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Potential Effects of the United States-Mexico Border Fence on Wildlife

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Abstract: *Security infrastructure along international boundaries threatens to degrade connectivity for wildlife. To explore potential effects of a fence under construction along the U.S.–Mexico border on wildlife, we assessed movement behavior of two species with different life histories whose regional persistence may depend on transboundary movements. We used radiotelemetry to assess how vegetation and landscape structure affect flight and natal dispersal behaviors of Ferruginous Pygmy-Owls (*Glaucidium brasilianum*), and satellite telemetry, gene-flow estimates, and least-cost path models to assess movement behavior and interpopulation connectivity of desert bighorn sheep (*Ovis canadensis mexicana*). Flight height of Pygmy-Owls averaged only 1.4 m (SE 0.1) above ground, and only 23% of flights exceeded 4 m. Juvenile Pygmy-Owls dispersed at slower speeds, changed direction more, and had lower colonization success in landscapes with larger vegetation openings or higher levels of disturbance ($p \leq 0.047$), which suggests large vegetation gaps coupled with tall fences may limit transboundary movements. Female bighorn sheep crossed valleys up to 4.9 km wide, and microsatellite analyses indicated relatively high levels of gene flow and migration (95% CI for $F_{ST} = 0.010–0.115$, $Nm = 1.9–24.8$, $M = 10.4–15.4$) between populations divided by an 11-km valley. Models of gene flow based on regional topography and movement barriers suggested that nine populations of bighorn sheep in northwestern Sonora are linked by dispersal with those in neighboring Arizona. Disruption of transboundary movement corridors by impermeable fencing would isolate some populations on the Arizona side. Connectivity for other species with similar movement abilities and spatial distributions may be affected by border development, yet mitigation strategies could address needs of wildlife and humans.*

Keywords: bighorn sheep, dispersal, pygmy-owl, flight behavior, gene flow, connectivity, least-cost path, transboundary conservation, U.S.-Mexico border

Efectos Potenciales de la Barda en la Frontera Estados Unidos-México sobre la Vida Silvestre

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Resumen: *La infraestructura de seguridad a lo largo de fronteras internacionales amenaza con degradar la conectividad para la vida silvestre. Para explorar los efectos potenciales de una barda en construcción a lo largo de la frontera Estados Unidos-México sobre la vida silvestre, evaluamos la conducta de movimiento de dos especies con historias de vida diferentes cuya persistencia regional puede depender de movimientos transfronterizos. Utilizamos radiotelemetría para evaluar el efecto de la estructura de la vegetación y el paisaje sobre las conductas de vuelo y dispersión natal de mochuelos (*Glaucidium brasilianum*), y telemetría por satélite, estimaciones del flujo de genes y modelos de camino de mínimo costo para evaluar la conducta de movimiento y la conectividad entre poblaciones de borrego cimarrón (*Ovis canadensis mexicana*). La altura de vuelo de los mochuelos promedió solo 1.4 m (ES 0.1) sobre el suelo, y solo 23% de los vuelos excedieron los 4 m. Los mochuelos juveniles volaron a menor velocidad, cambiaron más de dirección y tuvieron un bajo éxito de colonización en paisajes de vegetación con grandes claros o mayores niveles de perturbación (*$p \leq 0.047$*), lo que sugiere que los grandes claros de vegetación aunado a bardas altas pueden limitar los movimientos transfronterizos. Borregos hembras atravesaron valles de hasta 4.9 km de ancho, y los análisis de microsatélites indicaron niveles relativamente altos de flujo y migración de genes (95% IC para *$F_{ST} = 0.010–0.115$, $Nm = 1.9–24.8$, $M = 10.4–15.4$*) entre poblaciones separadas por un valle de 11 km. Los modelos de flujo de genes basados en la topografía regional y las barreras al movimiento sugirieron que nueve poblaciones de borrego cimarrón en el noroeste de Sonora están ligadas por dispersión con poblaciones en Arizona. La disrupción de corredores de movimiento transfronterizo por una barda impermeable aislaría algunas poblaciones del lado de Arizona. La conectividad para otras especies con habilidades de movimiento y distribuciones espaciales similares puede ser afectada por el desarrollo de la frontera, sin embargo las estrategias de mitigación podrían atender las necesidades de la vida silvestre y los humanos.*

Palabras Clave: borrego cimarrón, camino de mínimo costo, conducta de vuelo, conectividad, conservación transfronteriza, dispersión, flujo de genes, frontera Estados Unidos-México, *Glaucidium brasilianum*

Introduction

Animal movements are an important determinant of distribution, abundance, extinction, and colonization dynamics, and gene flow (Colbert et al. 2001; Hanski & Gaggiotti 2004). In highly fragmented environments, animal movements among resource patches may be of greater consequence to population persistence than the demographic potential of the patches themselves (Lande 1987). Landscape connectivity is the degree to which an environment facilitates movement among resource patches (Taylor et al. 1993) and is a function of landscape structure and organisms' ability to perceive and respond to it (Tishendorf & Fahrig 2000). Because species' distributions shift due to climate change (Parmesan 2006), landscape connectivity may be essential for persistence (Malcolm et al. 2006), especially near range margins where the size, quality, and proximity of resource patches often decline (Holt et al. 2005). Although human activity has degraded connectivity in many landscapes, forecasting effects on populations is complex because movement is difficult to study.

