



Current Bobcat Research and Implications for Management

Symposium Proceedings

from

The Wildlife Society 2000 Conference

Nashville, Tennessee
12–16 September 2000

A. Woolf, C.K. Nielsen, and R.D. Bluett, editors



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PREFACE

A colleague once referred to bobcats as “the louse of the Cat World.” While unflattering, his characterization rings true in many respects. Like lice, bobcats are adaptable, resilient, and nearly ubiquitous.

Our work started with a different premise. Considered rare and confined to the southernmost part of Illinois, the bobcat was listed as a state threatened species when we launched a research project under the Federal Aid in Wildlife Restoration program. Believing the odds were in my favor, I made a friendly wager which pitted researchers against a goal of radio-collaring 20 individuals during the course of the study. Much to my chagrin (and equal delight), researchers exceeded this goal long before the first field season came to a close. Success sparked youthful enthusiasm while experience brought a better understanding of ecological and behavioral underpinnings of the bobcat’s good fortunes.

Organizing a symposium at The Wildlife Society’s 7th Annual Conference was a natural extension of our interests in “Current Bobcat Research and Implications for Management.” We hope these proceedings help to foster an appreciation of the bobcat by contributing to current knowledge. After all, their strategies for survival merit respect—even if they attract comparisons with a louse.

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BOBCAT RESEARCH AND MANAGEMENT: HAVE WE MET THE CHALLENGE?

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Abstract: Bobcats (*Lynx rufus*) first attracted research attention for economic reasons related to predation, or their value as a furbearer. As late as 1971, bobcats were neither protected nor purposefully managed in 40 of the 48 contiguous United States. This laissez-faire attitude prevailed until the mid-1970s when attitudes toward predators changed and pelt values increased. Amid concerns that the species could be at risk, it became subject to management scrutiny and a surge of research projects. Concern for the species led to a 1979 conference at Front Royal, Virginia, where biologists presented research and shared information and insight. Papers summarized current research and management, and discussion provided ample opportunity to exchange information and viewpoints. A rapporteur noted that the species' natural history in diverse habitats was well known, but he identified serious problems and gaps in knowledge. Further, he criticized rigor of the science applied to better understand and manage bobcats and believed the information presented fell short of knowledge needed to properly manage the species throughout its range. Twenty-one years have passed and it is appropriate to meet, share our state of knowledge, and examine the purpose, approach, and rigor of bobcat research. This symposium presents bobcat research in an ecosystem context, and at spatial and temporal scales not possible 2 decades ago because our predecessors lacked the powerful tools of data acquisition and analyses we enjoy. Managers discuss challenges and their approaches to address conflicting public demands in a rapidly changing environment. We present this symposium so our audience can reflect on new knowledge, question our assumptions and methods, and help identify important questions and new approaches to improve management of bobcats and their ecosystems in the decades ahead.

Key words: bobcat, ecology, *Lynx rufus*, management, research.

The bobcat (*Lynx rufus*) first attracted management and research attention for economic reasons related either to its impact as a predator or its value as a furbearer. Increasing public awareness and ecological interest in native cats grew in the 1970s and led to heightened concerns for the species well being. Amid concerns that the bobcat could be at risk, it became subject to management scrutiny and prompted a surge of research projects covering a range of topics. This interest and concern led to the 1979 Bobcat Research Conference in Front Royal, Virginia, co-hosted by the National Wildlife Federation and the Endangered Species Scientific Authority. The conference was designed to provide a forum where biologists studying bobcats could present their work and share information and insight. Twenty-one years have passed and it is appropriate to again meet to share our state of knowledge and subject the purpose, approach, and rigor of bobcat research and management to peer scrutiny. The species seems to be faring well throughout its range (Woolf and Hubert 1998), but ecological understanding remains incomplete and science-based management faces new challenges in a rapidly changing landscape.

This symposium presents research on bobcats that was conducted in the context of the ecosystems they are components of, and at spatial and temporal scales not possible 2 decades ago. The research employed more powerful tools of data acquisition and analyses than were available to earlier biologists. Management issues addressed are those at the forefront of approaches used to address public concerns and conflicting demands in a rapidly changing environment. We present this symposium

so our audience can reflect on our new knowledge, question our assumptions and methods, and help identify important questions and new approaches to improve science-based management of bobcats and their ecosystems.

