Restoration of bobcats to Cumberland Island, Georgia, USA:
Lessons learned and evidence for the role of bobcats as keystone predators
Reintroducción del lince rojo en la isla de Cumberland, Georgia, EEUU:
Lecciones aprendidas y evidencia del papel del lince rojo como predador clave
Duane R. Diefenbach, Leslie A. Hansen, Robert J. Warren, Michael J. Conroy and M. Greg Nelms

The tree which moves some to tears
of joy is in the eyes of others only a green thing that stands
in the way. Some see nature all ridicule and deformity...
and some scarce see nature at all.
But to the eyes of the man of imagination, nature is
imagination itself.

William Blake
(1757-1827)

Restoration of bobcats to Cumberland Island, Georgia, USA: lessons learned and evidence for the role of bobcats as keystone predators

Reintroducción del lince rojo en la isla de Cumberland, Georgia, EEUU: lecciones aprendidas y evidencia del papel del lince rojo como predador clave

Duane R. Diefenbach, Leslie A. Hansen, Robert J. Warren, Michael J. Conroy and M. Greg Nelms

Resumen

Entre 1988 y 1989, durante un proyecto de reintroducción, reubicamos a 32 linces rojos (*Lynx rufus*; 3,1 linces rojos/10 km²) en una isla costera de Estados Unidos, la isla de Cumberland, en Georgia, con el fin de estudiar la reintroducción de un predador nativo. La supervivencia anual de los adultos fue del 93% (Error standard=2.6%) durante los tres primeros años. Los linces rojos recapturados tuvieron un aumento medio de peso de 0,8 kg (un incremento del 12% desde el momento de la suelta). Se documentó la reproducción de los ejemplares reintroducidos. Las presas principales fueron los conejos *(Sylvilagus palustris)*, los ciervos de cola blanca *(Odocoileus virginianus)* y las ratas de algodón *(Sigmodon hispidus)*. Entre 1997 y 1998 hubo un cambio en el tipo de presa y la presencia de ciervos y conejos en heces fue menos frecuente que la de las demás especies. Ningún lince rojo llegó a mantener un área de uso exclusivo, sin solapamiento con otros congéneres. Las estimaciones e índices de abundancia de ciervos indicaron que tras la reintroducción de los linces rojos hubo una disminución de la población de ciervos, que se mantuvo en niveles bajos, aunque el peso corporal medio de los ciervos aumentó una media de 11 kg entre 1989 y 1997. En nueve parcelas, que contenían un total de 87 robles, la regeneración de cada árbol fue medida entre 1990 y 1997; el número de árboles con plantones o brotes de raíces se incrementó de 52 a 86 y el número medio de plantones por parcela aumentó en 153,5. En aquellas parcelas que contenían plantones y brotes, tanto en 1990 como en 1997, la altura media se incrementó en 4,6 cm (95% IC=4.0–5.2). Nuestras observaciones sobre el consumo de ciervos como presa primaria de los linces rojos, la disminución de la abundancia de ciervos y la mayor regeneración del roble indicaban que los linces rojos reintroducidos causaron un efecto de cascada trófica de la isla. Los estudios previos a la reintroducción de los linces rojos indicaron que los ciervos eran abundantes y que su ramoneo impedía la regeneración de los árboles. Según los mismos estudios, los ciervos eran presas idóneas para los

423

linces rojos por su abundancia y su tamaño reducido. El seguimiento posterior a la suelta de una especie reintroducida proporciona información que nos permite comprender las razones por las cuales un proyecto de reintroducción pueda tener éxito o fracase. Asimismo, en los proyectos de reintroducción de poblaciones de predadores debe plantearse el posible seguimiento de las características relacionadas con los niveles tróficos del ecosistema, teniendo siempre en cuenta el escaso conocimiento que tenemos sobre el papel de los predadores en los ecosistemas, sobretodo el papel de los predadores vertebrados. Si se creasen programas de seguimiento para probar las teorías de la dinámica de las poblaciones comunitarias, habría mayores posibilidades de entender mejor las redes tróficas de los ecosistemas terrestres, así como sus interrelaciones.

PALABRAS CLAVE

Predador clave, lince rojo, *Lynx rufus*, reintroducción, organización espacial, cascada trófica

ABSTRACT

We translocated 32 bobcats (*Lynx rufus*; 3.1 bobcats/10 km^2) to a coastal barrier island, Cumberland Island, Georgia, USA, during 1988-1989 to restore a native predator. Annual survival of adults was 93% (SE=2.6%) for the first three years and recaptured bobcats exhibited an average weight gain of 0.8 kg (12% increase), and we documented reproduction. Marsh rabbits *(Sylvilagus palustris)*, white-tailed deer *(Odocoileus virginianus)* and hispid cotton rats *(Sigmodon hispidus)* were the principal prey species. By 1997-1998, prey use changed, in which white-tailed deer and marsh rabbits occurred less frequently in scats and all other species occurred more frequently. No bobcats retained areas of exclusive use from conspecifics of the same sex. Estimates and indices of deer abundance indicated that following reintroduction of bobcats the deer population declined and remained low but body weights of deer averaged 11.0 kg greater in 1997 compared to 1989. On nine plots containing 87 oak trees, where oak regeneration at each tree was measured in 1990, the number of trees with seedlings or root sprouts increased from 52 to 86 and the average number of seedlings per plot increased by 153.5. On plots that contained seedlings and sprouts in both 1990 and 1997, average height increased 4.6 cm (95% CI=4.0–5.2). Our observations of bobcat use of deer as a primary prey species, a decline in deer abundance, and an increase in oak regeneration indicated that bobcats caused a trophic cascade effect on the island. Research prior to the restoration of bobcats indicated deer were abundant and deer browsing suppressed tree regeneration, and apparently deer were suitable prey for bobcats because of their abundance and small size. Post-release monitoring of a reintroduced species provides information to understand why a reintroduction project succeeds or fails. Moreover, restoration projects of predator populations should consider monitoring trophic level characteristics of ecosystems because the role of predators in ecosystems in poorly understood, especially vertebrate predators. If monitoring programmes were developed to test theories of community population dynamics, there would be potential to better understand food webs of terrestrial ecosystems and trophic level inter-relationships.

