
Effectiveness of a Regional Corridor in Connecting Two Florida Black Bear Populations

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Abstract: *Corridors may mitigate the adverse effects of habitat fragmentation by restoring or maintaining connectivity between disjunct populations. The efficacy of corridors for large carnivores, however, has rarely been evaluated objectively. We used noninvasive sampling, microsatellite analysis, and population assignment tests to evaluate the effectiveness of a regional corridor in connecting two Florida black bear (*Ursus americanus floridanus*) populations (Osceola and Ocala). Bear movement was predominantly unidirectional, with a limited mixing of individuals from the two populations in one area of the corridor. We also documented bears in Osceola that were genetically assigned to Ocala and bears in Osceola that may be offspring from an Osceola-Ocala mating. Our results indicate that the Osceola-Ocala corridor is functional and provides a conduit for gene flow between these populations. Human development, however, may hinder the use of the Osceola-Ocala corridor by bears. The noninvasive sampling and genetic methods we used provide a means of evaluating corridor effectiveness that can help identify linkages necessary for maintaining metapopulation structure and population viability.*

Key Words: dispersal, population assignment test, population connectivity, regional corridors, *Ursus americanus floridanus*

Efectividad de un Corredor Regional para la Conectividad de Dos Poblaciones de Oso Negro de Florida

Resumen: *Los corredores pueden mitigar los efectos adversos de la fragmentación de hábitat mediante la restauración o mantenimiento de la conectividad entre poblaciones discontinuas. Sin embargo, la eficacia de los corredores para carnívoros mayores ha sido objetivamente evaluada pocas veces. Utilizamos muestreo no invasivo, análisis de microsatélites, y pruebas de asignación poblacional para evaluar la efectividad de un corredor regional para la conectividad de dos poblaciones (Osceola y Ocala) de oso negro de Florida (*Ursus americanus floridanus*). El movimiento de osos fue predominantemente unidireccional con una mezcla limitada de individuos de las dos poblaciones en un área del corredor. También documentamos osos en Osceola que estaban asignados genéticamente a Ocala y osos en Osceola que pudieran ser descendientes de un apareamiento Osceola-Ocala. Nuestros resultados indican que el corredor Osceola-Ocala es funcional y proporciona un conducto par el flujo de genes entre estas dos poblaciones. Sin embargo, el desarrollo humano puede impedir el uso del corredor Osceola-Ocala por los osos. El muestreo no invasivo y los métodos genéticos que utilizamos proporcionan un medio para evaluar la efectividad de corredores que puede ayudar a identificar las conexiones necesarias para el mantenimiento de la estructura de la metapoblación y la viabilidad poblacional.*

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Palabras Clave: conectividad de poblaciones, corredores regionales, dispersión, prueba de asignación poblacional, *Ursus americanus floridanus*

Introduction

Reversing the effects of habitat fragmentation is a wildlife conservation priority (Soulé & Orians 2001). Landscape linkages or corridors have been suggested to connect disjunct populations and mitigate the negative effects of habitat fragmentation (Harris 1984; Noss & Harris 1986). Corridors can increase movement of organisms among habitat patches (Hass 1995; Haddad 1999; Haddad et al. 2003), increase recolonization potential (Hale et al. 2001), provide additional habitat (Perault & Lomolino 2000), and facilitate plant and animal interactions (Tewksbury et al. 2002). Corridors may also enhance survival of individuals (Coffman et al. 2001), gene flow (Harris & Gallagher 1989), and population viability (Fahrig & Merriam 1985; Beier 1993).

Large carnivores are highly susceptible to the effects of habitat fragmentation because of low population densities, wide-ranging movements, and the potential for conflicts with humans (Noss et al. 1996; Crooks 2002). Many populations of large carnivores currently exist within fragmented habitats, encompassing areas much too small to support long-term population viability (Woodroffe & Ginsberg 1998). Additionally, the long-distance movements of large carnivores suggest they are more likely to use corridors for movements than species with limited dispersal capabilities (Lidicker & Koenig 1996; Harrison & Voller 1998). The effectiveness of corridors for large carnivores, however, has not been tested on a regional scale.

