

# Individual Behaviors Dominate the Dynamics of an Urban Mountain Lion Population Isolated by Roads

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## Summary

Large carnivores can be particularly sensitive to the effects of habitat fragmentation on genetic diversity [1, 2]. The Santa Monica Mountains (SMMs), a large natural area within Greater Los Angeles, is completely isolated by urban development and the 101 freeway to the north. Yet the SMMs support a population of mountain lions (*Puma concolor*), a very rare example of a large carnivore persisting within the boundaries of a megacity. GPS locations of radio-collared lions indicate that freeways are a near-absolute barrier to movement. We genotyped 42 lions using 54 microsatellite loci and found that genetic diversity in SMM lions, prior to 2009, was lower than that for any population in North America except in southern Florida, where inbreeding depression led to reproductive failure [3–5]. We document multiple instances of father-daughter inbreeding and high levels of intraspecific strife, including the unexpected behavior of a male killing two of his offspring and a mate and his son killing two of his brothers. Overall, no individuals from the SMMs have successfully dispersed. Gene flow is critical for this population, and we show that a single male immigrated in 2009, successfully mated, and substantially enhanced genetic diversity. Our results imply that individual behaviors, most likely caused by limited area and reduced opportunities to disperse, may dominate the fate of small, isolated populations of large carnivores. Consequently, comprehensive behavioral monitoring can suggest novel solutions for the persistence of small populations, such as the transfer of individuals across dispersal barriers.

## Results

### Movements, Mortality, and Dispersal in an Urban Landscape

We captured, genotyped, and radio-tracked 26 mountain lions in the Santa Monica Mountains (SMMs;  $n = 21$ ) and Santa Susana Mountains (including the Simi Hills;  $n = 5$ ) from July 2002 through July 2012 (Figure 1). We also genotyped 17 other mountain lions from opportunistically collected samples,

including from Angeles National Forest and the Verdugo Hills. Large freeways, including the 101 freeway (Figure 2A), the 5 freeway (Figure 2B), and the 405 freeway (Figure 2A), were significant barriers to movement (i.e., were almost never crossed by mountain lions) and often acted as home-range boundaries. One smaller freeway, the 118 freeway between the Simi Hills and the Santa Susana Mountains (Figure 1), was crossed at least 23 times by two radio-collared mountain lions in an area with a large tunnel and natural habitat on both sides [6]. In February 2009, subadult male P12 crossed the 101 freeway into the SMMs, the only time that a radio-collared mountain lion crossed 101, which separates the SMMs from all areas to the north.

Fourteen radio-collared lions died during the study period: six from intraspecific strife, two from vehicles, two of anticoagulant toxicosis from ingesting rodenticides, one from poaching, one from starvation as a young kitten, and two from unknown causes. Overall, 50% of mortalities of known cause were from intraspecific strife. An uncollared young male was also killed by another lion, for a total of seven instances of intraspecific killing. In five of these cases we were able to identify the surviving individual, and in all five we found that an adult male killed his offspring, his brother, or a previous mate (Table S1 available online).

We tracked the fate of young mountain lions, especially males, to assess dispersal. In the SMMs, we radio-tracked ten subadult male mountain lions and sampled five others that originated there (Table S1). Not one of these 15 young males was known to disperse from the SMMs to a home range with mating opportunities. Of the 12 young males from the SMMs whose ultimate fates are known, 11 died before or during dispersal from intraspecific strife ( $n = 5$ ), vehicle strikes ( $n = 4$ ), control action by police ( $n = 1$ ), and unknown causes ( $n = 1$ ). The only young male to successfully disperse from the SMMs, P22, settled in Griffith Park, requiring the crossing of two freeways (405 and 101; Figure 1). For more than 2 years, this male inhabited a home range of 26 km<sup>2</sup>, as compared to 500 km<sup>2</sup> for adult male P1 (Figure 1). P22's home range was entirely bounded by freeways and urbanization, and he was its sole occupant.