Along international boundaries, increasing concerns over national security and human migration complicate conserving landscape connectivity. Transboundary development, including fences, roadways, lighting, vegetation clearing, and increased human activity, threatens to alter connectivity at large scales in over 20 nations. In Asia, for example, a security fence recently built along the disputed India–Pakistan border may have already affected wildlife movements (Pahalwan 2006). In North America a 1125-km security fence along more than one-third of the U.S.–Mexico border (U.S. Public Law 109–367) is under construction. Although fence structures vary, most segments are ≥4 m tall, have vertical gaps 5–10 cm wide, and are associated with vegetation clearings and roads ≥25 m wide. Other sections consist of vehicle barriers often coupled with barbed-wire fences (Fig. 1). Mitigating the effects of these structures on wildlife requires information on movement behavior and landscape structures that foster connectivity.

The international boundary between the states of Arizona in the United States and Sonora in Mexico traverses a diverse region. Spanning over 600 km and a 10-fold gradient in annual rainfall, this region extends from coniferous forests near the northern Sierra Madre Occidental to vast deserts of the Colorado River Valley. In contrast to other regions along the U.S.–Mexico border, most areas directly north of Sonora are federally managed, often according to explicit conservation mandates, and in combination with reserves in Sonora form one of the largest networks of protected areas in North America (Felger & Broyles 2007). Transboundary connectivity is especially relevant to conservation in this region because several major biogeographic provinces converge and produce the range limits of many Neotropical and Nearctic taxa (Turner et al. 1995; Escalante et al. 2004). Moreover, broad elevation and moisture gradients produce fragmented distributions of many populations (Hoffmeister 1986; Flesch 2008) that presumably are linked by dispersal. Despite the biological significance of this region, virtually the entire

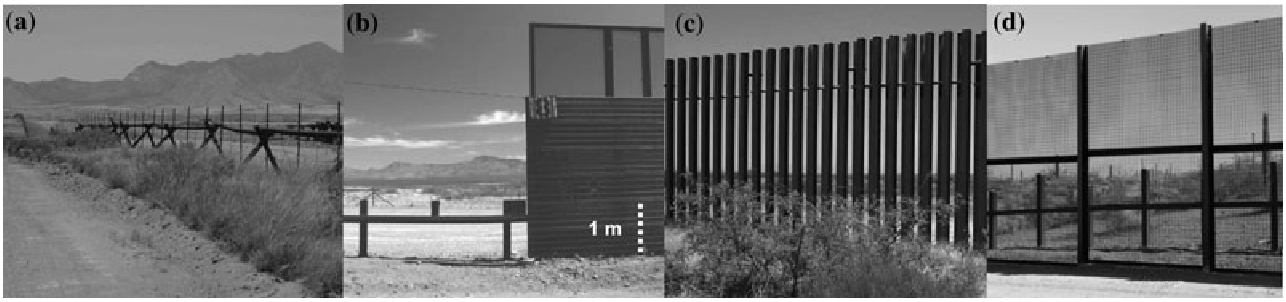

Figure 1. Examples of security fencing located along the international boundary between Arizona, U.S.A., and Sonora, Mexico. In the past, 4- to 6-strand barbed-wire fences traversed many portions of the boundary (a). Many wire fences have been fortified recently with vehicle barriers (b) or replaced with taller less permeable pedestrian fences (c, d).

Arizona–Sonora border has been fenced or is proposed for fencing.

To assess the potential effects of border development on wildlife, we selected two species of concern in the borderlands: Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) and desert bighorn sheep (*Ovis canadensis mexicana*). Each has very different life histories but represent species with fragmented distributions and movement behaviors that may be vulnerable to changes in landscape structure. We used data on movement behavior collected before construction of the border fence to develop descriptive and model-based inferences on the potential effects of border development.

Ferruginous Pygmy-Owls have declined to endangered levels in Arizona, yet are more common in adjacent Sonora (Flesch & Steidl 2006). Thus, persistence and recovery in Arizona may depend on transboundary movements. Although landscape connectivity for birds is often assumed (Dale et al. 2006), recent studies demonstrate that vegetation gaps can slow (Castellón & Sieving 2005) or restrict (Desrochers & Hannon 1997) movements, especially by nonmigratory birds (Harris & Reed 2002) such as Pygmy-Owls.

Desert bighorn sheep occupy mountainous terrain separated by broad valleys. Movements by desert bighorn sheep and other wide-ranging mammals such as Sonoran pronghorn (*Antilocapra americana sonoriensis*) and jaguar (*Panthera onca*) are likely to be disrupted by a continuous border fence (Cordova & de la Parra 2007). Because populations of bighorn sheep are often small and fragmented, connectivity among them is particularly important (Epps et al. 2007).

We assessed the influence of vegetation and landscape structure on (a) flight and dispersal behaviors of Pygmy-Owls, (b) movement rates and gene flow between two populations of desert bighorn sheep and the simulated effects of an impermeable border fence on regional interpopulation connectivity, (c) other species likely to be affected by border development, (d) and strategies to conserve transboundary connectivity.

Methods

Study Area

Lowland vegetation in the Arizona–Sonora borderlands is dominated by three vegetation communities: semidesert grassland at higher elevations to the north and east, Arizona Upland desert scrub at moderate elevations, and lower Colorado River Valley desert scrub at the lowest elevations in the west.

We studied movement behavior of Pygmy-Owls in north-central Sonora and movement behavior and gene flow of desert bighorn sheep in the Pinta and Cabeza Prieta mountains on Cabeza Prieta National Wildlife Refuge, two rugged mountain ranges separated by an 11-km-wide valley. We assessed interpopulation connectivity of desert bighorn sheep in western Arizona and Sonora within 60 km of the border.