Testing the effectiveness of regional corridors for carnivores is a challenge because long-distance dispersal is rare, and there is no guarantee that the sample of radio-tagged animals will contain dispersers (Koenig et al. 1996). Moreover, the movement of animals from one population to another does not indicate effective dispersal in the context of population genetics. Genetic data are better suited to detect effective dispersal (Frankham et al. 2002). The use of relatively inexpensive, noninvasive sampling techniques such as hair snares and genetic analyses provide data necessary for evaluating the functionality of corridors by elucidating genetic structure and dispersal of individual animals (Foran et al. 1997; Frankham et al. 2002). Recent advances in genetic analyses and statistical techniques, namely population-assignment tests, have made it possible to identify the origin of animals by assigning them to a population based on their multilocus genotypes (Paetkau et al. 1995; Waser & Strobeck 1998; Waser et al. 2001). These techniques can identify dispersal patterns and otherwise cryptic metapopulation boundaries,

which may indicate breaks in gene flow across populations or the reconnection of once isolated populations (Manel et al. 2003; Proctor et al. 2004). Additionally, some assignment tests have the potential to detect not only immigrants into a population but also their offspring, which enables researchers to directly detect and monitor gene flow (Rannala & Mountain 1997; Pritchard et al. 2000).

The Florida black bear (*Ursus americanus floridanus*) is a species that could benefit from the establishment of regional corridors. Once distributed throughout Florida and the southern portions of Georgia, Alabama, and Mississippi, its distribution and abundance were significantly reduced from the 1850s to the 1970s through habitat loss, fragmentation, and overhunting (Brady & Maehr 1985). The Florida black bear now occurs in several fragmented populations and is state-listed as a threatened species in most Florida counties (Maehr et al. 2001). Residential and commercial development throughout the range of the Florida black bear has created formidable obstacles to its movement (Brody & Pelton 1989; Maehr et al. 2003). Consequently, regional corridors may be needed to mitigate the detrimental demographic and genetic effects of habitat fragmentation before development precludes existing opportunities for connectivity (Harris & Scheck 1991; Noss 1993; Harris et al. 1996).

Dispersing black bears can travel hundreds of kilometers from where they were born (Rogers 1987; Maehr et al. 1988; Lee & Vaughan 2003). This long-range dispersal potential offers a mechanism by which population connectivity and metapopulation structure could be maintained. Documented dispersal and movement of individual bears (Florida Fish and Wildlife Conservation Commission [FWC], unpublished data) and geographic information systems (GIS) analysis (Hector 2003) suggest that the Osceola-Ocala regional corridor (see Study Area for details) may be the best option for reconnecting two of the largest Florida black bear populations.

Our objective was to evaluate the effectiveness of the Osceola-Ocala corridor for the Florida black bear. We used noninvasive sampling to obtain genetic material from bears within the Osceola-Ocala corridor and from the Osceola and Ocala populations. Population assignment tests were used to assign individuals sampled from the corridor to a population of origin (Ocala or Osceola) based on their multilocus genotypes. These techniques allowed us to characterize the dispersal of bears from the source populations and identify gaps in connectivity within the Osceola-Ocala corridor.

Study Area

This study was conducted in Ocala National Forest (Ocala), Osceola National Forest (Osceola), and the patchwork of land between the two (Osceola-Ocala corridor) (Fig. 1). Ocala encompasses approximately 1650 km² of habitat (Cox et al. 1994). Vegetation is dominated by sand pine forest and xeric oak scrub (Myers & Ewel 1991). Ocala harbors one of the largest populations of the Florida black bear (McCown et al. 2004), and its bear population has not been hunted since 1971 (Wooding 1993).

Bordered to the south by an interstate highway (I-10), Osceola National Forest encompasses 638 km² of habitat (Cox et al. 1994). The habitat of Osceola consists of pine flatwoods and hydric hammock interspersed with bay swamp, shrub bog, and mixed hardwood swamp (Myers & Ewel 1991). The Osceola black bear population is contiguous with the Okefenokee population in Georgia and represents one of the largest populations of the Florida black bear (Maehr et al. 2001). The Osceola bear population was last hunted in 1993 (Wooding 1993).