KEYWORDS

Food habits, keystone predator, *Lynx rufus,* reintroduction, spatial organization, trophic cascade

Restoration of bobcats to Cumberland Island, Georgia, USA: lessons learned and evidence for the role of bobcats as keystone predators

DUANE R. DIEFENBACH, LESLIE A. HANSEN, ROBERT J. WARREN, MICHAEL J. CONROY AND M. GREG NELMS

INTRODUCTION

The United States national park system is a network of nearly 400 natural, cultural and recreational sites across the nation designated to preserve and protect unique natural and cultural features. National parks designated for their natural resources have been mandated by the United States Congress to maintain the abundance, diversity, and ecological integrity of native plants and animals (16 United States Code 1, 2-4). The enabling legislation for Cumberland Island National Seashore (CINS) included directives to the National Park Service (NPS) on how the island should be managed, which included providing for public outdoor recreational use (including hunting, fishing and trapping), preserving related scenic, scientific and historic values, and conserving its primitive state together with its flora and fauna. Consequently, the Resources Management Plan for CINS (National Park Service, 1983) specifically identified extirpated species and the possibility of their reintroduction. Among extirpated predators, Harris (1984) identified the bobcat *(Lynx rufus)* as a species to receive highest priority for reintroduction because it would be least likely to cause human-related conflicts.

In 1988, the National Park Service funded the reintroduction of bobcats to Cumberland Island. However, because this project involved federal funding and public land, an Environmental Assessment (EA) was required under the National Environmental Policy Act (Public Law 91-190) to consider the environmental effects of reintroduced bobcats. We prepared the EA for the NPS (Warren et al., 1990) and justified the project from the standpoint of restoring ecological control over several species of native and exotic herbivores. We cited evidence of grazing and browsing effects from white-tailed deer *(Odocoileus virginianus)*, feral horses *(Equus caballus)*, and feral hogs *(Sus scrofa)* (Hillestad et al., 1975; Ambrose et al., 1983; Turner, 1986) and noted that bobcats can kill healthy, adult deer (McCord and Cardoza, 1982; Anderson, 1987). Furthermore, studies in the southeastern United States indicated that bobcats were effective predators on white-tailed deer fawns (Epstein et al., 1985). Other potential prey species on the island included hispid cotton rats *(Sigmodon hispidus)*, cotton deermice *(Peromyscus gossypinus)*, eastern gray squirrels *(Sciurus carolinensis)*, marsh rabbits *(Sylvilagus palustris)*, nine-banded armadillos *(Dasypus novemcinctus)*, and wild turkey *(Meleagris gallapavo)*. Of these species,

425

wild turkeys were not expected to be an important component of bobcat diets.

During fall of 1988 and 1989 we released a total of 32 bobcats throughout Cumberland Island. All bobcats were captured from the coastal plain of Georgia and fitted with a radio-collar to monitor post-release movements, survival, and reproduction. This translocation of bobcats to Cumberland Island afforded the opportunity to conduct a reintroduction experiment for a mid-sized felid, in which failure would have no adverse effect on the global status of the species. Furthermore, post-release monitoring provided an opportunity to study the genetics and population viability of an insular predator population, test a population monitoring technique with a known population size, monitor the social organization and spatial distribution of bobcats, study predator-prey dynamics, and monitor changes in community structure and trophic-level interactions.

In this paper we 1) identify key lessons we learned that could be useful for future felid reintroductions, 2) demonstrate the importance of post-reintroduction monitoring to learn more about the role of predators in ecosystem functioning and 3) summarize insights we have gained about bobcat prey selection and social organization in a solitary felid. Also, we present previously unpublished data we collected that provide evidence for bobcats initiating a top-down trophic cascade on the Cumberland Island forested ecosystem.

FIGURE 1. LOCATION OF CUMBERLAND ISLAND ALONG THE GEORGIA-FLORIDA, USA COASTLINE (INSET) AND REGIONS OF THE ISLAND DELINEATED FOR FOOD HABITS ANALYSES.

FIGURA 1. SITUACIÓN GEOGRÁFICA DE LA ISLA DE CUMBERLAND EN LA COSTA ESTADOUNIDENSE DE GEORGIA-FLORIDA (RECUADRO) Y DELIMITACIÓN DE LAS REGIONES DE LA ISLA PARA EL ANÁLISIS DE COSTUMBRES ALIMENTARIAS.
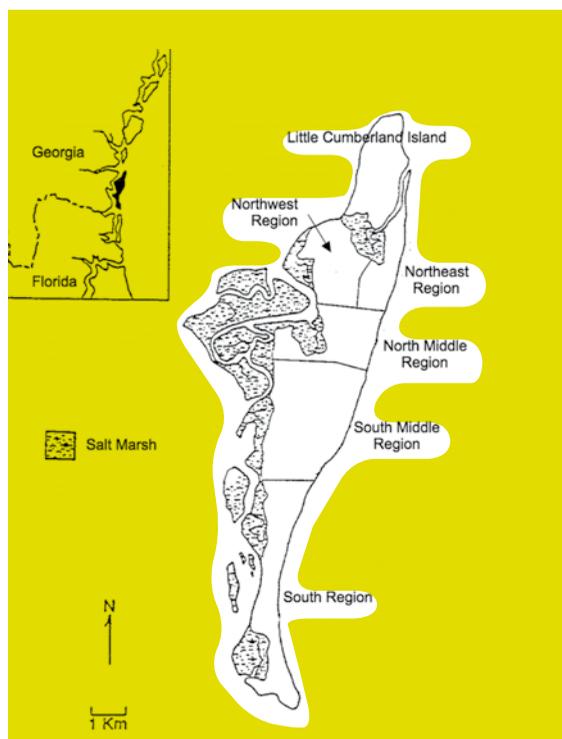
MATERIALS AND METHODS
STUDY AREA

Cumberland Island, a coastal barrier island 0.5 km north of the Georgia-Florida border (30°48'16"N, 81°27'36"W), is the largest among a series of barrier islands that extend along the Atlantic Ocean seaboard from Cape Hatteras, North Carolina south to Talbot Island, Florida (Figure 1). The island is 25 km long and varies in width from 1 to 6 km. It is separated from the mainland by 2–4 km of salt marsh and open water. To the north is Little Cumberland Island, which is separated from Cumberland Island by <0.25 km of salt marsh and a tidal creek.