North of 101, we radio-tracked three subadult males and sampled three others that were killed on roads (Table S1). All three collared animals successfully crossed roads and established home ranges as adults. P3 moved regularly between the Simi Hills and the Santa Susana Mountains across the 118 freeway. P12 crossed 101 and subsequently established himself as a dominant male in the SMMs. Perhaps most instructive, young male P16, who shared the eastern Santa Susana Mountains with his father, P21, dispersed north across highway 126 and established a home range (Figure 1). Among radio-collared animals of known fate, the least biased sample for mortality and dispersal, none of the seven subadult males from the SMMs successfully dispersed and established viable home ranges, while all three from the Santa Susana Mountains did.

### Population Genetics of a Small, Isolated Population

We found very low genetic diversity compared to large, contiguous populations in California and in other parts of the west

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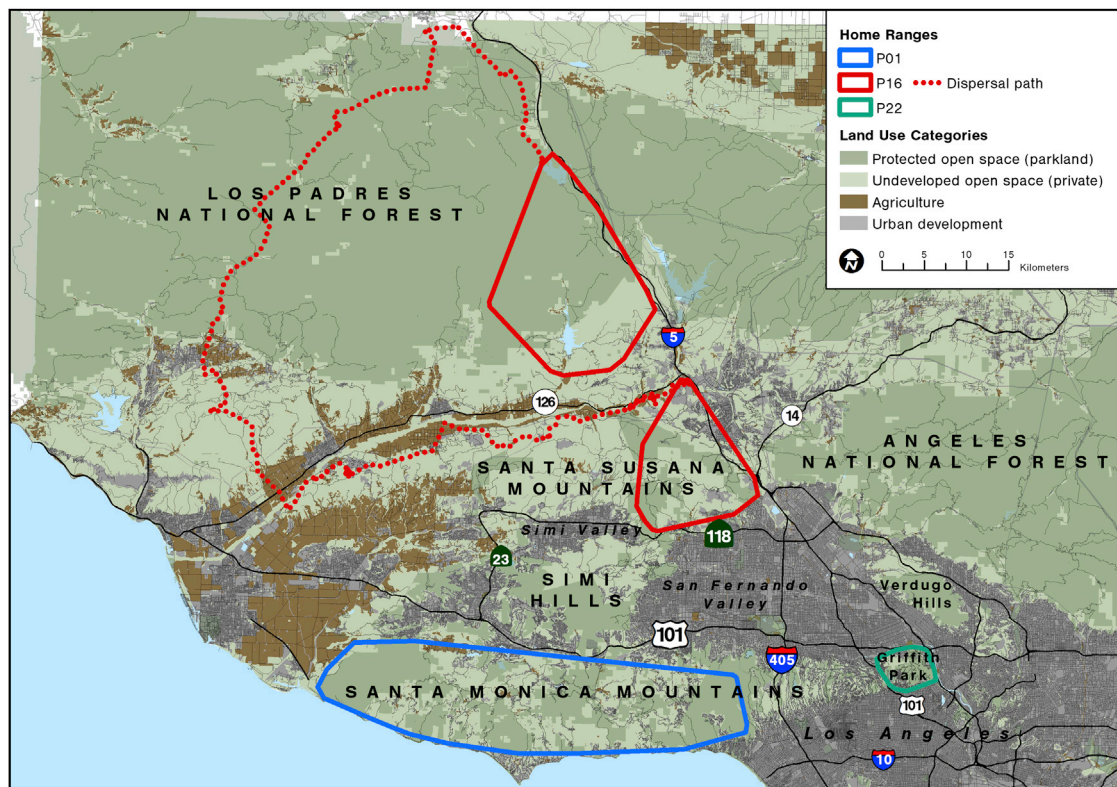


Figure 1. Study Area for Mountain Lion Movements and Population Genetics in and around Santa Monica Mountains National Recreation Area Northwest of Los Angeles

Large natural areas and major freeways are labeled. Home ranges are 100% minimum convex polygons for male P22 in Griffith Park, male P01 in the SMMs, and male P16 that dispersed from the eastern Santa Susana Mountains, across highway 126 to Los Padres National Forest. See also [Table S1](#).