THE PATH TO TODAY

The bobcats extensive distribution on the North American continent attests to its versatility and adaptability. In the early history of wildlife management, especially management of predators or furbearers, there was little incentive to consider need to manage its habitats or populations. As late as 1971, bobcats were not protected nor purposefully managed in 40 of the 48 contiguous United States (Faulkner 1971). The beginnings of public awareness and concern about mammalian predators was impetus for a symposium held at the North American Wildlife and Natural Resources Conference in 1971 to review status of the native felids of North America (Jorgensen and Mech 1971). The symposium consisted of 21 presentations with a strong focus on status and management; 8 included discussions of the bobcat. In a summary of the symposium, Cowan (1971) described the bobcat as an adaptable and successful species that was the most numerous of North American felids. Further, his review of the papers presented at the symposium led Cowan (1971:6) to conclude that management was in general not regarded as necessary. This laissez-faire approach toward management prevailed until changing attitudes toward predators and a dramatic increase in pelt value during the mid- to late-1970s led to public and

professional concern for the welfare of the species. This concern was magnified when the bobcat was listed in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 1975. The listing made state management subject to federal review and agencies had to prove that harvesting bobcats was not detrimental to populations (Rolley 1987).

Additional reviews of the bobcat's status followed (Woolf and Hubert 1998), but they did not allay either public or agency concern. The continued concern led to the 1979 Front Royal, Virginia, conference that focused just on the bobcat (Escherich and Blum 1979). Whereas the 1971 symposium and other surveys (e.g., Deems and Pursley 1978) were essentially a compilation of reports on status and management, the Front Royal conference sought to provide an opportunity for researchers to present and discuss recent research and work in progress. The conference took place at a time when interest in the bobcat was high, and there were a number of new research projects underway throughout the country. Researchers presented 29 papers; some discussed status and management, but a number addressed bobcat ecology. Not everyone was impressed with the scope and substance of the research presented. A rapporteur (Dyer 1979) noted that the species natural history in diverse habitats was well known, but he identified serious problems and gaps in knowledge. Further, he criticized rigor of the science applied to better understand and manage bobcats and believed the information presented fell short of knowledge needed to properly manage the species throughout its range.

A comprehensive compilation of bobcat literature by Tumlison et al. (1985) provided evidence of increasing interest in the bobcat, and a changing focus of research beginning in the 1970s. They assembled and cross-indexed citations into 11 major topics; we selected 4 to illustrate changing emphasis of research in the 1970s and 1980s compared to prior years. The topic "food habitats and predation" included 115 citations; 53% dated before 1970. "Behavior and home range" only included 54 citations, but 69% were dated after 1970. "Ecology and population characteristics" (this topic included population dynamics, techniques for population assessment, general ecology, density, and scent-station surveys) included 91 references of which 85% were dated after 1970. The category "miscellaneous references" also illustrated the increasing interest in bobcats in the 1970s and 1980s compared to prior years; 71% of the citations were more recent than 1970.

Although different research topics were emphasized beginning in the 1970s, bobcat populations remained a source of concern for resource managers. In 1990, the bobcat again was the focus of a review of its status and management (Kulowiec 1990). Finally, the status and management of bobcats spanning the last 3 decades was reviewed by Woolf and Hubert (1998). The path we took to arrive at this symposium is one that followed changing

public values, management models and emphasis, and better knowledge upon which to establish science-based management. One common thread has been concern for the well-being of the bobcat; a concern shared both by resource managers and the public they serve.

HAVE WE MET THE CHALLENGE?

Dyer (1979) was disappointed in the science he was asked to review at the Front Royal conference that represented the knowledge of the day. Whether one judges his criticisms as perceptive and insightful or the intellectual arrogance of a person who failed to appreciate the difficulties of studying a secretive carnivore, they deserve our introspection. He thought the papers presented lacked rigor as evidenced by a tendency to ignore study objectives, failure to state approaches in terms of hypotheses, and failure to utilize the breadth of pertinent scientific literature. He noted that nothing was said about niche/competition theory, and lamented that home range was discussed, but not in context. Another troublesome criticism, if true, was his perception that tools such as radiotelemetry were used as gimmicks rather than to address strong scientific questions. There were other criticisms as well, and overall, he believed it was necessary to consider major changes in the conduct of bobcat research and management to satisfy both CITES and local issues. Finally, he took exception that the bobcat population was a central focus of the Front Royal conference and maintained there was need for more expansive thinking and use of community and ecosystem function paradigms as the backbone leading to management strategies (Dyer 1979:135-136).

What would he say today if asked to summarize these proceedings? Few could have imagined the new tools now at our disposal and how computers, radiotelemetry, and remote sensing have combined to offer insight about bobcat ecology simply not possible 2 decades ago. Good science always begins with asking an important question, but without doubt, the tools now at our disposal have allowed such questions to be addressed as evidenced by the research presented at this symposium.

However, the real issue is the quality and rigor of our science; are the criticisms posed 21 years ago still an issue today? We believe the papers in this symposium are of a quality that can withstand critical peer evaluation. Hypotheses are in evidence, and most papers reflect studies of bobcats in context of the ecosystems they occupy, and at temporal and spatial scales previously unimaginable. Both niche and competition theory are addressed, and there is now meshing of theoretical and empirical approaches that Dyer (1979:135) found lacking. Perhaps most importantly, our powerful new tools have allowed insights into species-habitat relationships that offer promise of habitat-based management decisions not even envisioned 2 decades ago.