Pygmy-Owl

We selected owl territories across a range of vegetation and landscape structures. Between 2003 and 2005, we trapped 19 adult males early in the nesting season and 54 juveniles from 19 broods immediately after fledging. We attached harness-mounted radio transmitters (2.2 g) that averaged 4.1% (SE 0.04) of body mass to each owl.

We assessed flight behavior by monitoring owls continuously during mornings (dawn to 5 h after) and evenings (3 h before dusk to dark) at least one time per week until transmitter batteries failed (12–15 weeks) or owl mortality occurred. We monitored owls visually (84% of locations) when possible or used triangulation. For each flight, we used a rangefinder to measure flight distance and visually estimated minimum and maximum flight height and initial perch height to the nearest 0.1 m for heights <1.5 m above ground or 0.5 m otherwise. To minimize observer influence on owls, we stopped visual monitoring for 60 min if we flushed owls from consecutive perches. To assess observer influence, we noted owls that flushed in response to our presence, noticed us

Table 1. Attributes of vegetation and landscape structure considered as potential explanatory variables of flight and dispersal behaviors of Ferruginous Pygmy-Owls in northern Sonora, Mexico 2003–2005.

Spatial scale and explanatory variable	*Description*
Flight paths	±10° of flight direction
distance to nearest potential perch	distance from preflight location to nearest potential perch*
height of nearest potential perch	height of nearest potential perch*
Home ranges	95% minimum convex polygons
density of trees	mean distance^2 to nearest tree (>2 m tall) in each 90° quarter around potential perches*
height of trees	mean height of nearest tree (>2 m tall) in each 90° quarter around potential perches*
vegetation volume	mean percent vegetation obstruction on 1-m^2 board 6 m from potential perches and 0.5–1.5 m above ground in 90° quarters
proximity to vegetation edge	distance to nearest vegetation edge
Dispersal corridors	500 m wide, centered on lines between successive locations; potential corridors were $\leq$500 m from the endpoint of each corridor in the same direction
topography	dominant topographic formation; mountains or valley
vegetation community	dominant formation type; savannah, desert scrub, thorn scrub, riparian scrub, or woodland
disturbance intensity	proportion of area where vegetation had been cleared or significantly altered; high ($>$50%), moderate (10–50%), low ($<$10%), or none
size of largest vegetation opening	size of the largest human-made vegetation opening; large ($>$200 m wide), moderate (100–200 m), small ($<$100 m), or none

Woody plant >2 m tall and >1.5 cm wide 1 m above the ground.

but did not fly in response, or did not appear to notice us.

We assessed dispersal behavior by estimating the speed, route, direction, and success of natal dispersal. Because owls dispersed during dusk, dawn, and bright moonlit nights and roosted at other times, we calculated dispersal speed as the straight-line distance between pre- and postmovement locations from successive visits divided by the number of movement periods between visits. To assess landscape features encountered during dispersal, we supplemented visual observations with plots of successive locations and inferred dispersal routes based on movement trajectories. To quantify directional change between successive movement bouts, we calculated the absolute difference in orientation. Owls that settled in discrete areas for the life of transmitters and that paired were considered successful dispersers (pairing was inferred from courtship behavior). We located dispersers every 1.5 movement bouts on average and excluded observations if owls were not located for >2 successive bouts, settled for $\geq$36 h, or moved back to natal areas.

We described attributes of vegetation and landscape structure within flight paths, home ranges, and dispersal corridors (Table 1). Within flight paths, we measured distance and height of the nearest potential perch. Within home ranges, we estimated tree density, tree height, understory vegetation volume, and proximity to vegetation edges around the closest potential perch from 30 random points (Table 1). Within dispersal corridors, we used aerial photographs and on-site measurements to classify topography and vegetation and to measure intensity of disturbance and size of the largest vegetation opening. We also described areas that may have been avoided during dispersal by measuring those same features within potential corridors (Table 1).

We estimated flight height, flight distance, and perch height by averaging values for each individual with $\geq$10 observations and averaging estimates across the population. We used analysis of variance (ANOVA) to compare behaviors among individuals and correlation coefficients to assess associations. Because telemetry error was small ($<$25 m [SE 7]), we pooled all locations to estimate home ranges. We estimated total distance moved during dispersal by summing distances between locations from successive visits. We calculated dispersal distance by measuring distances between nests and edges of new home ranges. For one owl that did not settle, we used maximum distance moved.

We used generalized linear mixed models to explain variation in flight and dispersal behaviors within flight paths and dispersal corridors. Within flight paths, we considered flight height and distance as response variables, two potential explanatory variables (Table 1), and initial perch height as a covariate. Observers had no effect on flight behavior ($p \geq 0.16$) and were not considered covariates. Within dispersal corridors, we considered dispersal speed and directional change as response variables, four potential explanatory variables (Table 1), and sex as a covariate. We considered individuals as subjects and as random effects.

We used generalized linear models to explain variation in flight behaviors among home ranges and variation in dispersal success among landscapes. For flight behaviors, we considered mean flight height and distance as response variables and four potential explanatory variables (Table 1). For dispersal success, we considered dispersal distance, total distance moved, intensity of landscape disturbance, and size of the largest vegetation opening along routes as potential explanatory variables and sex as a covariate. We used stepwise variable selection ($p < 0.25$ to enter, $p \leq 0.10$ to stay).

Desert Bighorn Sheep

Between February 2002 and May 2004, we captured 37 adult females (19 in the Pinta and 18 in the Cabeza Prieta Mountains). Females are less likely to disperse long distances (Singer et al. 2000), yet are essential for recolonization and demographic rescue. We placed GPS telemetry collars (900 g) programmed to record one location every 13 h on each animal and captured additional sheep to maintain 6–10 radio-marked sheep in each range.