Immediately behind the eastern shore and primary dunes of the island is an interdune meadow, ≤200 m in width, dominated by grasses, sedges, and waxmyrtle *(Myrica cerifera)*. The interior of the island is dominated by live oak *(Quercus virginianus)* and pine *(Pinus)* forests with much of the understory dominated by stands of sawtooth palmetto *(Serenoa repens)*. Freshwater wetlands follow natural depressions between former dune ridges in the interior of the islands. The western edges of the islands are salt marsh.

Cumberland Island contains five major vegetation associations covering 84.5 km²: sandy beach and interdune meadow (14.7 km²); maritime forest, including lowland hardwoods (38.7 km²); scrub-shrub thickets that developed after natural fires (7.0 km²); freshwater wetlands (6.7 km²); and salt marsh (17.4 km²). Little Cumberland Island is 9.0 km² and contains sandy beach and interdune meadow (1.3 km²), maritime forest (4.8 km²), and salt marsh (4.8 km²). Hereafter, we refer to the two islands together as Cumberland Island.

The climate is warm temperate to subtropical, with normal mean temperature ranging from 12 °C in January to 28 °C in July (Johnson et al., 1974). The average annual rainfall is 134 cm, with the wettest months being June

through September ($\bar{x}$=16 cm/month) and the driest months being October, November, and April ($\bar{x}$=7 cm/month). Hillestad et al. (1975) described the study area in detail.

CAPTURE AND TRANSLOCATION

Details of the capture, handling, and translocation of bobcats are described in Diefenbach et al. (1993). We captured bobcats using hunting dogs *(Canis familiaris)*, foot-hold traps, and cage traps from the coastal plain of Georgia in the hope that these bobcats would have gene complexes adapted to the environment on Cumberland Island (Templeton, 1986). Captured bobcats were held in a facility for ≤1 month to monitor behavior and detect illness or injury. Only adult bobcats (≥1 year old) were reintroduced to Cumberland Island and all reintroduced bobcats were vaccinated for feline panleukopenia, rhinotracheitis, and calicivirus. Also, we held bobcats in captivity until we had 4-6 individuals to release so we could evaluate the scent-station population monitoring technique with a controlled increase in population size (Diefenbach et al., 1994).

Our goal was to release approximately 30 bobcats because this would result in a density similar to maximum densities on the mainland (1 bobcat/2.6 km²). All releases of bobcats were "hard releases" in which bobcats were transported to the release site and freed. Release sites occurred throughout the island that were easily accessible by vehicle and likely were outside the home range of previously reintroduced bobcats.

POST-RELEASE MONITORING

We began trapping on Cumberland Island to recapture bobcats a few months after the first bobcats were released on the island (Diefenbach et al., 1993). This recapture effort provided information on the physiological status of bobcats, allowed us to replace radio-collars before batteries failed, and capture bobcats born on the island to assess recruitment and survival of juveniles. We used only cage traps because they were less controversial than foot-hold traps even though they were inefficient and less effective. Captured juveniles were not vaccinated and were fitted with a radio-transmitter attached to a harness (Jackson et al., 1985) rather than a collar.

We monitored survival and locations of bobcats via triangulation of radio signals from the ground or by locating bobcats with fixed-wing aircraft throughout the year and the 24-hour day (Diefenbach et al., 2006). These data were used to assess habitat use (Baker et al., 2001; James, 1992) and spatial organization (Diefenbach et al., 2006). We monitored reproduction by conducting intensive telemetry monitoring of females during the denning season (see Ragsdale [1993] for details) to located dens and document reproduction.

To monitor food habits and prey selection we collected bobcat scats and measured prey abundance (Baker, 1991; Baker et al., 1993; Nelms, 1999; Baker et al., 2001). From November 1988 through July 1990 we surveyed prey abundance during a three-week period in November, March and July. We defined four habitats for purposes of analysis: woodlands with understories of saw palmetto (oak-palmetto), woodlands with understories not dominated by saw palmetto (open woodland), interdune meadow and an area that burned in 1981 (scrub thicket). These habitat types composed 26%, 37%, 9% and 10% of the island area, respectively, with the remainder of the island being bottomland hardwoods/shrubs, beach and residential areas.

Whenever possible, we used distance sampling methods (trapping webs or line transect surveys, Buckland et al., 2001) to estimate prey density (Baker et al., 2001). We used spotlight transects to estimate island-wide abundance of white-tailed deer and raccoons *(Procyon lotor)*. We walked eight permanent transects during early morning and late afternoon to assess habitat-specific abundance for white-tailed deer, eastern gray squirrels, nine-banded armadillos, marsh rabbits, feral swine, and raccoons. In November 1988 and March 1989 we walked each transect twice and alternated the starting point on consecutive days; four times thereafter. Each transect traversed multiple habitat types and pooled transect lengths in each habitat type were 11.5 km in oak-palmetto, 20.9 km in open woodland and 6.8 km in interdune meadow; vegetation in the scrub-thicket was too dense to observe animals. If we obtained too few observations or could not meet the assumptions of distance sampling we calculated indices of abundance (captures per 100 trap nights or numbers seen per km).

We collected bobcat scats by walking roads, trails, and dune/forest edges during a six week period encompassing each of the prey abundance surveys. Methods for identification of prey remains were described by Baker et al. (1993). Also, frequency of occurrence was estimated (no. of occurrences of a species/total

no. of scats) and diet diversity was calculated using (1 – Simpson's Diversity Index), in which greater values indicated greater diet diversity (Hall et al., 1984). We used prey abundance and bobcat diet data to examine differences in diet (prey use among species and spatial differences across the island) and changes in diet over time. Also, we tested predictions of functional relationships of bobcat diets, and if diets differed between males and females. Details of the analytical methods used are described in Baker et al. (2001).

The scat collection and analysis procedures used by Baker (1991) and Baker et al. (2001) were replicated during November-December 1997, March 1998, and August 1998 (Nelms, 1999). Seasonal diets during 1997-98 were compared with the corresponding 1988-90 data (Baker et al., 2001) using chi-square tests of homogeneity (Conover, 1980).

Trophic level changes

We used weight, sex and age data collected from deer harvested during public hunts on CINS from 1980 to 1997, in which most deer were harvested on the northern end of CINS. Because the final bobcat releases were in fall 1989, we designated the years 1980-89 as the prerelease (PRE) period and 1990-98 the postrelease (POST) period.