The single species approach persists, but is this really a valid criticism or concern? We do not apologize for

featuring the bobcat, because in truth, the research presented has focused on the species in an ecosystem context. Managers also focus on the species, but that is their charge. However, they too understand that the bobcat does not live in isolation, and their management decisions are increasingly habitat-based and cognizant of landscape-level scales.

A GLIMPSE AT TOMORROW

Those who will be charged with managing the bobcat in the future will start from a position of strength. By most accounts, the continental bobcat population is healthy (Woolf and Hubert 1998) and fears for its future well-being, professed in the 1970s, were unfounded. Bobcats were delisted as state threatened in Illinois in 1999 (Bluett et al. 2001), and in Pennsylvania, the Game Commission (Lovallo 2001) approved a legal harvest of bobcats for the first time in 30 years. Further, managers and their management strategies have adapted to changing times and needs. Better data are available upon which to implement science-based management, and agencies are making harvest management decisions on that basis capable of withstanding legal challenges (Rolley et al. 2001).

However, managers most likely will face more difficult issues to resolve, and the need for scientifically sound information upon which to formulate and defend management options will increase. Adverse impacts of humans and their activities on wildlife and their habitats also can only increase. Bobcats seem tolerant of human presence, but exurban development will intensify pressure on bobcat populations (Nielsen and Woolf 2001). Finally, public policy already shapes management decisions, but increasingly, human dimensions aspects will outweigh ecological considerations when formulating management strategies (Bluett et al. 2001).

In spite of increasing human pressure and increasingly contentious debates over management goals and objectives, we remain optimistic. The bobcat indeed is an adaptable species as Cowan (1971) noted long ago. Also, wildlife managers and researchers have always been up to challenges posed. We predict that both bobcats and those who manage them will prevail and we hope this symposium contributes to that outcome.

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MULTIVARIATE MODELS OF BOBCAT HABITAT SELECTION FOR PENNSYLVANIA LANDSCAPES

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Abstract: We used bobcat (*Lynx rufus*) locations, a geographic information system, multivariate statistical modeling techniques, and remotely sensed land cover and physiographic data to model bobcat habitat selection and to predict distribution of suitable habitat in Pennsylvania. Bobcats (27 F, 34 M) were radiocollared and monitored on a 2,320-km² study area during 1986–97. We developed Mahalanobis distance-based models of habitat selection on the study area and used logistic regression techniques to extrapolate patterns of habitat selection to larger scales. The models classified 70% and 54% of the study area as suitable for males and females, respectively. Cross-validation suggested 86% classification success for both males and females. The model was validated using independent locations collected from 7 female and 10 male bobcats. Validation suggested 78% classification success for females and 71% success for males. Female home range size was inversely correlated ($r = -0.67$, $P = 0.004$) with percent composition of areas classified as suitable habitat suggesting model predictions reflected habitat gradients that were linked to individual behavior and home range use. An area of 18,564 km² (15.8% of Pennsylvania) was classified as suitable for both male and female bobcats, whereas 39,067 km² (33.3%) was suitable for males but not females. Our results provide an information source for habitat-based management decisions and serve as a basis for hypotheses addressing local- and landscape-level habitat associations.

Key words: bobcat, distribution, habitat modeling, geographic information systems, logistic regression, *Lynx rufus*, Mahalanobis distance, multivariate statistics.

The use of quantitative habitat models and geographic information systems (GIS) in wildlife science is rapidly increasing for resource inventory, impact assessment, mitigation, and the development of wildlife management objectives (Schamberger and O'Neil 1986). Habitat models are usually developed from field investigations of species-habitat relationships and then extrapolated to evaluate habitat conditions in other regions. These models are often developed on a site-specific basis and are rarely validated beyond the geographic extent of their development (Lancia et al. 1982). Current interest by state and federal agencies in predicting the spatial occurrence of suitable habitats, as evidenced by the Gap Analysis Program (Scott et al. 1993), illustrates the need to make better use of site- and species-specific habitat relationship models in predicting broad-scale spatial distributions of animal species.

The geographic range of the bobcat includes most of the contiguous U.S., with the exception of major agricultural regions of the Midwest and Mexico (Anderson 1987, Boyle and Fendley 1987). Bobcat populations in Pennsylvania are established throughout the northern, central, and southcentral portions of the state (Giles 1986, Merritt 1987, Lovallo 1999) and provide an important geographic link between established populations in New York to those of the southeastern U.S. The bobcat was first classified as a game animal in Pennsylvania in 1970,

which empowered the Pennsylvania Game Commission (PGC) to set regulations to manage bobcat populations. Before 1970, bobcats were unprotected in Pennsylvania and bounties were paid during 1819–1937 (Giles 1986). Recent surveys of PGC field personnel and sportsmen suggest the geographic range of the bobcat is expanding and that bobcat density has increased since the 1970 reclassification (Lovallo 1999).