To describe topography and differentiate mountains from valleys, we used a digital elevation model (DEM) and ArcGIS 9.0 (ESRI 2005) to select contour lines at the base of each mountainous area. To quantify distance and rate of inter- and intramountain movements for each animal, we measured the proportion of lines connecting successive locations of each animal and the rate of valley crossings. We compared frequency of intramountain movements among seasons with chi-squared tests and assessed seasonal variation in length of intramountain movements with generalized linear mixed models.

We assessed gene flow between the Cabeza Prieta and Pinta populations by genotyping six females from each range at 14 microsatellite loci (loci and reaction conditions described in Epps et al. 2005*a*). We used program ARLEQUIN (Schneider et al. 2000) to estimate genetic distance (F_{ST}; Weir & Cockerham 1984) and converted F_{ST} to gene flow (Nm) because $F_{ST} = 1/(1 + 4Nm)$; Nm is the number of migrants per generation and provides an index of gene flow (Neigel 2002). We estimated migration rate M (Nm/marker mutation rate) with program MIGRATE (Beerli & Felsenstein 2001) (see Supporting Information).

We assessed potential effects of a border fence on movements with a least-cost path model of interpopulation gene flow that was developed from genetic analyses of 27 populations of desert bighorn sheep in southeastern California (Epps et al. 2007). That region, beginning 40 km west of our study area, is in the same physiographic province (basin and range) and floristic area (Sonoran) and includes mountain ranges of similar size and topography. The gene-flow model was parameterized by testing against observed genetic structure and provided an estimate of the maximum effective distance (ED) for gene flow among populations; ED among populations is a function of topography and distance (Supporting Information).

We applied this model to bighorn populations in Arizona and Sonora to estimate gene flow among habitat patches known or suspected to support resident populations of females (Lopez et al. 2001); population boundaries were delineated by basal contour lines with slopes ≥10%. We used PATHMATRIX (Ray 2005) to estimate location and ED of each least-cost route among populations within the maximum ED of 16.4 km. We scaled estimated ED among populations by gene flow (Supporting Information). We simulated the effects of an impermeable border fence on interpopulation connectivity by assigning cells along the border a dispersal cost exceeding the maximum value allowed by the model, repeating least-cost path analyses, and comparing predicted movement corridors with and without the fence. Because female desert bighorn sheep disperse shorter distances than males, we assumed this model largely reflects male-mediated gene flow. Therefore, we identified populations that likely were connected by female dispersal with and without the border fence by considering a maximum ED of 10 km, based on observations from California where females moved ≤8.5 km (Supporting Information).

Results

Pygmy-Owls

Flights involved rapid descent from perches followed by direct and level flight near the ground then rapid ascent to perches. On average, owls lost 53% (SE 2) of flight altitude when descending to the lowest point along flight paths ($n = 258$ flights by 15 owls) and descended more during longer flights ($r = 0.39$, $p < 0.001$). Flight height ranged from 0.1 to 12 m above ground. Only 23% of flights were >4 m above ground (Fig. 2), and only one flight was consistently above treetops. Minimum and maximum flight heights averaged 1.4 m (SE 0.1) and 3.2 m (SE 0.2), respectively, and varied among individuals ($F_{14,251} \geq 3.48$, $p \leq 0.001$). Within flight paths, flight height increased as height of the nearest potential perch increased; minimum flight height decreased and maximum flight height increased as distance to the nearest potential perch increased (Table 2). Within home ranges, mean flight height increased as height of trees and volume of understory vegetation increased ($t_{10} \geq 2.26$, $p \leq 0.048$).

Flights were direct and short; 97% ($n = 311$) were <80 m. Flight distance averaged 29 m (SE 2) but varied among individuals ($F_{14,279} = 1.67$, $p = 0.062$). The three longest flights were 120–210 m. Owls that flew longer distances reached higher maximum heights ($r = 0.23$, $p < 0.001$). Within flight paths, flight distance increased with distance to the nearest potential perch (Table 2). Within home ranges, mean flight distance decreased with tree density increased ($t_{10} = 2.74$, $p = 0.021$). Perch height averaged 2.7 m (SE 0.1) and increased with tree height ($t_{15} = 2.68$, $p = 0.017$). Flight and perch behaviors of juveniles were similar to those of adults, yet one dispersing juvenile flew 335 m across an open field.

