern house mosquito. *American Journal of Tropical Medicine and Hygiene*, **74**, 284–289.

Gaggiotti OE, Lange O, Rassmann K, Gliddon C (1999) A comparison of two indirect methods for estimating average levels of gene flow using microsatellite data. *Molecular Ecology*, **8**, 1513–1520.

Gibbs HL, Dawson RJG, Hobson KA (2000) Limited differentiation in microsatellite DNA variation among northern populations of the yellow warbler: evidence for male-biased gene flow? *Molecular Ecology*, **9**, 2137–2147.

Goodnight KF, Queller DC (1999) Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology*, **8**, 1231–1234.

Haavie J, Sætre G, Moum T (2000) Discrepancies in population differentiation at microsatellites, mitochondrial DNA and plumage colour in the pied flycatcher — inferring evolutionary processes. *Molecular Ecology*, **9**, 1137–1148.

Hawley DM, Hanley D, Dhondt AA, Lovette IJ (2006) Molecular evidence for a founder effect in invasive house finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. *Molecular Ecology*, **15**, 263–275.

Hedrick P (1999) Perspective: highly variable loci and their interpretation in evolution and conservation. *Evolution*, **53**, 313–318.

Ingram KK, Gordon DM (2003) Genetic analysis of dispersal dynamics in an invading population of Argentine ants. *Ecology*, **84**, 2832–2842.

Knight RL, Kawashima JY (1993) Response of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management*, **57**, 266–271.

Kolbe JJ, Glor RE, Rodríguez Schettino L, Chamizo Lara A, Larson A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**, 177–181.

Kristan WB III, Boarman WI (in press) Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. *Ecological Applications*.

Kristan WB III, Boarman WI (2003) Spatial distribution of risk of desert tortoise (*Gopherus agassizii*) predation by common ravens (*Corvus corax*). *Ecology*, **84**, 2432–2443.

Kristan WB III, Boarman WI, Crayon J (2004) Diet composition of common ravens across the urban–wildland interface of the west Mojave Desert. *Wildlife Society Bulletin*, **32**, 244–253.

Lee CE (2002) Evolutionary genetic of invasive species. *Trends in Ecology & Evolution*, **17**, 386–391.

Li S-H, Huang Y-J, Brown JL (1997) Isolation of tetranucleotide repeat microsatellites from the Mexican jay. *Molecular Ecology*, **6**, 499–501.

Liebezeit JR, George TL (2004) A *Summary of Predation by Corvids on Threatened and Endangered Species in California and Management Recommendations to Reduce Corvid Predation*. Humboldt State University, Arcata, California.

Lillandt BG, Bensch S, Hansson B, Wennerberg L, Von Schantz T (2002) Brief report—isolation and cross-species amplification of microsatellite loci in the Siberian jay (*Perisoreus infaustus*). *Hereditas*, **137**, 157–160.

Meekins JF, Ballard HE Jr, McCarthy BC (2000) Genetic variation and molecular biogeography of a North American invasive plant species (*Alliaria petiolata*, Brassicaceae). *International Journal of Plant Sciences*, **162**, 161–169.

Milot E, Gibbs HL, Hobson KA (2000) Phylogeography and genetic structure of northern populations of the yellow warbler (*Dendroica petechia*). *Molecular Ecology*, **9**, 667–682.

Novak SJ (2004) Genetic analysis of downy brome (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*): management implications. *Weed Technology*, **18**, 1417–1421.

Omland KE, Tarr CL, Boarman WI, Marzluff JM, Fleischer RC (2000) Cryptic genetic variation and paraphyly in ravens. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **267**, 2475–2482.

Omland KE, Baker JM, Peters JL (2006) Genetic signatures of intermediate divergence: population history of Old and New World Holarctic ravens (*Corvus corax*). *Molecular Ecology*, **15**, 795–808.

Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK: a computer program for detecting recent reductions in the effective population size using allele frequency data. *Journal of Heredity*, **90**, 502–503.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Simberloff D (2005) Non-native species do threaten the natural environment! *Journal of Agricultural and Environmental Ethics*, **18**, 595–607.

Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequencies. *Genetics*, **139**, 457–462.

Slatkin M (2005) Seeing ghosts: the effect of unsampled populations on migration rates estimated for sampled populations. *Molecular Ecology*, **14**, 67–73.

Tarr CL, Fleischer RC (1998) Primers for polymorphic GT microsatellites isolated from Mariana crow, *Corvus kubaryi*. *Molecular Ecology*, **7**, 253–255.

Tarr CL, Fleischer RC (1999) Population boundaries and genetic diversity in the endangered Mariana crow (*Corvus kubaryi*). *Molecular Ecology*, **8**, 941–950.

Tiedemann R, Paulus KB, Scheer M *et al*. (2004) Mitochondrial DNA and microsatellite variation in the eider duck (*Somateria mollissima*) indicate stepwise postglacial colonization of Europe and limited current long-distance dispersal. *Molecular Ecology*, **13**, 1481–1494.

US Fish and Wildlife Service (2007) *Draft Environmental Assessment to Implement a Desert Tortoise Recovery Plan Task: Reduce Common Raven Predation on the Desert Tortoise*. Ventura Field Office, Ventura, California.

Wang J (2005) Estimation of effective population sizes from data on genetic markers. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **360**, 1395–1409.

Webb WC, Boarman WI, Rotenberry JT (2004) Common raven juvenile survivorship in a human augmented landscape. *Condor*, **106**, 517–528.

Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4N_m+1)$. *Heredity*, **82**, 117–125.

Rob Fleischer is Head of the Center of Conservation and Evolutionary Genetics (CCEG) at the Smithsonian Institution and has interests in a wide range of questions in conservation and evolutionary biology that can be answered with the help of molecular tools. William Boarman is an adjunct professor of Biology at San Diego State University and proprietor of Conservation Science Research & Consulting. He has been studying the ecology and management of ravens and tortoises in the Mojave Desert since 1990. Elena G. Gonzalez was a visiting predoctoral scientist at the CCEG. Her research interest focuses on the mechanisms that drive population genetic structure and dispersal in various organisms, especially in highly migratory species. Alvaro Godinez was a technician for the CCEG and currently manages the Microarray Core Facility at the University of Maryland Biotechnology Institute. Kevin Omland is a faculty member at UMBC whose laboratory focuses on speciation, character evolution and sexual selection in birds. He is especially interested in recently derived groups at the interface between population-level divergence and species-level phylogenies. Sarah Young was a CCEG technician and is currently a research technician at the University of Pittsburgh studying vascular development in zebrafish. In addition to her work in molecular biology and genetics, she pursues work in the field of sustainable agriculture and food systems. Lauren Helgen is a technician for the CCEG, with research experience in the molecular systematics of marine invertebrates, mammals and birds. Gracia Syed is a graduate student at UNAM and a CCEG technician, and has interests in conservation genetics of endangered turtles. Carl McIntosh was the laboratory manager of the Genetics Program and is currently a biologist in the Laboratory of Genomic Diversity. He has long-term interests in evolutionary genetics and systematics, especially of Hawaiian birds.