The development of effective management strategies for Pennsylvania bobcats requires a fundamental understanding of bobcat-habitat relationships as they relate to abundance and distribution. The PGC is currently developing a habitat-based management plan for bobcats (Lovallo 2001). The development and implementation of this plan requires an understanding of bobcat habitat selection and a statewide assessment of the amount and distribution of suitable bobcat habitat. Despite a proliferation of field investigations on bobcat habitat selection during the late 1970s and early 1980s (Anderson 1987), there are no published reports of bobcat habitat selection in Pennsylvania.

We estimated bobcat habitat selection in northcentral Pennsylvania and used multivariate habitat modeling to predict the extent and distribution of suitable bobcat habitat. We compared models using Mahalanobis distance measures based on spectral reflectance and physiographic characteristics to logistic regression models

based on classified satellite imagery and physiographic characteristics. We evaluated model performance using cross-validation techniques and an independent sample collected beyond the geographic extent of model development. We also described the extent and distribution of suitable bobcat habitat using cell-by-cell, sex-specific, predictions of habitat suitability, and compared amounts of suitable habitat within bobcat home ranges to habitat composition within simulated bobcat home ranges statewide.

STUDY AREA

Field investigations were conducted in a 2,320-km² study area (hereafter, Study Area 1) in northern Lycoming County, Pennsylvania. The study area was located in the Allegheny Plateau province and was underlain with Devonian and Mississippian bedrock. The area was characterized by steep, forested slopes and narrow drainages. Soils were primarily incepticols originating from glacial till. The study area was primarily forested with active agriculture in the lower elevations. Forests were dominated by northern hardwood types including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*), and hemlock (*Tsuga canadensis*). Other prevalent species included white pine (*Pinus strobus*), basswood (*Tilia americana*), mountain laurel (*Kalmia latifolia*), and American ash (*Fraxinus americana*).

METHODS

Capture, Marking, and Monitoring

Bobcats were captured in offset #1.75 coil spring traps by trappers and PGC employees during 1986–95. Bobcats were immobilized with ketamine hydrochloride and equipped with radiocollars and numbered eartags. All bobcats were released immediately following capture. Initial efforts to capture bobcats during 1986–93 were focused on Study Area 1, whereas subsequent capture efforts (1993–95) were expanded to include areas within 150 km of Study Area 1 (hereafter, Study Area 2).

Bobcats were located using fixed-wing aircraft (Mech 1983) and ground-based triangulation using 2-element H-style antennas. Aerial-determined locations were periodically ground-truthed by PGC employees to verify telemetry accuracy. Bobcat locations were grouped by sex and season (sum: 15 May–31 Aug, win: 1 Oct–14 May). Seasonal designations were chosen based on the reproductive biology of bobcats. The summer period encompassed parturition and kitten rearing periods for females, whereas the winter period included the breeding season.

Habitat Variables

Measures of elevation, aspect, and slope were based on digital, statewide data derived from 2-arc-second (30 min), United States Geological Survey digital elevation models. Digital elevation models were produced via interpolation of digital line graph hypsographic and

hydrographic data and had an associated root-mean-square-error of 0.5 contour intervals. A GIS (ARC/INFO; ESRI, Redlands, California, USA) was used to resample digital elevation models into 30-m lattices and to interpolate elevation (m), aspect (degree of exposure), and slope (degrees) measures associated with bobcat locations. Spectral reflectance data (30x30-m resolution) were obtained from Landsat Thematic Mapper sensors during May 1993. A 31,470-km² scene that encompassed northcentral Pennsylvania was used to assign 6 bands of reflectance data to bobcat locations.

Univariate analyses of habitat selection and logistic regression models were based on classified land cover data and considered 7 land cover categories: coniferous forest, mixed forest, broadleaf forest, transitional areas, perennial herbaceous, annual herbaceous, and unvegetated areas. Land cover data were generalized to 1-ha resolution and stored at 30x30-m resolution as part of Pennsylvania's contribution to the National Gap Analysis Project (W. Myers, The Pennsylvania State University, unpublished data; Scott et al. 1993).

Univariate Habitat Selection

Univariate analyses of cover type selection were based on the actual use of cover types compared to their expected use based on proportional occurrence within Study Area 1 (Neu et al. 1974). Because sufficient numbers of locations were not available to test for habitat selection by individual bobcats, locations were pooled across individuals and habitat selection was estimated separately for males and females each during the summer and winter seasons. Availability of cover types was based on a minimum perimeter convex polygon estimated from all bobcat locations. Bonferroni z -tests were used to construct 95% confidence intervals to identify selection or avoidance of particular types. Chi-square contingency tests were used to compare habitat use between sexes and seasons (Zar 1984).

We used a modified goodness-of-fit to test for circular uniformity among aspect measures associated with male and female bobcat locations during summer and winter. This test is insensitive to the starting point of a circle and is widely applied to circular data (Batschelet 1965). Standard deviations for aspect measures were calculated according to Mardia (1972). Rayleigh's z -test was used to test for a mean aspect when distributions were unimodal (Zar 1984). Kuiper Chi-square tests of heterogeneity were used to compare aspect measures between seasons and sexes (Zar 1984).