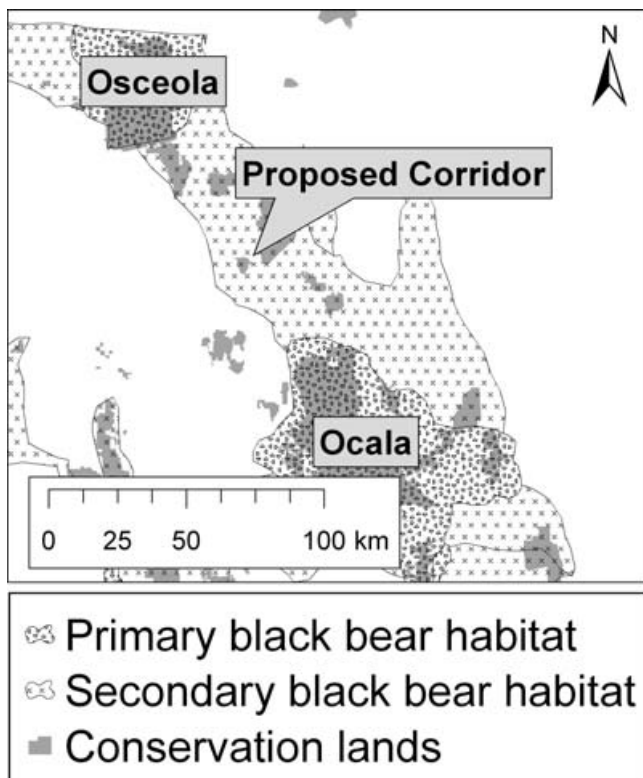


Figure 1. Area proposed as a regional corridor between Ocala National Forest and Osceola National Forest. Primary black bear habitats are those with documented presence of breeding females. Secondary habitats are those with documented bear sightings but no evidence of presence of breeding females (Florida Fish and Wildlife Conservation Commission, unpublished data).

The Osceola-Ocala corridor is a patchwork of public and private lands within a matrix of roads and development between the Ocala National Forest and the Osceola National Forest (Fig. 1). The corridor is approximately 30 km wide and 90 km long. The narrowest part of the corridor is located north of the city of Starke, near industrial mining operations. Vegetation consists of flatwoods, pine plantations, forested wetlands, riparian hammocks, and scrub covering 80 km² of potential black bear habitat (Maehr et al. 2001).

Methods

We used a GIS map of areas with known black bear sightings (FWC, unpublished data; Fig. 1) and a proposed statewide ecological network (Hector 2003) to identify study areas between the Ocala and Osceola bear populations. We overlaid a grid of 20-km² cells on a GIS map of the corridor and placed at least one hair snare within each cell (Woods et al. 1999).

Each hair snare consisted of two strands of standard four-pronged barbed wire attached to a perimeter of three or more trees. Each snare encompassed a total area of 10–30 m². We baited the center of the snare with pastries and corn, and placed two attractants (pastries and raspberry extract) ≥ 2.44 m above the snare. As bears entered the snare the barbed wire snagged hairs with follicles that were collected for genetic analyses. We operated hair snares an average of seven times from May to November 2002 and May to August 2003. Additionally, we collected hair samples within the corridor opportunistically from a complementary hair snare project in Osceola (May–August, 2002–2003), from existing fences (2001–2003), and from bears killed on roads (1998–2003). We also obtained black bear tissue and hair samples archived from previous studies and highway mortalities (1989–2003) from the Osceola and Ocala populations. Hair and tissue samples were analyzed at Wildlife Genetics International (Nelson, British Columbia, Canada). The DNA was extracted using QIAGEN's DNeasy Tissue kits (Valencia, California). Individual bears were genotyped using 12 microsatellite loci (G1A, G10B, G10C, G1D, G10L, G10M, G10P, G10X, G10H, MU50, MU59, and G10J) that were amplified with polymerase chain reaction (PCR) (Paetkau et al. 1995, 1998, 1999). The gender of each bear was determined using the length polymorphism in the amelogenin gene (Ennis & Gallagher 1994).

We used population-assignment tests (software program STRUCTURE, Oxford, United Kingdom) to assign individuals to a population of origin (Osceola or Ocala) based on their multilocus genotypes (Pritchard et al. 2000). STRUCTURE assumes Hardy-Weinberg equilibrium (HWE) within populations and linkage equilibrium between loci. To test these assumptions, we first used

Genepop 3.4 (Montpellier, France) to test for deviations from HWE (Raymond & Rousset 1995). For this test, if loci had fewer than four alleles, we computed exact p values using the complete enumeration method (Louis & Dempster 1987). If loci had four or more alleles, we used the Markov chain method (dememorization 1000; batches 100; iterations per batch 1000) (Guo & Thompson 1992). We also used Genepop 3.4 and the Markov chain method to test for linkage disequilibrium to identify nonrandom association between alleles of different loci.

We used STRUCTURE to assign bears to a cluster or population based on their genotypes without regard to where samples were collected. Allele frequencies were assumed independent and analyses were conducted with 100,000 iterations and 100,000 repetitions of Markov chain Monte Carlo. We used the admixture model, which assumes that each individual draws some proportion of membership (q) from each of K clusters, with the number of clusters set to two (Pritchard et al. 2000).