We aged deer via the tooth wear and replacement method (Severinghaus, 1949) except all deer estimated to be ≥4.5 years were classified as 4.5+ because of small sample sizes and greater error associated with aging older deer. Age distributions for harvested male and female deer were compared using chi-square tests for homogeneity. We conducted a nested ANOVA (PROC GLM, SAS Institute, 2003) to test for changes in mean eviscerated weight between 1984-89 and 1990-97, in which age-sex class and bobcat release period (PRE or POST) were main effects and year was nested within time period. To test the effect of bobcat release period, the mean square error for the nested year effect was the divisor for the F test. Also, we estimated the change in mean eviscerated weights for each age-sex class in the PRE versus POST periods via t-tests with means of individual years as the sample unit.

We conducted deer spotlight surveys using protocols established for CINS by Ford (1987) and modified by Baker (1991) to obtain estimates of deer density using distance sampling (Buckland et al., 2001). Deer density estimates were converted to abundance estimates assuming 6,110 ha of upland habitat. However, because deer population estimates based on distance sampling were available only for four years during 1980-98, other methods were used to obtain estimates to demonstrate population trends. We estimated annual deer abundance using hunt data with the DeLury technique (Roseberry and Woolf, 1991; Appendix I) using the number of hunters and deer kill from all hunts in each year.

Lieske et al. (1990) established plots in spring 1990 immediately following the final bobcat releases. They chose 10 sites throughout the island and at each site located 10 oak (*Q. virginiana* and *Q. hemispherica*) trees, five with associated root sprouts or seedlings and five without. A 2x4 m plot was established on opposite sides of each tree. The center line of each plot was treated as a transect, and they measured heights of the closest 10 oak sprouts and seedlings along each transect line at 0, 1 2, 3, and 4 m from the base of each tree. Seedlings and sprouts were counted in subplots but the total 16 m^2 was treated as a single sample unit. We repeated these measurements in spring 1997 at 9 of the 10 plots and conducted an ANOVA to test whether the number of seedlings and sprouts differed between 1990 and 1997 with year, plot, and tree nested within plot as explanatory variables in the model (PROC GLM, SAS Institute, 2003). We used McNemar's test to test whether the number of plots with seedlings and sprouts changed between 1990 and 1997. We used the difference in mean sprout height at each plot to calculate the change in mean sprout heights between 1990 and 1997 at each plot.

Results

The initial justification of the reintroduction for the EA, to control herbivores, was a mistake (Warren et al., 1990) because it elicited a variety of negative comments from the public. Some environmental organizations and individuals questioned whether herbivores should be controlled in national parks, whereas hunters voiced concern about bobcats preying on wild turkeys, a game species, and recommended that deer population control could be accomplished more cost-effectively using hunters. Consequently, in subsequent news releases and public meetings we emphasized the purpose of the project was to reintroduce a formerly native species to

restore biological diversity. This approach to justifying the reintroduction was successful in reducing much of the controversy, and subsequent newspaper articles de-emphasized the controversial aspects and emphasized the broader ecological significance of the project (Warren et al., 1990).

Following the public comment period, the NPS issued a Finding of No Significant Impact, which meant the project had no significant human impact and the project could move forward without further review. In hindsight, we underestimated public support for a reintroduction for its own sake, that of restoring a native predator. Had we conducted public scoping or human dimensions surveys prior to preparing the EA, we might have identified the diversity of public opinions that surrounded the proposed bobcat restoration project. Furthermore, a proactive role with the media could have minimized misconceptions about the project and resulting controversy, and personal contacts with influential people in the local community could have allowed us to identify opposition to the project prior to formally releasing the EA.

CAPTURE AND TRANSLOCATION

In fall 1988, we released 14 bobcats on the island (3 males, 11 females); four on 13 October, six on 3 November, and four on 28 November. Details of the capture, handling, and transporting of bobcats was described in detail by Diefenbach et al. (1993), and most aspects of this part of the project were successful. One bobcat died in captivity when it slipped its jaw through the radio-collar and suffocated; subsequently, bobcats were not fitted with a radio-collar until immediately prior to release. This resulted in additional handling of bobcats, but allowed us to assess bobcat condition immediately prior to release. Of those bobcats released in 1988, one female returned to the mainland in February 1989 and another died in January 1989, possibly due to injuries inflicted by a feral hog. In fall 1989, we released 18 bobcats (12 males, 6 females); six on 5 October, six on 25 October and six on 4 December. One male released in the interdune area swam into the Atlantic Ocean and presumably drowned.

POST-RELEASE MONITORING

The effort to recapture bobcats on the island resulted in recapturing eight of 12 bobcats from the first year's release and nine of 15 bobcats from the second year's release. Thus, for the first three years of the project we knew the fate of all but one female bobcat, due to transmitter failure. Annual survival of adult bobcats was 93% (SE=2.6%, Diefenbach, 1992). Diefenbach et al. (1993) reported that most bobcats exhibited weight gains, in which bobcats increased an average of 0.8 kg (12.3%). Therefore, we have no evidence that food was limiting during this time period.

In 1989 we documented 10 kittens born in four litters, of which we monitored three from 4-10 months of age, captured and radio-collared three as adults in 1990, and recovered the carcass of one that died at two years of age. In 1990, we located one den with two kittens, and in 1991 we found no evidence that any females denned, although later in the year we observed two 3- to 4-month-old kittens. Recaptures of females for which we did not find dens with kittens indicated that they were not lactating and were unlikely to have produced young (Ragsdale, 1993).

Bobcat prey abundance differed among regions and varied seasonally, but we detected no effect of season or year on diet composition during 1989-1990 (Baker et al., 2001). On an annual basis, marsh rabbits composed the largest proportion of the diet in three of four regions of the island in both years, whereas deer composed the largest proportion of the diet in the northwest region (Baker et al., 2001). Bobcats consumed marsh rabbit, white-tailed deer, cotton rat, grey squirrel, raccoon, unidentified bird species, cotton mouse and feral hogs (Table 1). Marsh rabbit, white-tailed deer and cotton rat were the only prey species identified in bobcat diets during all surveys; thus, we considered these species the principal prey.

