Bobcat Spatial Distribution and Habitat Use Relative to Population Reduction

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ABSTRACT Understanding interactions among bobcats (*Lynx rufus*) may lend insight into less understood life history traits of the bobcat and improve management of the species. Moreover, data from manipulative experiments pertaining to bobcat ecology are largely absent from the scientific literature. Therefore, we investigated bobcat spatial organization and habitat use after an experimental population reduction on an 11,735-ha study site in southwestern Georgia, USA. In response to an approximate 50% population reduction, male bobcats shifted their space use (26.4 ± 1.7% more shift relative to baseline) more ($F_{1,3} = 138.08$, $P = 0.001$) than males where no bobcat removal occurred (28.1 ± 5.5% less shift relative to baseline). Dispersion of radio locations for all female bobcats increased following the population reduction; however, females that were exposed to the removal of a potentially interacting male remained more ($F_{1,14} = 6.78$, $P = 0.021$) static (increase in dispersion = 7.8 ± 7.3%) than females that were not exposed to removed males (increase in dispersion 41.2 ± 11.1%). Male bobcats likely shifted their central tendency to increase breeding opportunities, whereas the difference in dispersion of female radio locations may be the result of decreased intraspecific competition. Alternatively, reduced dispersion of females following harvest of neighboring males may increase the likelihood that remaining males will interact with females for breeding purposes. Neither habitat use nor habitat selection differed as a function of removal, suggesting that density-dependent habitat selection was not occurring on our study site. Although it is generally accepted that male bobcats use space to increase breeding opportunities, our study suggests that male bobcats may also influence space use of females, but in counterintuitive ways. Because bobcat movements are altered by harvest of neighbors, we suggest that inferring habitat quality for bobcats based on their space use patterns should be avoided unless researchers incorporate knowledge of both short- and long-term population perturbations. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):107–112; 2008)

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Spatial organization of bobcats (*Lynx rufus*) is controlled by numerous factors including prey abundance, habitat quality, breeding opportunities, den sites, and time-in-residence (Bailey 1974, Griffith and Fendley 1986, Clutton-Brock 1989, Conner et al. 1999, Diefenbach et al. 2006). Bobcats may investigate areas outside of their normal home range, thereby allowing them to capitalize on resources that become available following the death or emigration of adjacent territory holders (Lovallo and Anderson 1995, Benson et al. 2004). These excursions also may increase a bobcat's familiarity with the surrounding landscape, allowing it to move to areas of better resources when they become available (Lovallo and Anderson 1995, Conner et al. 1999). Theoretically, at lower population densities species are able to select the best quality habitats so as to maximize their fitness (Fretwell and Lucas 1970). Thus, it follows that resource availability would need to be greater in surrounding areas for it to be beneficial for a bobcat to shift or expand into a recently vacated territory (Lovallo and Anderson 1995).

Benson et al. (2004) used a long-term telemetry data set to study reoccupation of home ranges following death of a resident bobcat. Although the study by Benson et al. (2004) was not a controlled experiment, they described 10 cases in which another bobcat assumed use of the area vacated following the death of the former resident. Anderson (1988) conducted a controlled removal of a single resident male bobcat and noted a neighboring resident male started using the vacated area within 6 days. Bailey (1974) and Litvaitis et al. (1987) each noted a range shift by neighboring females following the death of a resident. Each of these studies dealt with either the response of a few individuals to the death of one or very few neighbors in the short term (Bailey 1974, Litvaitis et al. 1987, Anderson 1988) or the response of multiple animals to the death of multiple neighbors over a period of multiple years (Benson et al. 2004). None of these studies evaluated the response of numerous animals to short-term, yet intensive, harvest as would be expected in association with a fur harvest or predator control program.

Our objectives were to quantify changes in space use, habitat use, and habitat selection associated with an experimental removal of bobcats. We predicted that the spatial pattern of bobcat locations would change (i.e., shift or become more dispersed) to use newly available resources following the removal of neighboring bobcats. Further, we predicted that bobcats would select or use different habitats in response to a population reduction, suggesting density-dependent habitat selection (Fretwell and Lucas 1970).