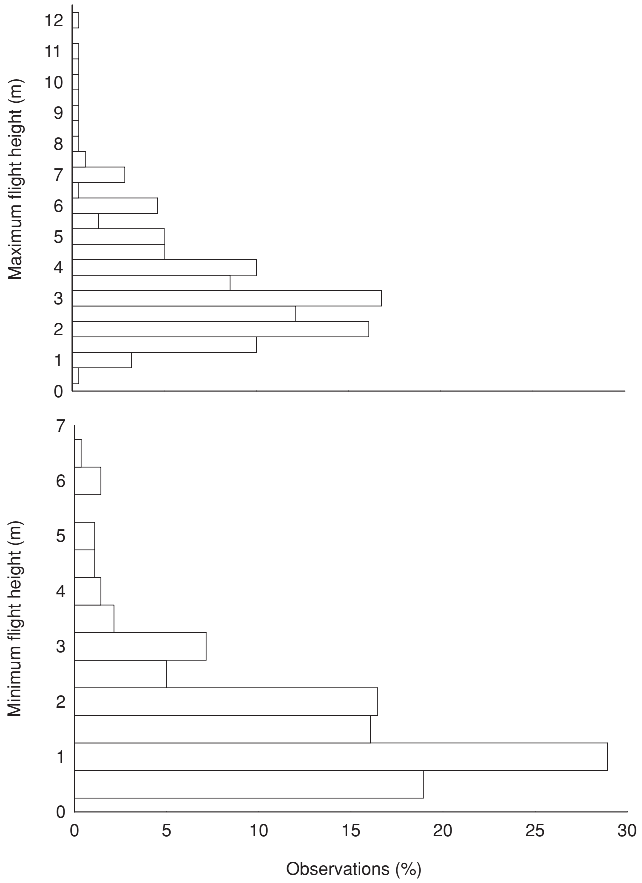

*Figure 2. Distribution of minimum and maximum flight heights (*n *= 280) of 19 radio-marked Pygmy-Owls in northern Sonora, Mexico, 2003-2004.*

All owls that survived the natal period (44% of 54) dispersed and moved an average of 1.2 km/bout (SE 0.1) (*n* = 81 bouts by 20 owls). Owls crossed mountains, roadways, agricultural fields, and fences, yet dispersal speed was 116 times slower (SE 47) in corridors with high levels of disturbance than in those with no disturbance (Table 3; Fig. 3). Highly disturbed corridors were often fragmented by agricultural fields (73%), and those with less disturbance included roadways (50%) or smaller vegetation openings (44%). Dispersal speed was faster through desert scrub (1.3 km [SE 0.2]) and savannah (1.1 [SE 0.2]) than through woodland (0.8 [SE 0.1]).

All owls crossed barbed-wire fences, yet none encountered other types of fences. All owls that encountered roadways eventually crossed them; 39% crossed two-laned paved highways and one (4%) crossed a four-lane divided highway. Number of roads crossed during dispersal increased with total distance moved ($t_{22} = 4.35$, $p < 0.001$), which suggests small to moderate-sized roads were not barriers.

Directional change between successive dispersal bouts varied with the size of vegetation openings and topography (Table 3). Owls that used corridors with large vegetation openings changed dispersal direction 2.0 (SE 0.7) times more than those that used corridors with no openings (Fig. 3). Owls that encountered mountains changed direction 1.7 (SE 0.8) times more than those that traversed valleys, indicating a tendency to move parallel to landscape contour.

Dispersal success averaged 50% within 35 d (SE 1) after the onset of dispersal, during which no mortality occurred. Odds of dispersal success were 92 (SE 7) times greater for owls that traversed landscapes with no disturbance compared with those with moderate disturbance ($\chi^2_{20} = 5.65$, $p = 0.017$), after adjusting for somewhat higher success for males (62% of 13) versus females (36% of 11; $\chi^2_{20} = 2.60$, $p = 0.11$). Success averaged 13% ($n = 8$), 64% ($n = 11$), and 80% ($n = 5$) in landscapes with moderate, low, and no disturbance, respectively. Success did not vary with dispersal distance or total distance moved ($\chi^2_{19} \leq 0.20$, $p \geq 0.65$).

Desert Bighorn Sheep

We observed no intermountain movements during 20,482 locations of 37 females, yet 14 of 18 sheep made 351 crossings of valleys within the Cabeza Prieta Mountains (0.4 [SE 0.1] crossings/week/individual). Frequency of intramountain movements varied seasonally ($\chi^2_3 = 44.09$, $p > 0.001$) and were more common in late summer (33% of observations) and fall (32%) than in winter (11%). Length of intramountain movements averaged 1.6 ± 0.1 km (max. = 4.9 km), and only 7% were >3 km. Length of movement did not vary seasonally

Table 2. Factors that explained variation in flight behavior in 267 flight events by 17 radio-marked male Ferruginous Pygmy-Owls in northern Sonora, Mexico 2003–2004.*

	Flight distance (m)				*Minimum flight height (m)*				*Maximum flight height (m)*			
Factor	*est.*	*SE*	t	p	*est.*	*SE*	t	p	*est.*	*SE*	t	p
Initial perch height (m)	0.088	0.026	3.41	<0.001	0.35	0.038	9.12	<0.001	0.73	0.050	14.64	<0.001
Height of closest available perch (m)	−0.041	0.026	1.57	0.12	0.090	0.038	2.34	0.020	0.13	0.050	2.60	0.010
Distance to closest available perch (m)	0.024	0.004	6.02	<0.001	−0.016	0.006	2.83	0.005	0.018	0.008	2.38	0.018

**Response variables in the top row: flight distance, minimum flight height, and maximum flight height.*

Table 3. Factors that explained variation in attributes of movement behavior during 81 movement bouts by 20 radio-marked Pygmy-Owls during natal dispersal in northern Sonora, Mexico 2003–2005.

Response and factor	*Estimate*	*SE*	t	p
Dispersal speed (km/bout)				
intensity of disturbance[a]				0.014
none (0%)	1.22	0.50	2.47	0.024
low (1–10%)	1.39	0.48	2.90	0.0095
moderate (10–50%)	0.95	0.05	1.98	0.063
vegetation community[b]				0.050
desert scrub	0.46	0.23	1.99	0.066
savannah	0.26	0.25	1.02	0.33
woodland	−0.03	0.20	0.14	0.89
riparian scrub	−0.22	0.36	0.62	0.55
Directional change (degree)				
size of the largest vegetation opening[c]				0.047
none (0 m)	−81.0	28.6	2.83	0.018
low (1–100 m)	−53.4	25.8	2.08	0.065
moderate (100–200 m)	−74.0	23.7	3.12	0.011
topography (Valley)[d]	−53.9	25.3	2.13	0.10

[a] *Reference level equals high intensity of disturbance (>50%).*
[b] *Reference level equals thorn-scrub vegetation.*
[c] *Reference level equals large vegetation opening (>200 m).*
[d] *Reference level equals mountainous topography.*

($F_{3,315} = 0.36; p = 0.79$). Dirt roads were the only human-made feature crossed during intramountain movements. One female crossed the U.S.–Mexico border nine times in an unfenced mountainous area.