Only marsh rabbits (Spearman's r=0.83, n=6, P=0.043) and hispid cotton rats (Spearman's r=0.84, n=6, P=0.036) in bobcat diets were correlated with their abundance, which suggests bobcats had a functional response to these prey species. Diet species diversity (Spearman's r=-0.87, n=6, P=0.023) and species richness in bobcat diets (Spearman's r=-0.82, n=6, P=0.046) were negatively correlated with marsh rabbit abundance. This agrees with the predictions of a diet optimization model, in which increased use of alternate prey species (raccoons, feral hogs, and cotton mice) increases with decrease in abundance of a preferred prey species. Finally, changes in bobcat density or sex ratio within regions were not correlated with prey use (Baker et al., 2001), which did not support the hypothesis of interference or differences in prey use by male and female bobcats.

Species	November/December			March/April			July/August		
	1988 (n=36)	1989 (n=84)	1997 (n=86)	1989 (n=39)	1990 (n=69)	1998 (n=82)	1989 (n=64)	1990 (n=65)	1998 (n=37)
Marsh rabbit	58	43	21	64	33	22	55	39	21
Deer	47	26	12	23	38	7	44	43	31
Cotton rat	3	7	11	15	19	5	3	9	5
Grey squirrel	0	16	13	5	10	11	3	6	5
Raccoon	3	7	10	3	3	5	2	5	12
Bird spp.	3	12	11	0	15	3	5	6	2
Cotton mouse	3	11	14	3	12	23	2	3	5
Feral hog	3	5	9	3	7	24	0	0	19

TABLE 1. NUMBER OF SCATS ANALYZED (N) AND PERCENT OCCURRENCE OF PREY SPECIES IN SEASONAL BOBCAT DIETS ON CUMBERLAND ISLAND, GEORGIA, USA, 1988-90 AND 1997-98.

TABLA 1. NÚMERO DE EXCREMENTOS ANALIZADOS (N) Y PORCENTAJE DE EXISTENCIA DE LAS ESPECIES DE PRESA EN LAS DIETAS ESTACIONALES DE LOS LINCES ROJOS EN LA ISLA DE CUMBERLAND, GEORGIA, EEUU, DURANTE 1988-90 Y 1997-98.
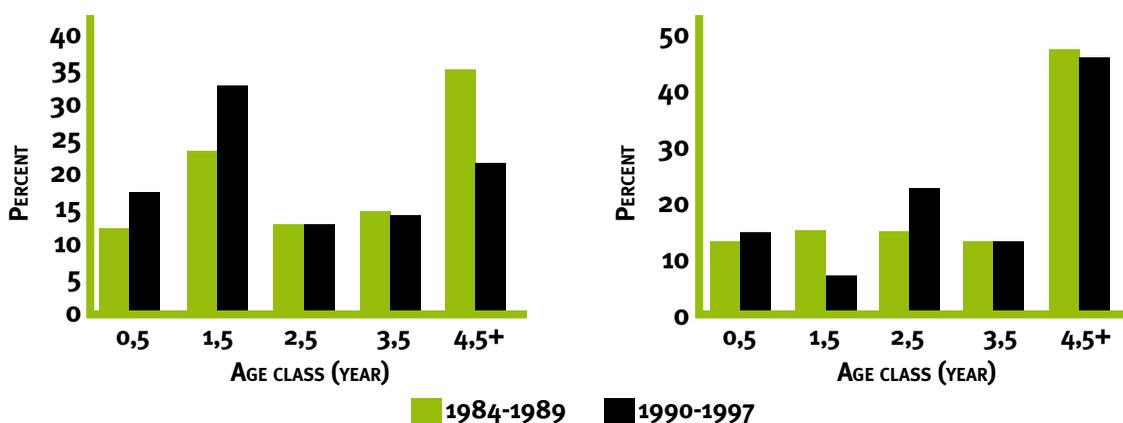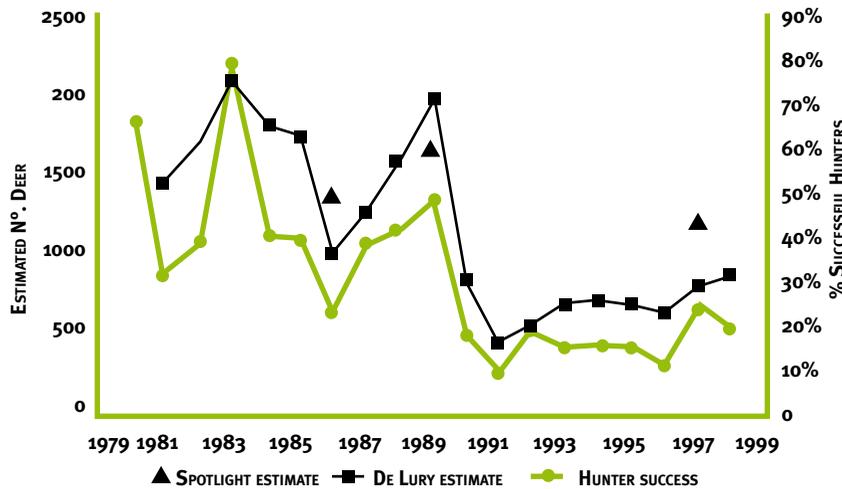

FIGURE 2. AGE-SEX STRUCTURE OF MALE (LEFT) AND FEMALE (RIGHT) WHITE-TAILED DEER HARVESTED ON CUMBERLAND ISLAND, GEORGIA, USA DURING 1984-1989 AND 1990-1997.

FIGURA 2. DISTRIBUCIÓN POR EDAD-SEXO DE LOS CIERVOS DE COLA BLANCA CAPTURADOS EN LA ISLA DE CUMBERLAND, GEORGIA, EEUU, DURANTE LOS AÑOS 1984-1989 Y 1990-1997: MACHOS (IZQUIERDA) HEMBRAS (DERECHA).

We found bobcats consumed the same prey species during 1997-98, but detected important changes in prey use compared to 1988-90 (Table 1). Prey use differed in 1997-98 in fall (x^2_{14}=40.0, P < 0.001), spring (x^2_{14}=67.8, P <0.001), and summer (x^2_{14}=42.5, P <0.001). By 1997, marsh rabbit and white-tailed deer occurred less frequently in scats and occurrence of all other species increased in scats (Table 1) and this pattern was consistent among all three seasons. Overall, relative occurrence of prey species in scats was more evenly distributed during 1997-98 compared to 1988-90 (Table 1).