An individual bear was placed in a cluster if $q > 0.85$ for that cluster. If $q > 0.40$ for both clusters, the genotype profile indicated mixed ancestry, suggesting the individual may be the result of a mating between individuals from the two clusters.

Results

We collected hair samples at 44 hair snare sites within the Osceola-Ocala corridor (Fig. 2). Fewer samples were collected toward the center of the corridor (Fig. 3). Of

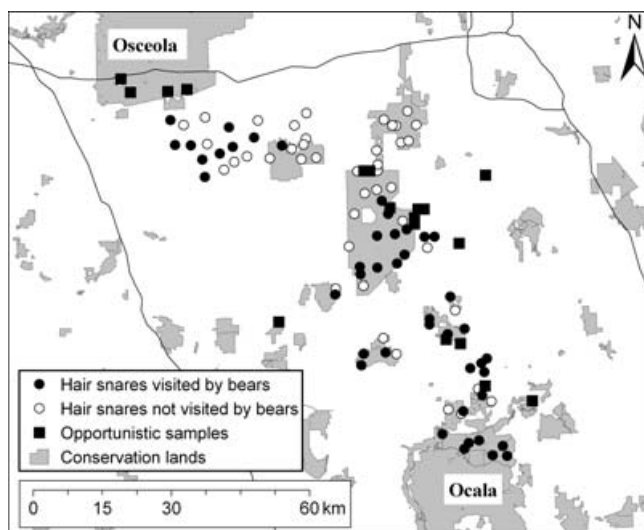


Figure 2. Locations where black bear hair samples were collected in the Osceola-Ocala corridor. Filled circles represent hair snares visited by bears and open circles represent hair snares not visited by bears. Squares represent location of samples collected opportunistically.

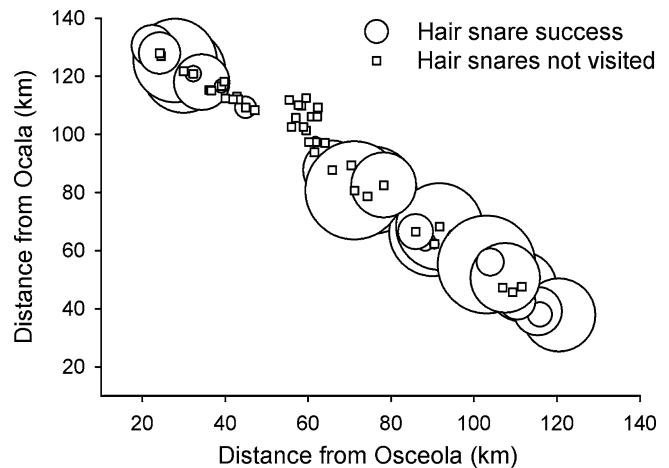


Figure 3. Trap success of hair snares in the Osceola-Ocala corridor. The size of the circle represents the number of bear visits relative to the number of trapping sessions. The distance is the linear distance from the populations' centroids (the harmonic mean of sample locations in the Ocala and Osceola populations) to the hair snares in the corridor.

the 629 samples collected, 129 were selected for genetic analysis (115 collected from hair snares, 9 from bears killed on highways, and 5 from existing fences). From these samples, 31 black bears were identified; of these, 11 were sampled at multiple locations. Only 3 females were identified in the corridor, and they were within 20 km of the Ocala population. Additionally, 41 (31 male and 10 female) bears were identified from samples collected at Osceola and 40 (26 male and 14 female) bears were identified from the Ocala population.

There were no significant departures from Hardy-Weinberg equilibrium for any locus or population ($p > 0.05$) and the linkage disequilibrium test indicated that 10% of loci pairings had significant nonrandom associations ($p \leq 0.05$). The population assignment tests revealed that all bears sampled in Ocala were assigned to cluster 1 (Ocala origin) ($q > 0.90$), indicating that none originated from Osceola. Bears sampled in Osceola had ancestry in both clusters, with 36 of the 41 bears assigned to cluster 2 (Osceola origin) ($q > 0.85$). Two individuals sampled in Osceola were assigned to cluster 1 ($q > 0.99$), suggesting they were dispersers from Ocala. Additionally, two bears sampled in the Osceola population were assigned to both clusters with $q > 0.40$, indicating that their parents were from Osceola and Ocala. The population assignment test for one bear in the Osceola sample was inconclusive. Of black bears sampled in the corridor, 28 were assigned to cluster 1 (Ocala) ($q > 0.85$) and 3 were assigned to cluster 2 (Osceola) ($q > 0.98$), suggesting a predominately one-way movement by bears from Ocala into the corridor (Fig. 4).