Genetic distance (F_{ST}) was 0.046 (95% CI 0.010–0.115) between the Pinta and Cabeza Prieta mountains. Gene flow (Nm) was 5.18 (95% CI 1.90–24.8) and migration rate was (M) 12.9 (95% CI 10.4–15.4).

We estimated that nine populations in Sonora are linked by gene flow and male dispersal with populations in Arizona and only two populations are completely isolated at this time (Fig. 4a). All predicted transboundary dispersal corridors would be disrupted by an impermeable fence, including several with high levels of predicted movement and gene flow.

The slope dispersal model for females predicted that without the border fence, all but four of the southernmost populations are linked by dispersal (Fig. 4b). A simulated border fence, however, disrupted at least 10 predicted transboundary dispersal corridors for females. Furthermore, the border fence would isolate the two westernmost populations in the U.S. portion of the study area because dispersal was predicted only through habitat in Mexico (Fig. 4b).

Discussion

Movement behavior and patterns of interpopulation connectivity we observed in the U.S.–Mexico borderlands suggest border fencing and associated vegetation clearing could degrade landscape connectivity for some species of wildlife. Although our findings rely on observations of movement behavior obtained before the border fence was constructed and require experimental approaches to corroborate, they highlight priorities for monitoring and mitigation as border development continues. Fences similar to those now being constructed along the U.S.–Mexico border have restricted wildlife movements and negatively affected populations in other regions (Whyte & Joubert 1988; Scott 1992; Baines & Summers 1997). Security infrastructure will have the greatest influence on wildlife when effects on individuals are manifested at population-level scales, yet these effects depend largely on species-specific movement abilities, the spatial and temporal arrangement of resources, and the type, location, and intensity of development. Although we focused on physical barriers, associated lighting, vehicle traffic, and human activity may further degrade connectivity (Forman & Alexander 1998; Rich & Longcore 2006) and warrant detailed consideration.

Pygmy-Owl

Flight behaviors of Pygmy-Owls suggest that large vegetation gaps coupled with tall fences could limit transboundary movements. Flights by Pygmy-Owls involved steep descents from low perches followed by direct-level flight near the ground. Flights leveled off only 1.4 m above the ground on average, and only 23% exceeded the approximate height of transboundary fences (4 m). These and other data suggest that nonmigratory birds such as Pygmy-Owls have more limited perceptual abilities than species that move at higher elevations (Dale et al. 2006). Other species of woodland owls also have U-shaped flight

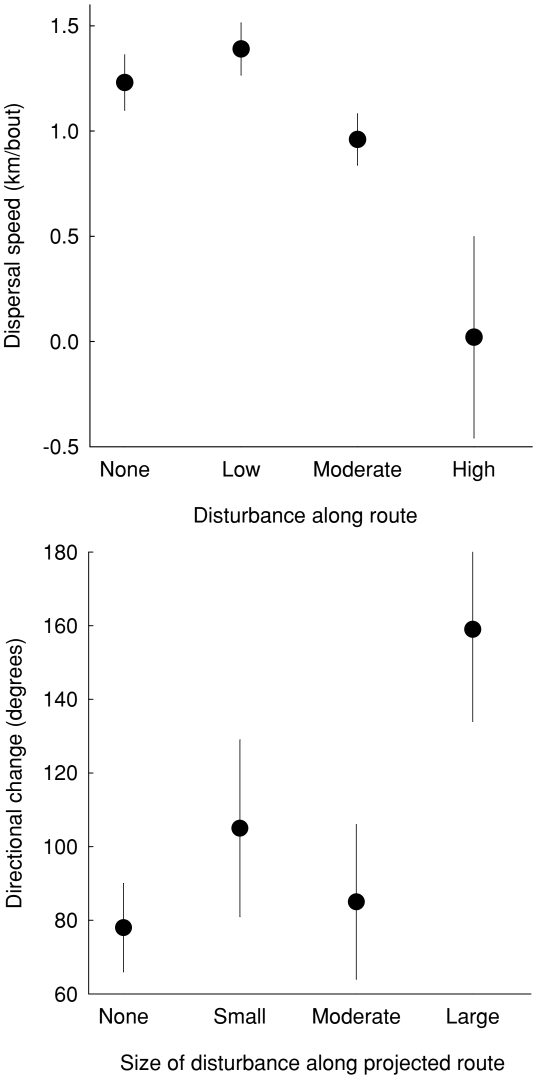

Figure 3. Dispersal speed and directional change between successive movement bouts of juvenile Ferruginous Pygmy-Owls during natal dispersal in northern Sonora, Mexico, 2003–2005. Disturbance along route indicates the proportion of natural vegetation that was cleared (low, <10%; moderate, 10–50%; high, >50%), and size of disturbance indicates width (small, <100 m; moderate, 100–200 m; high, >200 m) of the largest vegetation opening within 500 m of the endpoint of each dispersal bout in the same direction of the bout.