STUDY AREA

The Joseph W. Jones Ecological Research Center at Ichauway was located in Baker County, 16 km south of Newton,

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Georgia, USA. The research facility encompassed 11,735 ha. Average temperatures ranged from 11.1° C in winter to 27.2° C in summer. Average annual rainfall totaled 132 cm (L. R. Boring, The Joseph W. Jones Ecological Research Center, 1991–1996 development report, unpublished report).

Land managers at Ichauway burned 4,000–5,000 ha annually, resulting in a 2-year burn rotation (Davis 2001). Northern bobwhite quail (*Colinus virginianus*; hereafter quail) management practices were used at the study site. Management practices included planting and maintaining food plots, supplemental feeding of quail, and limited predator removal. No bobcats were removed from our study area during 1999–2004.

For purpose of this experiment, we divided the study area into control (3,521 ha) and treatment (7,041 ha) areas separated by a major highway (United States Highway 200). Treatment and control areas received identical management and contained similar habitats. The most notable differences between the 2 areas were that the treatment area was twice as large as the control and the treatment area was bordered by the Flint River.

METHODS

Bobcat Capture and Handling

We captured bobcats with laminated, offset-jaw number 1.75, and number 3 Victor soft-catch traps (Victor Inc., Ltd., Cleveland, OH). We restrained captured animals using a net and sedated them with an intramuscular injection of ketamine hydrochloride (10 mg/kg of body wt; Seal and Kreeger 1987). We used length and weight to differentiate juveniles from adults (Crowe 1975). We fitted adult animals with a 180-g very high frequency (VHF) radiocollar (Advanced Telemetry Systems, Isanti, MN). We monitored bobcats for 8–24 hours after sedation and released them at their capture site. Bobcat trapping began on the study area in December 2000 and continued periodically to replace lost animals and failed collars.

Bobcat Removal

Removal trapping began on 1 January 2005 and we removed the last bobcat on 14 February 2005. We placed foot-hold traps throughout the treatment area. We set and checked traps daily and dispatched trapped animals using a .22-caliber handgun. We also used a Johnny Stewart Wildlife Call (Hunters Specialties, Cedar Rapids, IA), a thermal-imaging camera (Raytheon Company, Waltham, MA), and a shotgun to attract and remove 2 radiocollared individuals that were known to be spatially adjacent to a number of other radiomonitored bobcats. All animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (IACUC no. A990159).

Scent Stations

We developed a scent station survey for the study area using 224 stations (179 in the treatment area and 55 in the control area) to 1) quantify relative abundance of bobcats before and after removal, 2) determine if visitation rates before and after removal were independent of treatment and control areas, and 3) ensure that rapid recolonization or immigration did not occur. We obtained scent station data on the treatment and control areas from 11–17 December 2004 before bobcat removal and then again from 16–22 February 2005 following the removal. We placed stations on alternating sides of roads at known points throughout control and treatment areas, maintaining a buffer of ≥0.32 km between stations. We cleared and smoothed an area of 1 m^2 using a garden rake and placed a cotton ball saturated with bobcat urine in the center of the cleared area. We checked scent stations for 3 consecutive mornings and re-established any stations that were disturbed or missing the urine-saturated cotton balls. We set up station checks as run A and run B, which enabled us to check all stations in the treatment and control areas during a 6-day period. We sampled treatment and control areas during both runs, and we used the same scent-station locations before and after the experimental bobcat removal.

Bobcat Monitoring

We triangulated bobcats using a 3-element yagi antenna, and a VHF-receiver (Wildlife Materials Inc., Carbondale, IL). We took ≥2 azimuths from known reference points throughout the study area. We limited time intervals between bearings to <15 minutes to minimize error resulting from movement between readings (White and Garrott 1990); 87% of our bobcat locations were based on <6 minutes between bearings. We did not use maximum likelihood estimators of animal locations because these estimators require ≥3 bearings (White and Garrott 1990). Furthermore, because we were not able to obtain multiple simultaneous bearings, we chose to get close to the animal and obtain bearings with a minimum of time between azimuths to reduce error from animal movement (White and Garrott 1990). We kept ≥8 hours between consecutive locations of individual bobcats to maintain independence among consecutive locations. We performed accuracy tests for all field personnel; these tests suggested that the standard deviation associated with bearing accuracy was 7°. We recorded ≥30 locations per bobcat, spaced equally throughout the diel period, during each season.