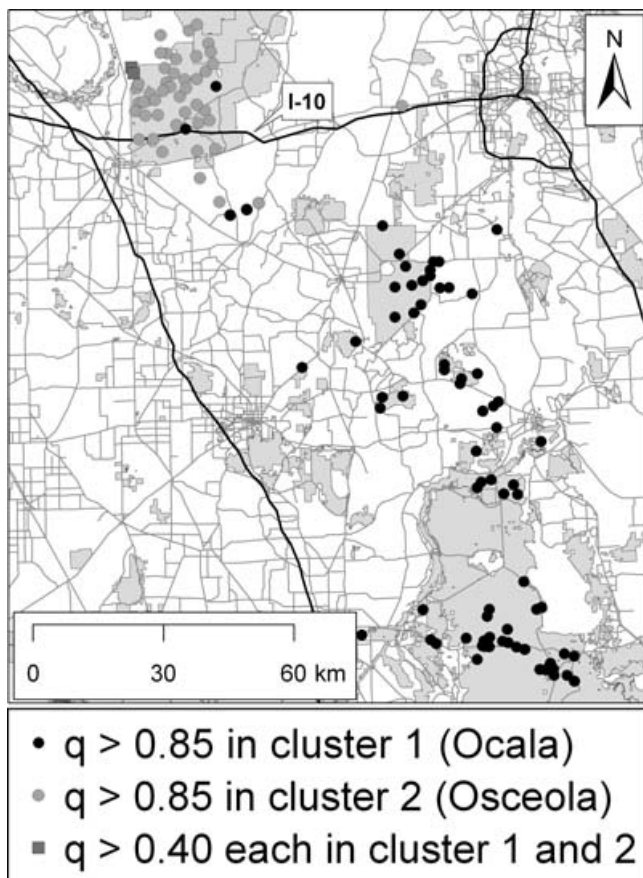


Figure 4. Spatial pattern of the proportion of membership (q) for bears sampled in Osceola, Ocala, and the Osceola-Ocala corridor: For Osceola and Ocala, 40 individuals each are displayed. Within the Osceola-Ocala corridor, 31 bears sampled at 50 different locations are displayed. Black bears with $q > 0.85$ in a cluster are labeled as belonging to that cluster. Bears with mixed ancestry have $q > 0.40$ in both clusters.

Discussion

Although the role of corridors in conservation planning has been debated (Simberloff et al. 1992; Rosenberg et al. 1997; Niemela 2001), the importance of connectivity has been well established in conservation biology (Harris 1984; Noss & Harris 1986; Noss 1987; Beier & Noss 1998). Conservation plans focusing on protecting regional networks of connected lands have been developed in recent years, although more data are needed to evaluate the functionality of corridors to better guide such planning efforts in the future (Noss & Harris 1986; Hctor et al. 2000; Larkin et al. 2004).

Functional corridors provide habitat for foraging or searching for a mate and serve as conduits for natal dispersal and seasonal migration (Harris & Scheck 1991;

Noss 1993; Rosenberg et al. 1997; Hess & Fischer 2001). Few researchers, however, have evaluated functionality of corridors for large carnivores. We evaluated the functionality of a regional corridor (Osceola-Ocala corridor) for the Florida black bear with noninvasive sampling, genetic analyses, and population assignment tests.

The presence of bears in multiple locations within the corridor indicates that some individuals may be corridor residents. Additionally, the substantial disparity in the sex ratio of bears sampled in the corridor (which also reflects the sex ratio of road-killed bears in the corridor [FWC, unpublished data]) and the sample locations of females suggest that the corridor is primarily used as a conduit for gender-biased dispersal. Although our sample from the corridor included three females, we do not know whether a reproducing population inhabits the Osceola-Ocala corridor. A reproducing population within the corridor would facilitate connectivity between Ocala and Osceola populations because bears born in the corridor could potentially disperse to the former populations (Noss 1993; Noss et al. 1996; Rosenberg et al. 1997; Beier & Noss 1998).