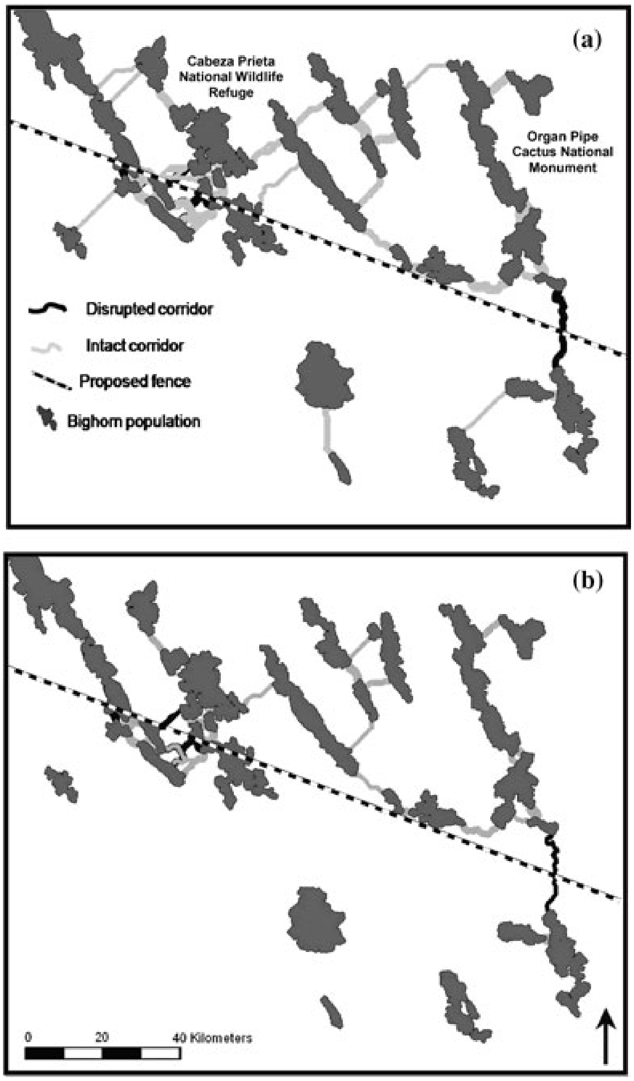

Figure 4. Predicted least-cost paths for movement and gene flow among desert bighorn sheep populations for (a) males and (b) females on the basis of distance and topography among populations in the study area from a connectivity model fitted to gene-flow estimates among populations in neighboring southern California. Corridors disrupted by construction of an impermeable border fence are indicated by black lines and corridors not disrupted are indicated by gray lines. Widths of lines are scaled by the quantity of gene flow predicted.

patterns (Gehlbach 1994) that may reduce potential for crossing fences. Because flights >4 m were observed, the border fence would not eliminate transboundary gene flow.

Because landscape structure influenced the speed, direction, and success of natal dispersal, large vegetation gaps associated with the border fence could further reduce transboundary movements. Dispersal success was lower in more-disturbed landscapes, probably because habitat availability was lower and locating mates was more difficult. Compared with the effects of landscape structure, distance moved during dispersal had no apparent effect on dispersal success, which suggests matrix structure and not proximity largely determines the effective isolation of resource patches (Ricketts 2001). Dispersing Pygmy-Owls that encountered vegetation gaps >200 m moved at much slower speeds, often made only one to two flights per movement bout, and tended to drastically change direction. Thus, vegetation gaps can slow movements or pose barriers to pygmy owls and other nonmigratory birds (Harris & Reed 2002; Castellón & Sieving 2005). Reduced dispersal from Sonora could have strong demographic effects on populations in Arizona, which should be monitored closely.

Because flight behavior was explained by local vegetation features, appropriate management could enhance landscape connectivity. Flights were longer when initiated from higher perches, flight height increased as tree height and understory vegetation volume increased, and maximum flight height increased as distance to potential perches increased. Therefore, tall stands of trees and dense understory vegetation near fences should augment transboundary connectivity. Because Pygmy-Owls have declined to endangered levels in Arizona yet are more common in adjacent Sonora, maintaining transboundary connectivity should aid recovery of owl populations in Arizona.

Desert Bighorn Sheep

Although we did not observe intermountain movements by females, such movements have been documented in this (Witham & Smith 1979) and other regions (Bleich et al. 1990). In our region females frequently crossed valleys within mountainous areas that were ≤ 2 km wide, whereas movements >4 km were rare. Documented intermountain movements in the southwestern United States suggest that bighorn sheep tend to take the shortest route across valleys and often use intervening hills as "stepping stones" (Jaeger 1994). Continued monitoring could better characterize long-distance movements yet may be difficult now that construction of the border fence is underway.

Despite no direct observation of intermountain movements, genetic analyses suggested fairly high levels of gene flow and a history of recent dispersal between the Cabeza Prieta and Pinta mountains ($F_{ST} < 0.05$; Nm = 5.2; $M = 12.9$). Estimates of Nm (<1 migrant/year) indicate the difficulty of observing intermountain movements over short time scales. The slope dispersal model of gene flow predicted Nm = 3.6 between those populations, which suggests that intermountain movement in the study area was similar where the model was developed. Populations in California among which dispersal was verified by radiotelemetry had similarly weak genetic structure ($F_{ST} < 0.05$; Epps et al. 2005*b*) and equivalent gene flow (Nm >1.2, $M > 11.8$) at the same loci (Epps et al. 2007).