([Tables 1](#) and [S2](#)). Genetic diversity was particularly low in the SMMs south of the 101 freeway, which is the largest and busiest road to the north (175,000 vehicles/day versus 115,000 for the 118 freeway and 22,000 for highway 126; [7]). This population is also farthest away from the putative source populations in Los Padres and Angeles National Forests. The expected heterozygosity ( $H_E$ ), total number of alleles ( $N_A$ ), and number of effective alleles ( $N_E$ ) were all significantly lower in the SMMs than north of the 101 freeway ([Table 1](#)). For private alleles (defined here as those present only in one study population), 67 of 172 discovered alleles were absent from the SMM population, and 78% of loci (42 of 54) had at least one private allele north of 101.

Genetic differences between local populations were also apparent from Bayesian cluster analyses ([Figure 3A](#)). Despite the small sample sizes, the program STRUCTURE [8] indicated strong clustering into three groups ( $K = 3$  by the Evanno  $\Delta K$  method [9]; [Figure S1](#)). The  $F_{ST}$  value between populations north and south of the 101 freeway was 0.12 ( $p < 0.05$ ), three times larger than that previously found for other carnivores in the area [10]. The SMM mountain lion population showed evidence of having experienced a genetic bottleneck based both on significant heterozygote excess (program Bottleneck [11]; single-step mutation probabilities of 90%,  $p = 0.00044$  and 78%,  $p = 0.00004$ ) and Garza and Williamson's  $M$  ratio test ([12]; average  $M = 0.75$ ; for single-step mutation proportion, 90%,  $p < 0.0001$ ). The current effective population size,  $N_E$ , for mountain lions south of 101 was just six individuals.

### The Influence of Specific Behavioral Events on Population Demography and Genetics

Our analysis of a genetically based pedigree showed that specific behavioral events greatly affected population dynamics and genetic composition ([Figure 3B](#)). For example, the migration into the SMMs of P12, who was genetically assigned to the population north of 101 ([Figure 3A](#), blue cluster) and had private northern alleles at 33% of microsatellite loci, demonstrated that the 101 freeway can be traversed. Critically, P12 then survived in the SMMs and bred with resident females, including female P13 twice and his daughter, P19 ([Figure 3B](#)). This was the second instance of father-daughter mating, as P13 was the result of male P01 mating with his daughter, female P06 ([Figure 3B](#)) [13].

The immigration and subsequent matings of male P12 increased the genetic diversity and decreased the internal relatedness (IR) of the SMM population ([Table 1](#)) and thus is an example of a genetic rescue. P12 possessed 20 private alleles from north of the freeway, 19 of which he passed on to his offspring, such that private alleles absent from the SMMs decreased from 67 to 47, loci with private alleles to the north decreased from 42 to 32, and monomorphic loci in the SMMs decreased from 13 to 9. Bayesian clustering analysis also clearly showed the impact of P12's immigration ([Figure 3A](#)). Ninety-seven percent of P12's genome was assigned to the Santa Susanna Mountain population, and he fathered eight offspring based on our pedigree ([Figure 3B](#)). Six of these, including the five with P13 (99% assigned to the SMMs) exhibited a near equal mix of the