Data Analysis

Scent station data.—We determined whether there was a detectable difference in bobcat abundance within the treatment and control areas using a chi-square test in a contingency table analysis (PROC FREQ; SAS Institute, Cary, NC) of our scent station data. We considered a station visited if we recorded a bobcat track within the 1-m^2 cleared area. We report scent station data as a percentage of scent stations visited to standardize for different sizes of treatment and control areas and associated differences in sampling intensity.

Spatial data.—We established time periods for the study: baseline (30 Apr–31 Aug 2004), preremoval (1 Sep–31 Dec 2004), removal (1 Jan–14 Feb 2005), and postremoval (15 Feb–15 Jun 2005). We converted compass bearings to Universal Transverse Mercator coordinates using the FORTRAN program EPOLY (L. M. Conner, Joseph W. Jones Ecological Research Center, Newton, GA). Because it is preferable to base inferences on data rather than models of the data (White and Garrott 1990), we calculated central tendency (Berry et al. 1984) and dispersion (Van Valen 1978) for each bobcat's point distribution before and after the removal using the FORTRAN program FIDELITY (L. M. Conner). We used the bivariate median as our measure of central tendency to ensure that the measure of central tendency fell within the actual point distribution collected on the animal (Berry et al. 1984). We calculated bivariate medians for each bobcat during baseline, preremoval, and postremoval periods.

We calculated dispersion (i.e., mean distance between bivariate medians and animal locations; Van Valen 1978) for each bobcat for pre- and postremoval time periods. A change in dispersion indicated that the distribution of bobcat locations became either more or less dispersed as a function of removal. We standardized dispersal by reporting the change in dispersal (i.e., the difference between pre- and postremoval dispersal) as a proportion of preremoval dispersal, thereby reducing variation associated with individual bobcat behavior.

We considered a change in the bivariate median as a change in central tendency. We defined the shift in central tendency during time 1 as the change in bivariate medians between the baseline and preremoval time periods (i.e., the shift occurring between the 2 preremoval seasons). We defined the shift in central tendency during time 2 as the change in bivariate medians between the preremoval and postremoval time periods (i.e., the shift occurring following the removal). However, to be considered meaningful, a shift in central tendency must be interpreted relative to the dispersion of locations, which is analogous to comparing means relative to the associated variance. Therefore, we standardized the shift in central tendency by subtracting the shift during time 2 from the shift during time 1 and dividing by dispersion during the preremoval period so that difference in shift could be evaluated relative to dispersion. We used these data as the dependent variable in our statistical analyses associated with changes in central tendency.

Habitat data.—We organized habitats into 8 categories: pine, mixed pine–hardwood, agriculture–food plot, hardwood, wetland, pine regeneration, shrub–scrub, and urban–barren. Habitat use and selection were tested at Johnson's (1980) second (i.e., within the study area) and third (i.e., within the home range) orders. We used a Euclidean distance technique to test for changes in habitat use and selection in response to removal (Conner and Plowman 2001). We analyzed habitat selection by comparing distances from animal locations to habitat types relative to the distances that would be expected at random, whereas habitat use was simply a comparison of distances to habitats before the removal treatment to the distances to habitats following the removal, without regard to expected distances. We used a 2-factor multivariate analysis of variance to quantify differences in habitat use and habitat selection as a function of sex, treatment, and sex × treatment interaction.