Home Range Estimates

We used 3 independent methods, including the adaptive kernel estimator (Worton 1989), harmonic mean estimator (Dixon and Chapman 1980), and minimum convex polygon technique (Mohr 1947), to estimate annual home range size for male and female bobcats. Because sample size was limited for some individuals, only annual ranges were constructed. All home range methods used 95% probability distributions. We used

program CALHOME (Kie et al. 1996) to estimate home range size and to export resulting polygons to a GIS. We used a Wilk-Shapiro test to assess normality of home range estimates.

Habitat Modeling

We used 2 independent approaches and a combined approach to model bobcat habitat selection within Study Area 1. The first approach used Mahalanobis distances as measures of habitat similarity and considered 8 variables including 6 measures of spectral reflectance, slope (degree change), and aspect (circular measure of exposure in degrees). The second approach was based on logistic regression that evaluated cover type, slope, and aspect measured at bobcat locations relative to habitat conditions at random locations within the study area. The combined approach also used logistic regression and compared used versus random locations. However, only random locations that occurred in areas classified as unsuitable, based on the Mahalanobis distance-based model, were used in the regression. Hereafter, we refer to this randomization scheme as "conditional."

Mahalanobis Distance Mode.—We developed a multivariate habitat selection model based on Mahalanobis distances that was similar to Clark et al. (1993). This model was fundamentally based on the use of Mahalanobis distance as a relative measure of habitat similarity. Mahalanobis distance calculations were used to assign various levels of habitat suitability for female and male bobcats on a cell-by-cell basis (Seber 1984). This procedure used the covariance matrix from each set of locations to produce a multi-space transformation in which distance between the reflectance, aspect, and slope of a geographic cell and the mean reflectance, aspect, and slope associated with radiolocations represented an index to habitat similarity. Kolmogorov-Smirnoff tests were used to determine distributions that best fit sample distances in Mahalanobis space (Zar 1984). Geographic cells were classified as selected habitat if they fell within the upper 90% of the distribution associated with a given sex. Our methods differed from Clark et al. (1993) in 2 respects: (1) models were developed independently for males and females to assess intersexual variation in habitat selection and to identify sex-specific patterns in habitat distribution, and (2) habitat models were developed, in part, from direct spectral reflectance rather than from classified land cover types.

Logistic Regression Models.—Logistic regression models of habitat suitability were developed according to the approach outlined by Hosmer and Lemeshow (1989). Logistic regression models were developed as the logit of probability of presence as a linear function of categorical and continuous regressor variables. Logistic regression models were based on habitat conditions associated with cells classified as used, based on the occurrence of bobcat locations ($n = 804$ for M; $n = 1,518$ for F), and at randomly selected cells within the study area. These models considered the 7 cover-type variables, slope, and aspect.

Aspect was represented as 4 categorical variables, each encompassing 90° intervals. The first aspect variable, Aspect(I), was centered on the estimate of the circular mean and consecutive aspect intervals (i.e., Aspect(II), Aspect(III), and Aspect(IV)) were assigned clockwise. We fit univariate logistic regression models and examined likelihood ratio tests to determine inclusion in multiple logistic regression models.

We used 2 approaches to select random points for the development of logistic regression models: a completely random approach and a conditional random approach. The completely random approach used all randomly selected points ($n = 2,893$) within the study area boundary. The conditional random approach used only randomly selected points believed to be located in poor habitat ($P \leq 0.10$) based on sex-specific, Mahalanobis distance-based models of habitat selection ($n = 804$ for M, $n = 1,518$ for F). Random coordinates were generated using algorithms described by Press et al. (1992).

We examined relationships between home range size and percent composition of suitable habitat, as determined from Mahalanobis distance and logistic regression models, to determine whether distribution and amounts of suitable habitat affected home range size. Home range boundaries were overlaid onto maps of predicted habitat suitability and the percent composition of suitable habitat in each range was determined. We hypothesized that home range size would be inversely related to the percent composition of suitable habitat within the home range and that the magnitude of inverse correlations would relate various levels of habitat suitability.

Model Validation

Bobcat habitat selection models were validated at 2 scales: within Study Area 1, and regionally throughout northcentral Pennsylvania. Within the study area, jackknife cross-validation techniques were used to estimate reclassification success using the initial set of bobcat locations (Lachenbruch and Mickey 1968). In the case of Mahalanobis distance-based models, we compared the actual habitat components (i.e., cover type, slope, aspect) associated with patches classified as suitable habitat to results from univariate habitat selection analyses.

At the regional level, habitat selection models were applied to areas occupied by bobcats radiocollared in Study Area 2. Locations ($n = 158$ for F, $n = 200$ for M) were attributed by predicted bobcat suitability scores and classification success rates were calculated.