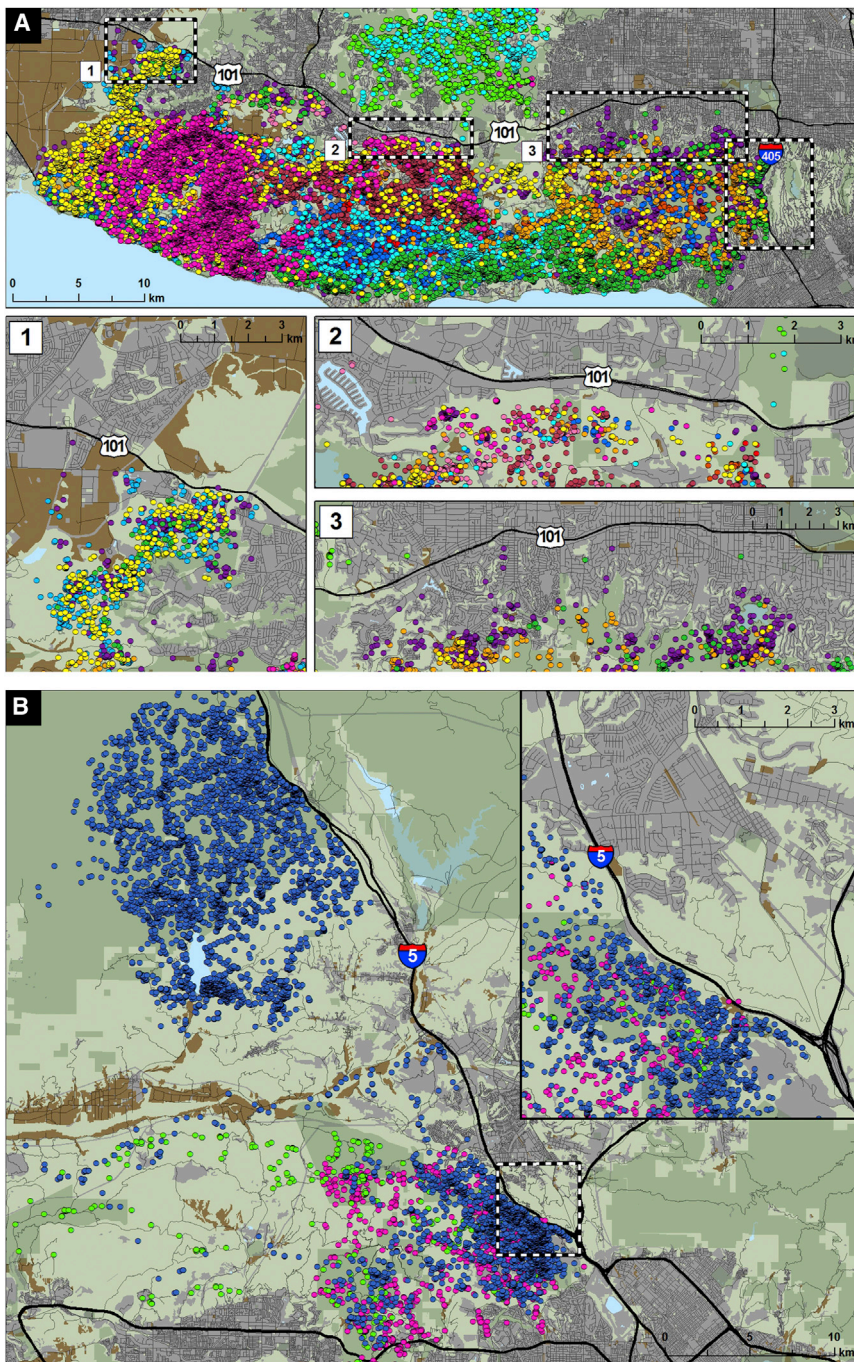


Figure 2. Locations of Mountain Lions along Freeways in Southern California from GPS Radio Collars, 2002–2012

(A) Locations near the 101 freeway, which runs east-west north of the Santa Monica Mountains. Because there is urban development along most of this freeway, in many areas (insets 2 and 3) animals do not approach the freeway. Toward the east end of the SMMs, the 405 freeway passes north-south through the mountains. This freeway is also a major barrier to mountain lion movement.