Levels of analysis.—We analyzed spatial data using 2 experimental approaches (hereafter, levels of analysis). We first compared bobcats in the control area ($N = 5$) to bobcats in the treatment area ($N = 16$) using analysis of variance. Because it is generally accepted that male and female bobcats establish and maintain home ranges for different reasons (Anderson 1987, Sandell 1989, Conner et al. 1999), we performed a separate analysis for each sex. It is likely that some of the removed animals interacted with animals in the control area because most of the removed animals had not been previously monitored using radiotelemetry. Similarly, it is possible that monitored animals in the treatment area did not interact with an animal that was subsequently removed. To account for these potential interactions, we analyzed the data at a second level of analysis by buffering capture sites of removed bobcats and considering monitored bobcats that used areas within these buffers as potentially interacting with the removed animal.

We derived our buffers by first estimating home range size of radiomonitored bobcats. We used ArcGIS 9 with the Hawth's Analysis Tools (Beyer 2004) to create 95% minimum convex polygon home ranges for individual bobcats during the 4 months preremoval. We placed a buffer zone that was 1.5 times larger than the radius of the average bobcat home range size in our study around each location where an animal was harvested (1,875-m radius for removed M and 1,156 m radius for removed F) using the buffer command in ArcGIS 9. We then used the intersect command in ArcGIS 9 to determine which bobcats potentially interacted with removed adult bobcats. We repeated the above analysis using bobcats that potentially interacted with removed bobcats as treatment and remaining bobcats as control animals. When analyzing data using potentially interacting animals, we did not analyze data for male bobcats because we considered all monitored males to have interacted with removed bobcats; thus, there were no control animals.

RESULTS

Bobcat Removal

We radiotracked 25 bobcats from 30 April to 31 December 2004. We removed 13 adult and 12 juvenile bobcats between 1 January and 14 February 2005. Of the 13 adults, 4 were previously radiocollared bobcats, leaving 21 remaining radiocollared bobcats for the postremoval time period (15 Feb–15 Jun 2005).

Scent Station Data

Bobcats visited 16% of stations in the control area before removal and 20% of stations after the removal. In contrast, bobcats visited 23% of stations before the removal in the treatment area and only 11% following the removal, resulting in a relative reduction of about 52% (Fig. 1). Bobcat visits were dependent ($P = 0.068$) on treatment and

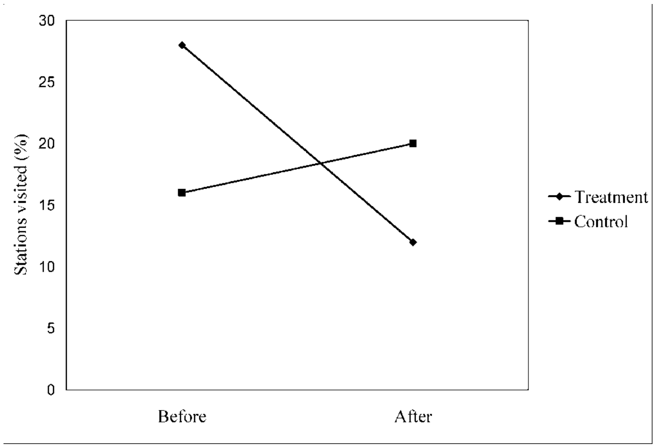

Figure 1. Bobcat scent-station visits for control and treatment areas, both before and after removal of bobcats from the treatment area, Ichauway, Georgia, USA, 2005.

time, suggesting that removed bobcats were not replaced by rapidly colonizing individuals.

Spatial Data

In our first level of analysis using predetermined control and treatment areas, we found that dispersion did not vary as a function of removal for females ($F_{1,14} = 0.67$, $P = 0.428$) or males ($F_{1,3} = 0.51$, $P = 0.528$). Shift did not differ ($F_{1,14} = 0.01$, $P = 0.915$) as a function of removal for females but did differ ($F_{1,3} = 138.08$, $P = 0.001$) for males, with males in the treatment area having a larger shift (26.4 ± 1.7% [$\bar{x}$ ± SE]) following harvest than did males in the control area (–28.1 ± 5.5%; Fig. 2).