Statewide Model Application

Regional validation results were used to determine which modeling approach would perform best for statewide extrapolation. We used existing statewide geographic data including slope, aspect, and classified land cover to make cell-by-cell (30x30-m resolution), sex-specific predictions of bobcat habitat suitability. We estimated amounts of suitable male and female bobcat habitat within counties, furbearer management zones, and

Wildlife Conservation Officer (WCO) districts to provide a geographic basis for future refinement of bobcat management zones.

Home Range Size Versus Habitat Predictions

We used estimates of percent composition of suitable habitat within actual female home ranges and a moving window approach to evaluate potentials of simulated home ranges throughout Pennsylvania to support female bobcats. Although habitat selection models were developed for males and females, we based the statewide analyses of home range potential only on females because females generally use higher quality habitat than males (Bailey 1974), and female home range size is directly related to habitat quality whereas male home range size may be influenced by breeding opportunities (e.g., the spacing pattern of females) (Anderson 1987). We developed circular home ranges of approximately the same area as median female home range sizes observed in our study. These simulated home ranges were developed statewide and served as the spatial units for comparison to actual home range characteristics. Home range centers were spaced at 2,500-m horizontal and vertical intervals. We used this sampling strategy to identify fine-scale gradients in the potential of simulated home ranges to support female bobcats and to negate random effects due to the placement of simulated ranges.

Statewide Model Validation

We used a questionnaire to survey WCOs concerning their perceptions on the distribution and status of bobcat populations within their respective districts. In most cases, the 67 counties in Pennsylvania are patrolled by 2 or 3 WCOs; each is assigned to 1 of 138 districts in the state. In districts where WCOs were relatively new, we requested that advice be sought from the previous WCO or from WCOs in surrounding districts. Survey results were compared to the predicted habitat composition of each district.

Existing information on reported bobcat mortalities was also used to identify bobcat presence/absence within counties. Pennsylvania Game Commission staff collected reports of bobcat mortalities during 1986–99. Recovered bobcats were weighed and sex and age (juv vs. ad) were determined. Date of death, cause of death (if possible), and location were recorded by county and township. A spatial data layer containing county boundaries was attributed by numbers of bobcat mortalities and was compared to the statewide distribution of suitable habitat.

RESULTS

Capture, Marking, and Monitoring

Sixty-one bobcats (27 F, 34 M) were captured and radiocollared in northcentral Pennsylvania during 1986–95. Initial efforts to model habitat suitability were based on radiolocations collected from 20 females and 24 males on Study Area 1. Extrapolation beyond Study Area 1 was evaluated using locations collected from 7 females and 10 male bobcats captured and radiocollared on Study Area 2 during 1993–95.

Univariate Habitat Selection

Slope measures associated with bobcat locations revealed differences by sex ($F_{3,2318} = 44.71$, $P < 0.001$) and season ($F_{3,2318} = 5.74$, $P = 0.017$). Females spent more time on steeper slopes during winter ($\bar{x} = 8.2^\circ$, $SE = 0.2$) than during summer ($\bar{x} = 7.3^\circ$, $SE = 0.3$). Regardless of season, males used steeper slopes than females ($\bar{x} = 8.4^\circ$, $SE = 0.2$ during winter; $\bar{x} = 8.3^\circ$, $SE = 0.5$ during summer). Comparison of aspect measures associated with bobcat locations revealed circular non-uniform distributions for both males and females during summer and winter periods. Plotting aspect measures by 30° intervals suggested distributions were unimodal and mean angles and circular standard deviations could be calculated. Aspect measures associated with bobcat locations differed between males and females regardless of season. Females were most often located on eastern aspects, whereas males were associated with eastern aspects during summer and southeastern aspects during winter (Fig. 1).

Female bobcats did not use cover types in proportion to their availability ($\chi^2_6 = 35.62$, $P < 0.001$ during summer; $\chi^2_6 = 55.71$, $P < 0.001$ during winter) (Table 1). Females selected broadleaf deciduous forests and avoided herbaceous and unvegetated areas during summer and winter. There was no seasonal difference in habitat selection for females ($\chi^2_6 = 10.62$, $P = 0.060$). Males also used cover types disproportionately to their availability ($\chi^2_6 = 42.13$, $P < 0.001$ during winter; $\chi^2_6 = 12.15$, $P < 0.001$ during summer) (Table 1). Male bobcats selected broadleaf deciduous forest during summer and winter. Males avoided conifer forests and annual herbaceous areas during summer and avoided mixed forest, unvegetated areas, and perennial herbaceous areas during winter. There was no seasonal difference in cover type selection for males ($\chi^2_6 = 3.57$, $P = 0.140$).