(B) Locations north of 101 in the Santa Susana Mountains and Los Padres National Forest near the 5 freeway, which runs north-south through the region.

the SMMs, and then rose again in 2013 after P12 bred with his daughter. Similarly, gene diversity showed the opposite pattern, decreasing after the first close inbreeding event, rising in 2010 after P12 bred, and then decreasing with the second inbreeding event (Table S3). The dramatic shifting values of these coefficients over short time periods demonstrate how important individual matings are to the levels of inbreeding and relatedness in the population (Figure S2).

Finally, the IR, a measure that has the potential to provide novel insight about inbreeding and genetic health [15], reflected both the initial bottleneck and the effects of the inbreeding and genetic rescue events. The mean IR for SMM animals dropped from 0.09 (SE = 0.014) to 0.03 (SE = 0.036) when P12 and his offspring were included, as IR values for the initial offspring of the genetic rescue event were low and averaged  $-0.16$  (range  $-0.10$  to  $-0.35$ ). For P23 and P24, the incestuous offspring of P12 and his daughter, IR values rose again to 0.10 and 0.09, indicating that one close inbreeding event may have reversed much of the value of the genetic rescue.

Our results from this small, isolated population also indicate how individual male mountain lions can monopolize breeding opportunities and

SMM (green) and Santa Susanna Mountain (blue) clusters (Figure 3A). Interestingly, P23 and P24, the offspring of P12 and his daughter, P19, each had about three-quarter assignment to the Santa Susana Mountains, as expected (Figures 3A and 3B).

The effects of individual mating events on population genetic measures were also evident as quantified with our pedigree by gene-drop analysis (program PMx [14]) applied for the first time to a wild population. Both the mean inbreeding coefficient (F) and mean kinship increased in 2007 after male P1 bred with his daughter, decreased in 2010 after migrant P12 began to produce offspring in

genetically dominate future generations. Two males, first P01 and later P12, had very high reproductive success based on the pedigree (Figure 3B). Specifically, P01 fathered  $\geq 15$  offspring, P12 fathered  $\geq 8$  offspring, and no individual in the SMM population was fathered by any other male. The pedigree and PMx analyses indicated that P01 had 22 descendants, including six of the seven animals known in the population in 2013, and that P12 had eight descendants, including four of the seven current animals; 33.9% of the copies of the genome in the current population are derived from P01 and 35.7% from P12 (see Table S4).

Table 1. Genetic Diversity Based on 54 Microsatellite Loci for Mountain Lions in and around the Santa Monica Mountains, California, 2002–2012

Population	$N_A$	$N_E$	Poly (%)	$H_E$	$H_O$	IR
Santa Monica Mountains only, south of the 101 freeway before P12 crossing (n = 17)	1.9 ± 0.2	1.6 ± 0.1	76%	0.31 ± 0.03	0.38 ± 0.04	0.09 ± 0.04
North and east of the Santa Monica Mountains, north of the 101 freeway (n = 15)	3.1 ± 0.1	2.1 ± 0.1	100%	0.48 ± 0.02	0.42 ± 0.02	0.17 ± 0.05
Santa Monica Mountains only, south of the 101 freeway after P12 crossing (n = 26)	2.3 ± 0.1	1.8 ± 0.1	83%	0.36 ± 0.03	0.36 ± 0.03	0.03 ± 0.04

Populations are from the SMMs before the genetic rescue event (the dispersal of subadult male P12 from north to south), from north of 101 in the Santa Susana Mountains and San Gabriel Mountains, and from in the SMMs after the genetic rescue event.  $N_A$  is the total number of alleles,  $N_E$  is the number of effective alleles, poly (%) is the percentage of loci that are polymorphic,  $H_E$  is expected heterozygosity,  $H_O$  is observed heterozygosity, and IR is individual heterozygosity or internal relatedness (see the [Supplemental Experimental Procedures](#) for details).  $N_A$ ,  $N_E$ , and  $H_E$  are significantly lower (nonoverlapping 95% confidence intervals) for the SMMs before P12 crossed than for north of the 101 freeway. Mean ± SE is shown. See also [Table S2](#).