In our second level of analysis of using female bobcats that potentially interacted with removed bobcats, removal of female bobcats had no effect on either dispersion ($F_{1,14} = 0.43$, $P = 0.522$) or shift ($F_{1,14} = 0.57$, $P = 0.461$) for remaining females. However female dispersion changed ($F_{1,14} = 6.78$, $P = 0.020$) in response to removal of male bobcats, with potentially interacting females having much less change in dispersion (7.8 ± 7.3%) relative to females that did not interact with removed males (41.2 ± 11.1%; Fig. 3). Removal of male bobcats had no effect ($F_{1,14} = 0.03$, $P = 0.855$) on central tendency of female bobcat locations (i.e., spatial patterns of animal locations did not shift).

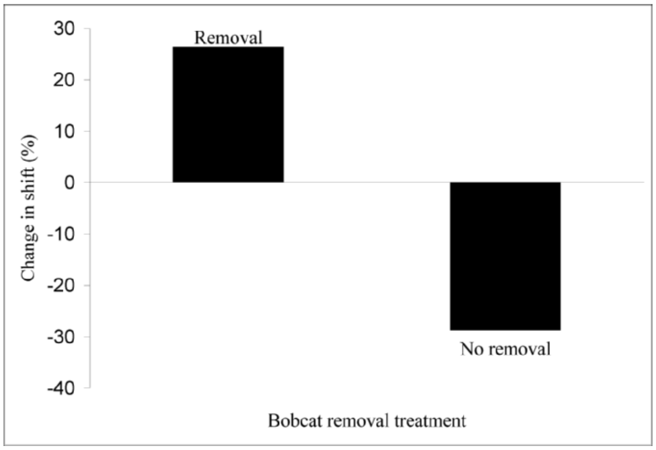

Figure 2. Shift in central tendency of male bobcats following an approximate 50% reduction of the bobcat population on the treatment area, Ichauway, Georgia, USA, 2005.

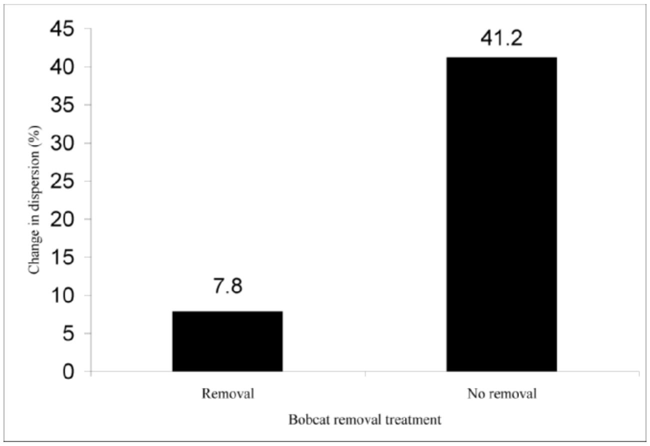

Figure 3. Changes in dispersion of radiolocations obtained from female bobcats that potentially interacted with male bobcats that were subsequently removed, Ichauway, Georgia, USA, 2005.

Habitat Data

We analyzed effects of bobcat harvest on habitat use and selection for 1) all animals using the treatment and control areas, 2) female response to female harvest, and 3) female response to male harvest. For each of these major areas of analysis, we performed hypothesis tests at 2 of Johnson's (1980) hierarchies (second and third order). Finally, within each hierarchy we tested to see if habitat use and habitat selection (i.e., habitat use relative to habitat availability) differed as a function of harvest. This resulted in 12 analyses to determine whether bobcat habitat use or habitat selection was influenced by harvest. We detected no evidence (all cases $P > 0.2$) that harvest of bobcats affected habitat use or selection of remaining animals.

DISCUSSION

Although others have documented bobcats usurping home ranges following death of the former residents or a shift in a bobcat's home range following the death of a neighbor (Bailey 1974, Litvaitis et al. 1987, Benson et al. 2004), ours is the first study of the behavioral response of bobcats to a pulsed harvest effort, such as would be expected following a fur trapping season or a predator control effort. Our results suggest that bobcats alter their space use patterns in response to harvest of neighboring animals and that these changes are sex-specific. We expected bobcat space use to shift or increase in dispersion to take advantage of newly available resources; male bobcats responded as expected, but female bobcat space use became more concentrated in response to harvest of males.