Home Range Estimates

We only used home ranges estimated from ≥ 20 locations in the analyses. Home ranges were calculated for 17 of 34 males and 17 of 26 females (Table 2). Home range size was non-normal ($P < 0.01$) for males and females, regardless of the estimator used. Median male home ranges were 2.5, 2.8, and 4.8 times greater than those of females based on minimum convex polygon, harmonic mean, and adaptive kernel estimators, respectively. Median home ranges and associated quartiles were similar between minimum convex polygon and harmonic mean estimators, whereas home ranges estimated using the adaptive kernel method were approximately twice as large as those estimated by other methods.

Habitat Modeling

Mahalanobis Distance Model.—Mahalanobis distance-based models classified 69.6% of the initial study area as suitable ($P \geq 0.10$) for males and 54.0% suitable ($P > 0.10$) for females (Fig. 2). Suitable habitat areas were dominated by forest cover types (approximately 85% and 95% for M and F, respectively). Percent composition of conifer and mixed cover types in suitable

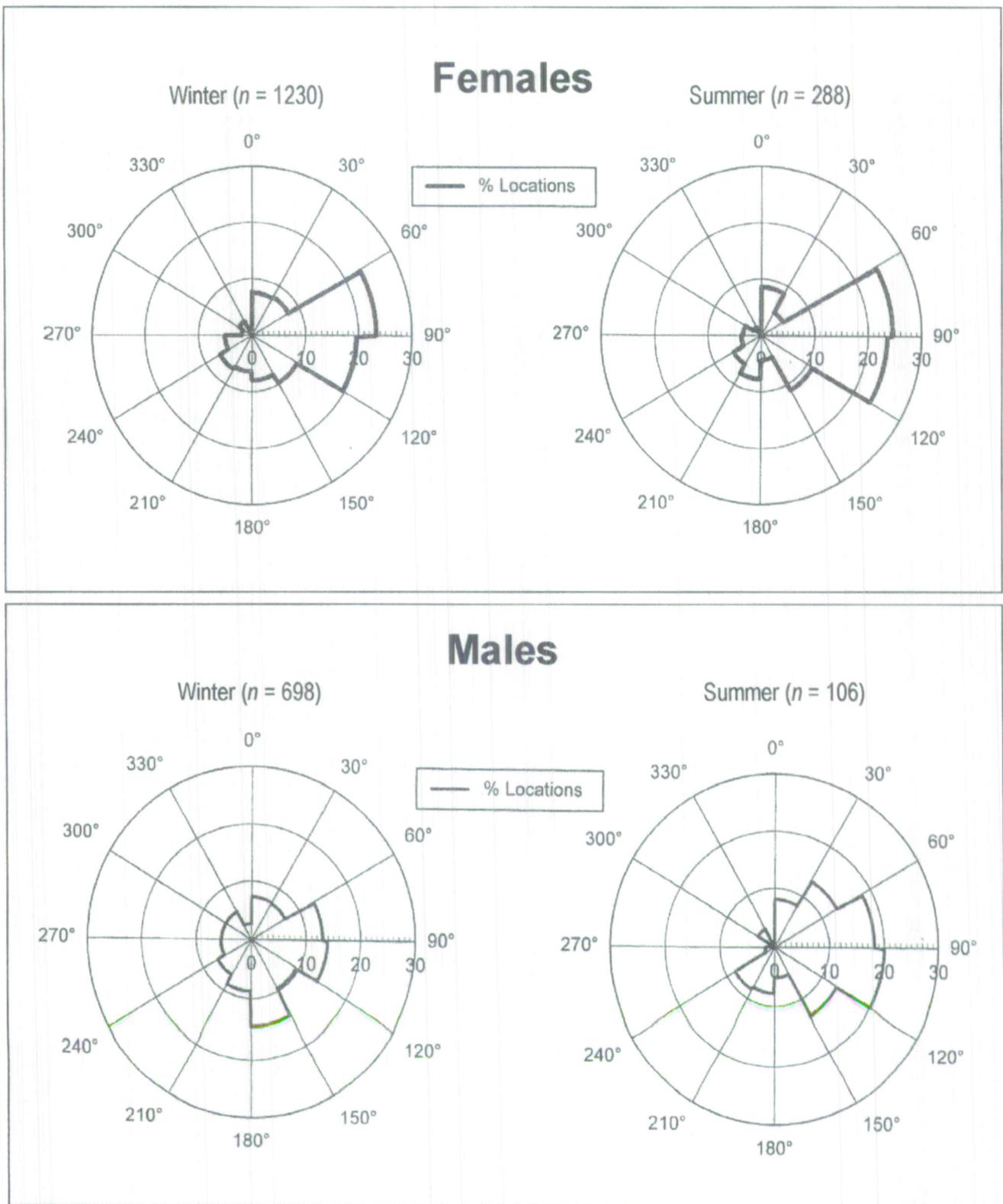


Fig. 1. Circular distributions of aspect measures associated with male and female bobcat locations in northcentral Pennsylvania during 1986–93.

patches gradually decreased as habitat suitability increased. Percent composition of broadleaf deciduous forest in suitable patches remained relatively constant and high in the most suitable habitats. Areas classified as unsuitable ($P < 0.10$) contained a mix of cover types including several types avoided by bobcats as indicated by univariate measures of cover type selection (e.g., unvegetated and herbaceous areas).