## Discussion

### Individual Effects on Population Dynamics and Genetic Diversity

Urban environments are generally inhospitable for large carnivores. Therefore, it is remarkable that a population of a large carnivore extends into the metropolitan area of Los Angeles, one of 30 world megacities (metropolitan areas of >10,000,000 people). However, the challenges for the long-term persistence of this population are substantial. Freeways in the area are almost complete barriers to mountain lion movement ([Figure 2](#)). This severe isolation most likely caused a striking assignment of lions to a single genetic cluster in the SMMs ([Figure 3A](#)). SMM lions were also clearly differentiated from those east of the 5 freeway (red cluster in [Figure 3A](#)), which separates the Angeles National Forest from the Santa Susana Mountains and Los Padres National Forest ([Figure 1](#)). The  $F_{ST}$  value of 0.12 across the 101 freeway is high given its relatively recent age (1949) and given that other studies of *Puma concolor* microsatellite loci have found  $F_{ST} < 0.10$  among 15 subpopulations across the state of Idaho (distances of  $\geq 500$  km; [16]) and an average  $F_{ST}$  of 0.041 among 20 subpopulations from four southwestern states (700 by 700 km; [17]).

Genetic diversity in SMM mountain lions also is very low relative to populations north of the 101 freeway and elsewhere in California and the western US ([Table S2](#)). A measure that is less affected by sample size, the expected heterozygosity, is 0.31 for the SMMs before the immigration event, a value that is the lowest ever reported for western mountain lions, with the exception of another isolated population in the Santa Ana Mountains of Southern California that has comparable variability (H.B.E., unpublished data). The average number of alleles per locus ( $N_A$ ) was also lower in the SMMs than north of 101 and was one-half to two-thirds of the average value from other populations across the western range ([Table S2](#)). The sole population with lower genetic diversity than the SMM population across all of these measures is the Florida panther, *Puma concolor coryi*, a federally endangered subspecies that suffered from substantial inbreeding depression and had been isolated for more than a century before lions from Texas were introduced to alleviate inbreeding depression ([Table S2](#)) [4, 5].

In the small, isolated SMM population, individual behavioral events can have a significant impact on population dynamics and genetics. We documented only one movement across the 101 freeway, by subadult male P12. But after his establishment as a dominant breeding male, new alleles entered the

population, and, particularly for his mixed offspring, genetic diversity increased and measures of inbreeding decreased. However, first-order inbreeding events (father-daughter matings) by males P1 and P12 had the opposite effect, increasing inbreeding and reducing diversity. This kind of close inbreeding has only rarely been documented in mountain lions, specifically in the small and isolated southern Florida population [3, 4].

We also found significant effects of individual behavior on two other critical aspects of population dynamics, dispersal and mortality. Although typically every young male and half of young females disperse out of their natal range [18], not a single subadult mountain lion has successfully dispersed out of the SMMs. Instead, young males have died, principally from intraspecific strife and vehicles. In the one dramatic case, male P22 dispersed from the SMMs into the Hollywood Hills and has lived for 2 years in a home range of 26 km<sup>2</sup>, the smallest annual range ever reported for an adult male. In this range, P22 was surrounded by roads and development ([Figure 1](#)) and had no opportunity to mate. Male mountain lion home ranges are typically an order of magnitude larger, at 300–400 km<sup>2</sup> or more [18, 19], and overlap with those of multiple females. By contrast, all three of the young males that we radio-tracked in the Santa Susanna Mountains successfully dispersed and established home ranges.