Most bears sampled within the Osceola-Ocala corridor were assigned to Ocala, indicating a predominantly unidirectional pattern of movement from Ocala into the corridor. This pattern is most likely due to the relatively high density of bears in Ocala, perhaps a consequence of population growth following hunting prohibition in 1971. Results of many studies of carnivores suggest that directional patterns of dispersal are related to the presence of habitat suitable for dispersal (Smith 1993; McLellan & Hovey 2001; Poole et al. 2001; Maehr et al. 2002). For instance, bears from Ocala probably used the Osceola-Ocala corridor for dispersal because there is available habitat in which to disperse. Other areas surrounding the Ocala population have less suitable habitat and more human-bear interactions (Eason 2000).

There was limited mixing of Ocala-assigned individuals with Osceola-assigned individuals in one area of the corridor (Fig. 4). Three of the Ocala-assigned individuals were previously sampled in Ocala and provide strong evidence of dispersal from Ocala into the corridor and further validate the accuracy of population assignment tests. This, along with presence of bears with both Ocala and Osceola genotypes in the corridor, suggests that the Osceola-Ocala corridor is functional.

The presence of two Ocala bears and two bears with mixed ancestry in the Osceola population is equivocal. During 1986–2002, seven nuisance bears were translocated from Ocala into Osceola, and these may be partially responsible for aforementioned observations. We eliminated one of these bears as a possible match based on genetic data. The fates of five of the translocated bears are known (two hunter harvest, one nuisance capture, one road kill, and one illegal kill [FWC, unpublished data]), but the fate of one bear remains unclear. We believe that

the Ocala bears sampled in Osceola were dispersers from Ocala, although the possibility that one of these might have been the translocated bear with unknown fate cannot be ruled out with certainty. Likewise, we cannot rule out the possibility that one or both of the bears with mixed ancestry sampled in Osceola were offspring of the translocated bears, although it is likely that these were sired by dispersers from Ocala.

The spatial pattern of hair samples (Figs. 2 & 3) and assignment tests (Fig. 4) indicated a filter with less suitable habitat toward the middle of the corridor. This filter may have been caused by residential, commercial, and industrial development and a four-lane highway that intersects the corridor. These land uses have been identified as potential barriers to bear dispersal (McLellan & Shackleton 1988; Maehr et al. 2003).

Only three bears with Osceola genotypes were sampled south of the interstate highway (I-10), despite the large population of bears just north of I-10 (Osceola). One of those three bears also was sampled north of I-10 (FWC, unpublished data), suggesting that although the highway is not a complete barrier to movement, it may represent a significant filter allowing only a few individuals to cross successfully. These observations are consistent with the evidence that high-speed highways can limit movements of bears (Brody & Pelton 1989; Proctor et al. 2002; Kaczensky et al. 2003). The filtering effect of I-10 may also have contributed to the unidirectional pattern of movement of bears from Ocala into the corridor.

Conservation Implications

Our results suggest that the Ocala and Osceola black bear populations were recently reconnected, primarily through unidirectional movement of bears from Ocala to Osceola and that some of the dispersers may have successfully reproduced. We speculate that the predominantly unidirectional dispersal of bears from Ocala to Osceola may be a result of a relatively high density of bears in Ocala, but factors such as the filtering effect of high-speed highways might contribute to it (FWC, unpublished data). Moreover, presence of bears throughout the Osceola-Ocala corridor (including females) provides evidence that at least some of the bears were corridor residents. Based on these results, we conclude that the Osceola-Ocala corridor is functional and provides genetic and demographic connectivity between Ocala and Osceola black bear populations. The connection of the Osceola and Ocala populations allows gene flow between these populations through male-biased dispersal, which maintains metapopulation structure, and may increase population viability. However, increasing development pressure near this regional corridor may thwart functional connectivity of these populations if the habitat within the corridor is not protected.

Maintaining or restoring demographic and genetic connectivity among populations may require multiple strategies, including encouraging recolonization of the corridor by maintaining high densities in the source populations, minimizing habitat loss and fragmentation, and managing for high-quality habitat. Sufficient habitat for recolonization, however, would require easements, purchasing conservation lands, fostering agreements with private landowners, and reducing human activity (Beier 1995; Duke et al. 2001). Providing connectivity may also require retrofitting highways to allow safe passage for bears (Foster & Humphrey 1995; Larkin et al. 2004).

The use of noninvasive hair snares and population-assignment tests is an efficient method for evaluating the existence and effectiveness of regional corridors. These techniques allow identification of functional corridors and can be used for conservation planning. Given the rapid pace of development in the southeastern United States, fragmentation of remaining wildlife habitat is likely to continue. The reconnection of wildlife populations with corridors may be the best option for mitigating the adverse impacts of habitat fragmentation on the black bear and other wildlife species.

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