Female bobcats reintroduced during the first year of the reintroduction exhibited little change in the location or size of their home range, but failed to exclude newcomers from either their home range or core areas (Diefenbach et al., 2006). No bobcats retained areas of exclusive use from conspecifics of the same sex. We observed increasing intrasexual overlap among females during 1989-91, such that overlap of home ranges (95% fixed kernel utilization distributions) was equivalent to each female sharing her home range with >2 other

Restoration of bobcats to Cumberland Island, Georgia, USA:
Lessons learned and evidence for the role of bobcats as keystone predators
Reintroducción del lince rojo en la isla de Cumberland, Georgia, EEUU:
Lecciones aprendidas y evidencia del papel del lince rojo como predador clave
Duane R. Diefenbach, Leslie A. Hansen, Robert J. Warren, Michael J. Conroy and M. Greg Nelms

Figure 3. Population estimates (DeLury population estimate and spotlight surveys, see Methods) of white-tailed deer and an index of abundance (hunter success rate) on Cumberland Island, Georgia, USA, 1980-1998.

Figura 3. Estimaciones poblacionales de ciervos de cola blanca (utilizando el método DeLury y censos nocturnos con focos, véanse Métodos) e índice de abundancia (porcentaje de éxito de caza) en la isla de Cumberland, Georgia, EEUU, 1980-1998.

females. Overlap of core areas (50% fixed kernel utilization distributions) was equivalent to each female sharing her core area with nearly one other female.

Trophic level changes

The POST age distribution of harvested male deer was different from the PRE distribution (x^2_{14}=11.1, P=0.025), in which the proportion of fawns and yearlings increased, 2.5- and 3.5-year-old deer did not change, and 4.5+-year-old deer decreased (Figure 2). The POST age distribution of harvested female deer did not change (x^2_4=8.0, P=0.093; Figure 2). Body weights of deer increased after the reintroduction ($F_{18,819}$=100.93, P <0.001) and the effect of release period was significant ($F_{1,12}$=13.82, P=0.003). Mean eviscerated body weights increased 5.0–7.6 kg for males and 2.0–4.9 kg for females between the PRE and POST years Eviscerated body weights were 11.0 kg greater in 1997 compared to 1989 (average difference of means by age-sex class).

Estimates and indices of deer abundance indicated that following reintroduction of bobcats the population declined and remained low (Figure 3). The DeLury population estimates and hunter success rates declined following the bobcat reintroduction, even though the number of hunters during the PRE period ($\overline{x}$=270 hunters/year) differed little from the POST period ($\overline{x}$=278 hunters/year).

Of 10 plots established by Lieske et al. (1990), we re-visited nine plots and except for two trees (one dead and one not found) counted seedlings and sprouts. In 1997, 53 of 87 trees had ≥1 seedling or sprout within the 16-m² plot, but in 1990, 87 of 88 plots had ≥1 seedling or sprout (McNemar's test, x^2_1=33.0, P <0.001). The ANOVA indicated the overall F statistic was significant ($F_{87,88}$=3.44, P <0.001), the number of seedlings on plots increased an average of 153.5 between 1990 and 1997 ($F_{1,87}$=39.04, P <0.001) and we detected no differences among plots ($F_{8,79}$=0.64, P=0.742).

Discussion

We were able to successfully capture and translocate approximately 15 bobcats per year, and the complete reintroduction was completed in a short period of time and at low cost. Diefenbach et al. (1993) identified three important factors that reintroduction efforts should consider: 1) the source and genetic relatedness of individuals, 2) the age-sex structure of restored populations and 3) the method of releasing translocated individuals.

We captured bobcats from throughout the coastal plain of Georgia to obtain bobcats with gene complexes adapted to regional environmental conditions (Templeton, 1986), although multiple bobcats were captured from the same area. Consequently, some bobcats may be closely related genetically and may result in significant genetic founder effects on the population. We collected genetic samples (blood) from all bobcats, but these samples have not been analyzed. However, the opportunity exists to investigate the genetic changes in the population over time, which should be a priority of restoration efforts of an endangered species.

We were not able to capture enough bobcats on the mainland to control the sex ratio of the population of reintroduced bobcats. Consequently, at the conclusion of the translocations in 1989 the reintroduced population consisted of 14 males and 15 females, although it was female-biased (11 females, 3 males) after the translocations in 1988. These changes in the sex ratio of the population introduced potential confounding effects when interpreting results of our post-release monitoring of food habits and spatial organization (Baker et al., 2001; Diefenbach et al., 2006). Obviously, reintroductions of an endangered species should take greater care in the age-sex structure of the reintroduced population as well as the genetic relatedness of individuals.

We strongly recommend that reintroduction projects establish a means of conducting "slow-releases" whereby animals are held in captivity at the release site and allowed to leave captivity following a holding period. We believe that slow releases might have prevented the disorientation of the one bobcat that swam into the Atlantic Ocean and presumably drowned. However, the logistics of such an effort for our project were prohibitive (Diefenbach et al., 1993). We do not believe hard releases are justified in most reintroduction situations; for example, Brocke et al. (1991) reported movements of hundreds of kilometers for Canada lynx *(Lynx canadensis)* reintroduced to the Adirondacks in New York, USA.

Post-release monitoring is critical to evaluating the success or failure of a reintroduction project. We believe monitoring the physiological condition of animals after release and monitoring their movements, spatial distribution, survival and reproduction should be a mandatory aspect of any reintroduction effort. Future efforts to restore native species should endeavor to increase our knowledge about the effects of spatial distribution, genetics, demography, population size, mechanisms of population regulation, behavior and environmental conditions on the viability of populations. Most of our post-release monitoring occurred within three years of the reintroduction, which may not have been long enough to detect important changes in the bobcat population or its effects on the island. In their evaluation of prey selection, Baker et al. (2001) noted "Further studies of prey abundance and prey use…are needed to determine the long-term effect of the bobcat reestablishment on the island's fauna". To a great extent, research by Nelms (1999) conducted eight years post-reintroduction provided important insights into the effect of bobcats on the island ecosystem.