Male bobcats both shifted central tendency and increased their dispersion in response to population reduction as predicted. If male bobcats establish home ranges to increase breeding opportunities (Anderson 1987, Sandell 1989, Conner et al. 1999), then removal of females whose home ranges were overlapped by a given male should result in the male shifting his central tendency and increasing his dispersion in an attempt to encounter more females. Bobcats on our study site typically breed during January and February, which is when we conducted our removals. Therefore, we suggest that males shifted their central tendency and increased dispersion in an attempt to increase breeding opportunities in response to the reduction in the number of breeding-age females, the decrease in female dispersion, or possibly a combination of these factors. Notably, Diefenbach et al. (2006) observed a similar increase in home range shift for males in response to an increasing bobcat population density, suggesting that any sudden change in bobcat density may lead to increased wandering among male bobcats.

In contrast to male bobcat response to harvest, the reduction in dispersion of female bobcat locations in response to harvest of neighboring males is perplexing. Perhaps females sensed the loss of adjacent males and restricted their movements in an attempt to be more easily located by remaining males. Alternatively, removal of male bobcats may have reduced competition for resources resulting in a space use response similar to that expected following an increase in prey availability. However, this is unlikely given the relatively dense prey resources of the study area (Godbois et al. 2003).

Some of our statistical tests failed to provide sufficient evidence for rejecting the null hypothesis. As with any study, small sample sizes and lack of statistical power can be used to explain nonsignificant results; however, we suggest that our results also may be interpreted using generally accepted ideas concerning bobcat spatial behavior. We found no evidence that female bobcats altered their space use patterns in response to harvest of neighboring females. On our study area, bobcat prey were both abundant and diverse (Godbois et al. 2003). Because prey abundance is considered the most important determinant of female bobcat fitness (Anderson 1987, Sandell 1989, Conner et al. 1999) and it would not be to a bobcat's advantage to alter space use patterns unless the change resulted in increased fitness, we suggest that there was no reason for female bobcats to alter space use patterns following harvest of neighboring females.

Finally, we predicted that a reduction in density would result in remaining bobcats altering habitat use and habitat selection to increase their utilization of better habitats, as predicted under a density-dependent model of habitat selection (Fretwell and Lucas 1970). However, we found no difference in habitat use or selection following removal, indicating that either habitat selection by bobcats is not density dependent or that habitat quality on our study area did not vary appreciably.

Interestingly, harvest of same-sex neighbors seemed to have little effect on spatial behavior of remaining animals, suggesting that intrasexual competition may not play a significant role in the spatial ecology of bobcats on our study area. We expected the male response to removal of females because male space use patterns are thought to be most influenced by access to females (Anderson 1987, Sandell 1989, Conner et al. 1999). However, female bobcats responded to removal of males but not females, suggesting that neighboring male bobcats play a greater role in female space use than do neighboring females.

MANAGEMENT IMPLICATIONS

Differences in bobcat space use patterns are often explained based on habitat quality or prey abundance (Bailey 1974, Anderson 1987, Knick 1990, Conner et al. 2001). Our data suggest that bobcat space use patterns are also influenced by neighboring animals. Our results when coupled with the study by Diefenbach et al. (2006) of a rapidly increasing population, suggest that any sudden change in a bobcat population, whether an increase or decrease, can lead to increased wandering of male bobcats; thus large male home ranges do not necessarily indicate poor habitat. Likewise, because females restricted their space use in response to harvest of male bobcats, small female home ranges should not be interpreted as indicative of quality habitat. Because bobcats exhibit changes in spatial behavior in response to harvest of neighbors, bobcat movement patterns and home range size are best interpreted when coupled with knowledge of short- and long-term population trends.

Our removal took place during the bobcat breeding season. Further research should address bobcat response to harvest during other seasons to determine if our results apply to other seasons. Finally, additional work is necessary to determine how quickly removed predators are replaced by adjacent animals; such research would prove valuable for timing predator control efforts.

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