Intraspecific strife, the most common cause of mortality, can also be important in other populations, particularly those that are not hunted [20, 21]. However, in the SMMs, we documented repeated cases of males killing their offspring, their brothers, and previous mates. Little has been reported about paternity or kin recognition in mountain lions [18, 22], but clearly this is rarely a sound evolutionary strategy as the survivorship of offspring or siblings is traded against the probability of future reproduction [23]. It is particularly hard to imagine an advantage from killing potential mates or female offspring ([Table S1](#)). In fact, in the Santa Susanna Mountains, we observed the opposite pattern. Male P21 was the father of subadult males P12 and P16 ([Figure 3B](#)), both of which successfully emigrated and established long-term home ranges: P12 south into the SMMs and P16 north across highway 126 ([Figure 1](#)). None of the young males originating in the SMMs, dominated by adult males P1 and P12, have lived beyond age 2, so with respect to male mountain lions, the SMMs are a population sink. In other aspects of ecology and behavior, including home-range size (males, 300–500 km<sup>2</sup>; females, 100–200 km<sup>2</sup>), diet ( $\geq 90\%$  deer), annual adult survival ( $\geq 75\%$ ), and litter size (two to four) [6], the SMM lion population is similar to those throughout the southwest [20].

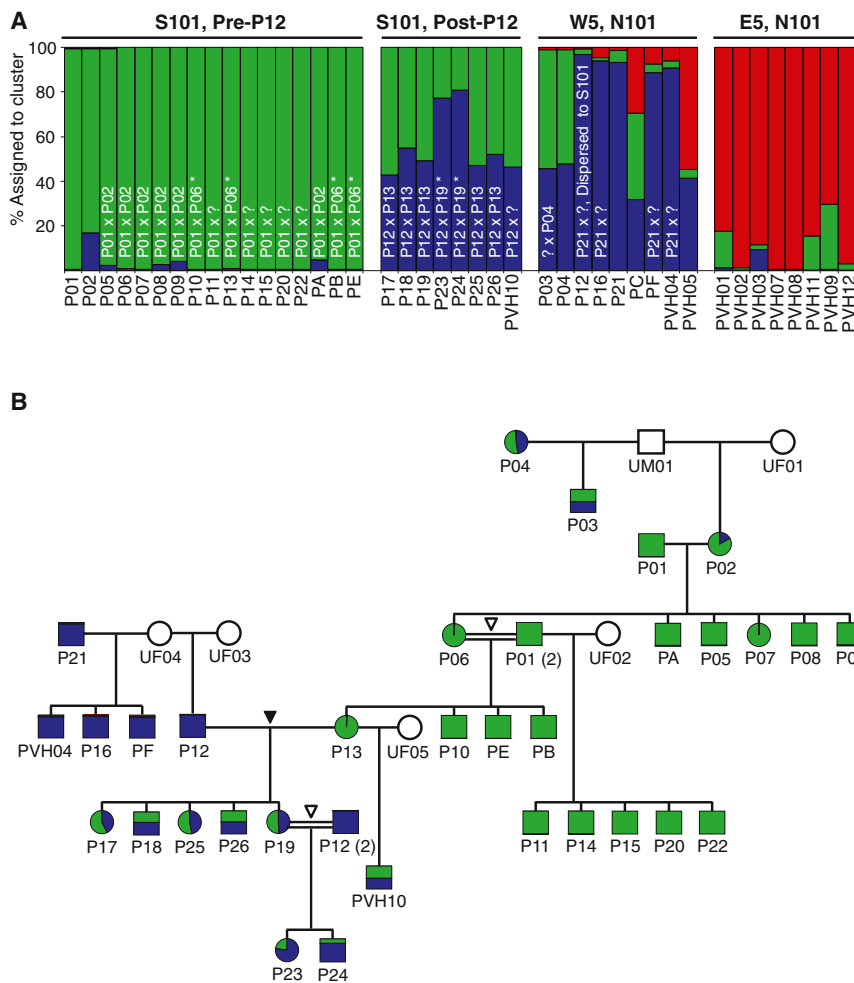


Figure 3. Genetic-Based Cluster Assignments and Recreated Pedigree Based on 54 Microsatellite Loci