A 14-fold population decline in marsh rabbits, caused by above-normal rainfall from a hurricane, allowed us to detect changes in bobcat diets and identify a functional response to prey abundance and evidence for diet optimization (Baker et al., 2001). The frequency of occurrence of deer in bobcat diets year-round (23–47%) was greater than reported for other studies in the southeastern United States (0–8%; Maehr and Brady, 1986). Although we did not have sufficient data to identify the shape of these functional relationships, bobcat diets in 1997-1998 had lower occurrence of marsh rabbits and deer and a more even distribution of occurrence of all prey species in their diet (Table 1). Also, there was no evidence the frequent occurrence of deer in the diet was

Restoration of bobcats to Cumberland Island, Georgia, USA:
Lessons learned and evidence for the role of bobcats as keystone predators
Reintroducción del lince rojo en la isla de Cumberland, Georgia, EEUU:
Lecciones aprendidas y evidencia del papel del lince rojo como predador clave
Duane R. Diefenbach, Leslie A. Hansen, Robert J. Warren, Michael J. Conroy and M. Greg Nelms

Figure 5. Interdune meadow and maritime forest of Cumberland Island (and Atlantic Ocean).

Figure 5. Pradera interdunar y bosque marítimo en la isla de Cumberland (con el océano Atlántico de fondo).

Photo: Duane Diefenback

because of a lack of food availability because bobcat survival was high, recaptured bobcats exhibited weight gains and bobcats maintained normal home range sizes (Diefenbach et al., 1993, Diefenbach et al., 2006).

Observation of the spatial organization of bobcats was consistent with the hypothesis that bobcats maintain home ranges via a system of land tenure established by prior rights (Diefenbach et al., 2006). However, we observed significant intrasexual overlap of both home ranges and core areas. Furthermore, we observed declining reproduction with an increase in home range overlap. Similarly, Lembeck and Gould (1979) observed a negative relationship between population density and reproduction, in which they reported 100% of females produced young when population densities were least and only 50% produced young when densities were greatest. We believe that successful reproduction in bobcats may be related to access by females to exclusive use areas even under conditions of adequate or good food availability. Under the conditions of this study (moderate bobcat density, adequate food availability and limited dispersal) bobcats exhibited no evidence of an ability to exclude other adult individuals from their home ranges or core areas. Given the inverse relationship Diefenbach et al. (2006) observed between home-range overlap and reproduction, we suggest that establishment of exclusive use areas by females may be important for successful reproduction, and that the social conditions necessary for maintaining these exclusive areas are less likely to occur at greater population densities or in the absence of dispersal opportunities, thereby reducing population productivity even without food limitation.

Previous researchers noted the adverse effects of grazing and browsing by feral horses, white-tailed deer and feral hogs (Hillestad et al., 1975; Ambrose et al., 1983; Turner 1986; Miller 1988). Bourdeau and Oosting (1959) reported live oak seedling densities of 0.28 seedlings/m² on Smith Island, North Carolina, USA and noted "the understory and shrub layers were very dense," whereas Hillestad et al. (1975) reported a seedling density of 0.055 seedlings/m² on CINS. Eight years after bobcats were reintroduced to CINS, we estimated an oak seedling density of 0.76 seedlings/m² on the same plots that Lieske et al. (1990) noted seedlings were rare or absent. We believe the changes we observed in oak regeneration are related to a decline in the abundance of white-tailed deer.

Consequently, our observations of bobcat use of deer as a primary prey species following their reintroduction, a decline in deer abundance, and an increase in oak regeneration suggest that bobcats caused a trophic cascade effect on the island. We did not expect to observe such strong trophic level changes on the island ecosystem because deer generally are not considered primary prey for bobcats (Maehr and Brady, 1986; but see Epstein et al., 1985). However, deer on CINS were suitable prey for bobcats because of their abundance and small size.

A keystone species is defined as one whose abundance is relatively low but whose effect on the ecosystem is relatively large (Power et al., 1996), and there are few examples of mammals as keystone species (Estes, 1996). McLarin and Peterson (1994) documented changes in vegetation via wolf *(Canis lupus)* predation on moose

433

(Alces alces), but there are few examples of trophic cascades involving mammalian predators, herbivores, and plants in terrestrial ecosystems (Shurin et al., 2002). We believe bobcats on CINS act as keystone predators. Given that Breitenmoser and Haller (1993) reported deer populations declined following a reintroduction of European lynx *(Lynx lynx)*, and our evidence of a trophic cascade caused by bobcats on CINS, any restoration of a felid population should consider trophic cascade effects as a real possibility.

In conclusion, we believe our research on bobcats on CINS provides strong justification for post-release monitoring of a reintroduced species. Not only does post-release monitoring provide data to better understand why a reintroduction project may have succeeded or failed, but it also can provide fundamental knowledge regarding population and community dynamics. In general, the role of predators in ecosystems is poorly understood, especially vertebrate predators (Shurin et al., 2002), and restoration projects of predator populations should consider monitoring trophic level characteristics of ecosystems. If such a monitoring programme were developed to test theories of community population dynamics, there would be potential to better understand food webs of terrestrial ecosystems and trophic level inter-relationships.

ACKNOWLEDGEMENTS

REFERENCES

Ambrose, J., Stoneburner, D., Bratton, S.P., 1983. Vegetation response to release from grazing in two Cumberland Island plant communities. Technical Report 2. U.S. Department of the Interior, National Park Service, Cooperative Park Studies Unit, Athens, Georgia, USA.

Anderson, E.M., 1987. A critical review and annotated bibliography of literature on bobcat. Colorado Division of Wildlife, Special Report 62.

Baker, L.A., 1991. Feeding ecology of reintroduced bobcats on Cumberland Island, Georgia. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

Baker, L.A., Warren, R.J., James, W.E., 1993. Bobcat prey digestibility and representation in scats. Proceedings of 47th Annual Conference of Southeastern Fish and Wildlife Agencies 47, 71-79.

Baker, L.A., Warren, R.J., Diefenbach, D.R., James, W.E., 2001. Prey selection by reintroduced bobcats *(Lynx rufus)* on Cumberland Island, Georgia. American Midland Naturalist 145, 80-93.

Bourdeau, R., Oosting, B., 1959. The maritime live oak forests of North Carolina. Ecology 22, 274-279.

Breitenmoser, M, Haller, H., 1993. Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57, 135-145.