Construction of an impermeable border fence would disrupt an extensive population network of desert bighorn sheep. In addition to preventing transboundary movements, that barrier would eliminate or weaken linkages among some populations on the same side of the border (Fig. 4b). Small population sizes and high environmental stochasticity in populations of desert bighorn sheep cause frequent population extinctions (Bleich et al. 1990). Fenced barriers such as interstate highways have disrupted dispersal and caused rapid genetic divergence and loss of diversity (Epps et al. 2005*a*). A continuous border fence would also reduce probability of recolonization after local extinction, compounding effects of changing resource availabilities due to climate change. Detailed demographic data and metapopulation models could shed further light on the probability of local extinctions. Finally, if pursued immediately, genetic sampling of bighorn populations or other species on both sides of the border could test for evidence of previous connectivity even after construction of the fence is completed.

Implications for Other Species

Results of our case studies suggest other species may be significantly affected by security infrastructure in the Arizona–Sonora borderlands if they are terrestrial and large enough to be physically excluded by security infrastructure (cannot pass through a 5- to 10-cm gap), deterred by vegetation openings, or fly at heights <4 m during dispersal. Furthermore, although bighorn sheep and many other species in discontinuous habitat patches can disperse across nonbreeding habitat, those species are most likely to experience loss of connectivity at larger scales when linkages incorporating transboundary movements are disrupted (e.g., Fig 4b). For instance, desert tortoise (*Gopherus agassizii*) also occupy disjunct rocky habitat separated by valleys and make interpopulation movements approximately once per generation (Edwards et al. 2004); those characteristics could increase vulnerability to disruption by border fencing. Among nonmigratory birds, ground dwellers such as Wild Turkey (*Meliagris gallopavo*) and quail (Phasianidae) may not readily cross fences unless gap widths facilitate movement (Fig. 1). Nevertheless, bats such as endangered lesser-long nosed bat (*Leptonycteris curasoae*) and migratory birds likely will fly over fences.

Among wide-ranging mammals, persistence and recovery of other species present in low numbers such as jaguar and Sonoran pronghorn may depend on transboundary movements (Krausman et al. 2005; McCain & Childs 2008). Persistence of black bears (*Ursus americanus*) in northern Sonora and Texas may depend, respectively, on movements from Arizona (Varas 2007) and northern Coahuila (Onorato et al. 2004). Population-level consequences for species that are more widespread and abundant such as pumas (*Puma concolor*) and mule deer (*Odocoileus hemionus*) are likely to be less severe. Detailed information on distribution, movement behavior, and the effects of interpopulation connectivity on local persistence are required to fully assess the potential effects of transboundary development on wildlife and to develop effective mitigation strategies.

Mitigation and Management

In transboundary landscapes internationally implemented, information-based strategies can augment connectivity and meet security needs. For bighorn sheep and other wide-ranging mammals that use mountainous terrain, crossing structures or fence gaps focused in the mountains may foster transboundary movement, yet placement of these structures requires careful evaluation of regional connectivity such as that initiated here. For Ferruginous Pygmy-Owls and other species of nonmigratory birds, tall trees, limited vegetation disturbance, and fences that are permeable by small animals should enhance connectivity.

In regions with continuous impermeable fencing, wildlife crossing structures should be considered. Although crossing structures can foster wildlife movement across roadways (Clevenger & Waltho 2005), security concerns along international boundaries and the effects of human traffic on wildlife may limit their efficacy. Nevertheless, if such structures are coupled with remote-surveillance technologies such as cameras, radar, and electromagnetic and motion sensors, they can enhance connectivity and provide data on wildlife movement without compromising security. Where pedestrian fencing is not needed, vehicle barriers may be more permeable by wildlife, yet designs for these structures should be considered carefully. As a last resort, targeted translocations of the most sensitive species could be implemented. Careful evaluation of strategies to meet conservation and security objectives in transboundary landscapes is needed for optimal solutions, including consideration of the economic and social factors that drive human migration.

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Supporting Information

Detailed descriptions of genetic analyses are available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Supplementary Material

Parameters used in MIGRATE to estimate gene flow between the Cabeza Prieta and Sierra Pinta desert bighorn sheep populations

We used the Brownian motion approximation of 10 short and 3 long chains of 500 and 5,000 genealogies respectively, a burn-in of 10,000 genealogies for each chain, and averaged results among three simulations.

The slope dispersal model of gene flow

The slope dispersal model used least-cost paths based on a model where all terrain with ≥15% slope was weighted as having 1/10th the dispersal cost of terrain <15% slope; those values best explained observed variation in gene flow. The estimated least-cost paths are reported in units of "effective distance" (ED), which is: (linear distance over terrain <15% slope) + (linear distance over terrain ≥15% slope*0.1). Gene flow (*Nm*) was detectable between populations separated by ED <16.4 km and declined to that point in negative exponential fashion (Epps et al. 2007):

$$Nm = 9.141 * e^{-0.112*ED} - 0.219 \qquad \text{(Eqn. 1)}$$

Adapting the slope dispersal model to model female movement

We assumed observed declines in gene flow with increasing ED indicated lower probability of inter-population dispersal, particularly for wider-ranging males, and that dispersal by females would decrease with increasing ED at the rate predicted by Equation 1 yet at a lower initial level due to tendency to disperse shorter distances. Subtracting 1.53 from the right side of Equation 1 resulted in a dispersal model for females with identical shape and a maximum dispersal distance of 10 km. Although observed female movements in California were <8.5 km (Epps et al. 2005b), we chose a larger maximum ED of 10 km to reduce the likelihood of overestimating the effect of the border fence on female movements.