(A) Results of program STRUCTURE for 42 mountain lions in the SMM region in Southern California, 2002–2012. The “S101, pre-P12” group is mountain lions from the SMMs, south of the 101 freeway (see Figure 1), before male P12 crossed the 101 freeway from the Simi Hills to the SMMs. The “S101, post-P12” group includes animals sampled in the SMMs that are the offspring of male P12 after he crossed the 101 freeway. “W5, N101” includes animals from the Simi Hills and Santa Susana Mountains, north of the 101 freeway. “E5, N101” includes mountain lions east of the 5 freeway in the San Gabriel Mountains and Verdugo Hills. White lettering for the first three groups indicates the known parentage based on the recreated pedigree. See also Figure S1.

(B) Pedigree for mountain lions in and around the SMMs, 2002–2012. The pedigree was constructed using the programs CERVUS and Colony (see the Supplemental Experimental Procedures). Colors for individual animals correspond to the genetic cluster assignments determined using STRUCTURE: green is the SMM cluster, and blue is the “W5, N101” or Santa Susana Mountains cluster. Symbols with two colors indicate animals with assignment to both clusters. Animals that were not sampled but whose presence is presumed are labeled “UF” for unknown females or “UM” for unknown males. Double lines and open triangles between animals indicate close inbreeding events, specifically father–daughter mating. The black triangle indicates the outbreeding event when P12, from north of the 101 freeway, bred with P13, from the SMMs. See also Figure S2 and Tables S3 and S4.

Very small populations are subject to Allee effects in which low growth rates result from low density, often caused by social disruption as individuals are too sparse to form social groups or find mates [24]. In the SMMs, the inverse has occurred as a small mountain lion population is at high density but lives in a spatially constrained area, resulting in social disruption through negative interactions between close relatives that normally would be rare or nonexistent. The result is reduced population health as indicated by low genetic diversity and increased inbreeding. Such “inverse Allee effects” leading to social disruption could be an important but largely unrecognized problem in isolated and densely packed urban environments.

#### Implications for Management and Conservation of Large Carnivores in Urban Landscapes

The importance of specific behavioral events such as dispersal, inbreeding, and killing of close relatives in this small, isolated mountain lion population has implications for conservation in fragmented landscapes. First, detailed behavioral and genetic monitoring may be critical for understanding the factors that threaten population persistence. Only through the collection of extensive demographic and behavioral data on most of the population were we able to identify the most important behaviors affecting population dynamics and genetic diversity.

Second, the maintenance and restoration of habitat connectivity is vital for small populations of large carnivores. Migration events between populations may not have to be frequent to maintain genetic diversity [25], and we have observed that one successful migrant can have a significant impact, especially in mountain lions, where individual males can have high reproductive success. However, the skewed reproduction in small mountain lion populations [26] can result in dominance of the gene pool by individual males, especially when close inbreeding is also occurring, which may be detrimental to population persistence. In the wolves at Isle Royale National Park, although a single male wolf immigrated into the population and increased genetic diversity, the effects were reversed by reproductive dominance of this individual and associated inbreeding [27, 28]. Connectivity is also important because stochastic effects, such as the loss of one dominant male through a vehicle collision, are more extreme and can result in extinction. Previous research on mountain lions in the Santa Ana Mountains suggested that an area of less than 1,100 km<sup>2</sup> was unlikely to support mountain lions without some immigration [29], and the SMMs are only about 660 km<sup>2</sup>. In highly developed areas, the conservation of natural habitat on both sides of freeways and effective corridors across them [30] or translocations may be necessary if large carnivores are to persist in proximity to the megacities of the future.

## Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.07.029>.

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