Brocke, R.H., Gustafson, K.A., Fox, LB., 1991. Restoration of large predators: potentials and problems, in: Decker, D.J., Krasny, M.E., Goff, G.R., Smith, C.R., Gross, D.W. (Eds.), Challenges in the Conservation of Biological Resources. Westview Press, Boulder, Colorado, USA, pp. 303-315.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling. Oxford University Press, Oxford, United Kingdom.

Conover, W.J., 1980. Practical nonparametric statistics. 2nd edition. J. Wiley, New York, New York, USA.

Diefenbach, D.R., 1992. The reintroduction of bobcats to Cumberland Island, Georgia: validation of the scent-station survey technique and analysis of population viability. Ph.D. dissertation. University of Georgia, Athens, Georgia, USA.

Diefenbach, D.R., Baker, L.A., James, W.E., Warren, R.J., Conroy, M.J., 1993. Reintroducing bobcats to Cumberland Island, Georgia. Restoration Ecology 1, 241-247.

Diefenbach, D.R., Conroy, M.J., Warren, R.J., James, W.E., Baker, L.A., Hon, T., 1994. A test of the scent-station survey technique for bobcats. Journal of Wildlife Management 58, 10-17.

Diefenbach, D.R., Hansen, L.A., Warren, R.J., Conroy, M.J., 2006. Spatial organization of a reintroduced population of bobcats. Journal of Mammalogy 87, 394-401.

Epstein, M.B., Feldhammer, G.A., Joyner, R.L., 1985. Predation on white-tailed deer fawns by bobcats, foxes and alligators: predator assessment. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 37, 161-172.

Estes, J.A., 1996. Predators and ecosystem management. Wildlife Society Bulletin 24, 390-396.

Ford, C.R., 1987. Spotlight survey for white-tailed deer population trends on Cumberland Island National Seashore. Technical Report 42, National Park Service, Cooperative Park Studies Unit, Athens, Georgia, USA.

Hall, L.K., DeCalesta, D.S., Downing, R.L., Everest, F.H., Harlow, R.F., Harshbarger, T.J., Kroll, J. C., Lindzey, J.S., Meyer, J.M., Scott, V.E., 1984. Forest wildlife and fish management, in: Wegner, K.F. (Ed.), Forestry Handbook., Wiley, New York, New York, USA, pp. 679-7373.

Harris, E.P., 1984. Possible extirpated mammals and reptiles of Cumberland Island, Georgia: a survey of five species being considered for reintroduction. Technical Report 9, National Park Service, Cooperative Park Studies Unit, University of Georgia, Athens, Georgia, USA.

Hillestad, H.O., Bozeman, J.R., Johnson, A.S., Berisford, C.W., Richardson, J.I., 1975. The ecology of the Cumberland Island National Seashore, Camden County, Georgia. University of Georgia, Georgia Marine Science Center, Technical Report Series 75-5.

Jackson, D.H., Jackson, L.S., Seitz, W.K., 1985. An expandable drop-off transmitter harness for young bobcats. Journal of Wildlife Management 49, 46-49.

James, W.E., 1992. Bobcat movements and habitat use on Cumberland Island, Georgia during two years of controlled population increases. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

Johnson, A.S., Hillestad, H.O., Shannholtzer, S.F., Shannholtzer, G.F., 1974. An ecological survey of the Coastal Region of Georgia. United States Department of the Interior, National Park Service, Science Monograph Series 3.

Lieske, S., Hoeldtke, J.E., Bratton, S.P., 1990. Live oak regrowth monitoring data base. Technical report 57, National Park Service, Cooperative Park Studies Unit, University of Georgia, Athens, GA, USA.

Lembeck, M., Gould, G.I., 1979. Dynamics of a harvested and unharvested bobcat population in California, in: Blum, L.G., Escherich, P. C. (Eds.). Bobcat Research Conference Proceedings: Current Research on Biology and Management of Lynx rufus. Scientific Technical Series 6, National Wildlife Federation, Washington, D. C., USA, pp. 53-54.

Maehr, D.S., Brady, J.B., 1986. Food habits of bobcats in Florida. Journal of Mammalogy 67, 133-138.

McCord, C.M., Cardoza, J.E., 1982. Bobcat and lynx (*Lynx rufus* and *F. lynx*), in: Chapman, J.A., Feldhammer, G.A. (Eds.), Wild Mammals of North America. Johns Hopkins Press, Baltimore, Maryland, USA, pp. 728-766.

McLarin, B.E., Peterson, R.O., 1994. Wolves, moose, and tree rings on Isle Royale. Science 266, 1555-1558.

Miller, S.K., 1988. Reproductive biology of male and female white-tailed deer on Cumberland Island, Georgia. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

National Park Service, 1983. Cumberland Island National Seashore Natural Resources Management Plan. U.S. Department of the Interior, National Park Service, Southeast Region Office, Atlanta, Georgia, USA.

Nelms, M.G., 1999. Deer herd trends, bobcat food habits and vegetation change on Cumberland Island, Georgia following bobcat reintroduction. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J. C., Lubchenko, J., Paine, R.T., 1996. Challenges in the quest for keystones. BioScience 46, 609-620.

Ragsdale, L.L., 1993. Den characteristics, activity patterns and habitat use of reintroduced female bobcats on Cumberland Island, Georgia. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

Roseberry, J.L., Woolf, W., 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117.

SAS Institute, 2003. SAS Version 9.1. Cary, North Carolina, USA.

Severinghaus, C.W., 1949. Tooth development and wear as a criteria of age in white-tailed deer. Journal of Wildlife Management 13, 195-216.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5, 785-791.

Templeton, A.R., 1986. Coadaptation and outbreeding depression, in: Soule, M.E. (Ed.), Conservation Biology. Sinnaur Associates, Sunderland, Massachusetts, USA, pp. 105-116.

Turner, M.G., 1986. Effects of feral horse grazing, clipping, trampling and a late winter burn on a salt marsh, Cumberland Island National Seashore, Georgia. Technical Report 23, National Park Service, Cooperative Park Studies Unit, Athens, Georgia, USA.

Warren, R.J., Conroy, M.J., James, W.E., Baker, L.A., Diefenbach, D.R., 1990. Reintroduction of bobcats on Cumberland Island, Georgia: A biopolitical lesson. Transactions of the North American Wildlife and Natural Resources Conference 55, 580-589.

435