As habitat suitability increased, aspect associations within patches classified as suitable habitat approached the average measures for both males and females, as determined from univariate tests of aspect measures. The measure of circular uniformity of aspect measures (r) decreased at a constant rate as suitability ranged from 0 to 1.0 and became very directional at high suitability scores. Average slopes in high suitability areas approached mean values associated with bobcat locations.

Mahalanobis distance-based habitat suitability models identified 49% of forested areas as suitable for both male and female bobcats; 40% of these areas were

composed of broadleaf deciduous forest. However, not all stands of broadleaf deciduous forest were identified as suitable. Nineteen percent of broadleaf deciduous forest was classified as unsuitable for males and females due to unfavorable slope and aspect conditions. Male habitat suitability models identified an additional 10% of broadleaf deciduous forest type and 3% of mixed forest type that were not suitable for females. Conversely, only a very small proportion (0.2%) was identified as suitable for females but not for males.

Logistic Regression Model (Complete Randomization).—Evaluation of univariate logistic regression models resulted in the elimination of 3 variables for males (coniferous forest, transitional areas, and Aspect[IV]). Broadleaf deciduous forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates. All other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model resulted in the elimination of mixed forest and annual herbaceous types. Broadleaf deciduous forest, slope, and

Table 1. Cover type selection by bobcats based on radiolocations in northcentral Pennsylvania during 1986–93.

Cover type	Prop. of study area	Summer				Winter			
		n	P_i	95% CI (P_i)	Preference	n	P_i	95% CI (P_i)	Preference
Females									
Conifer forest	0.015	9	0.031	(0.003–0.058)	-	17	0.014	(0.005–0.023)	-
Mixed forest	0.159	32	0.111	(0.061–0.161)	-	176	0.143	(0.116–0.170)	-
Broadleaf forest	0.698	226	0.785	(0.720–0.850)	Selected	940	0.764	(0.732–0.797)	Selected
Transitional vegetation	0.045	19	0.066	(0.027–0.105)	-	62	0.050	(0.034–0.067)	-
Perennial herbaceous	0.031	1	0.003	(0.000–0.013)	Avoided	15	0.012	(0.004–0.021)	Avoided
Annual herbaceous	0.027	1	0.003	(0.000–0.013)	Avoided	16	0.013	(0.004–0.022)	Avoided
Unvegetated	0.022	0	-	-	Avoided	4	0.003	(0.000–0.008)	Avoided
Males									
Conifer forest	0.015	0	-	-	Avoided	7	0.010	(0.000–0.020)	-
Mixed forest	0.159	12	0.113	(0.030–0.196)	-	84	0.122	(0.089–0.156)	Avoided
Broadleaf forest	0.698	89	0.840	(0.744–0.935)	Selected	548	0.797	(0.755–0.837)	Selected
Transitional vegetation	0.045	3	0.028	(0.000–0.072)	-	28	0.041	(0.020–0.061)	-
Perennial herbaceous	0.031	1	0.009	(0.000–0.035)	-	6	0.009	(0.000–0.018)	Avoided
Annual herbaceous	0.027	0	-	-	Avoided	12	0.017	(0.004–0.031)	-
Unvegetated	0.022	1	0.009	(0.000–0.035)	-	3	0.004	(0.000–0.011)	Avoided

Table 2. Home range sizes (km^2) of bobcats in northcentral Pennsylvania during 1986–93 using adaptive kernel, harmonic mean, and minimum convex polygon (MCP) methods. Only home ranges based on >20 radiolocations were used for analysis.

Method	Males ($n = 17$)				Females ($n = 17$)			
	Norm. ^a R (P)	Med.	Range	Q1 - Q3	Norm. ^a R (P)	Med.	Range	Q1 - Q3
Adaptive kernel	0.78 (<0.01)	114.5	14.3–1,048.0	25.3–229.5	0.78 (<0.01)	23.5	3.3–442.3	15.6–71.8
Harmonic mean	0.72 (<0.01)	44.4	7.7–625.1	13.1–86.1	0.85 (<0.01)	16.1	2.2–179.2	11.0–52.2
MCP	0.82 (<0.01)	42.2	7.2–430.6	15.7–102.6	0.81 (<0.01)	17.2	2.8–169.8	10.3–35.8

^aShapiro and Wilk test for normality. Small P -values indicate a non-normal distribution.

Aspect(I) had positive parameter estimates, suggesting favorable contributions to habitat suitability. Unvegetated areas, perennial herbaceous areas, and Aspect(III) had negative parameter estimates with unvegetated areas providing the greatest influence (Table 3).

Evaluation of univariate logistic regression models for females resulted in the elimination of transitional areas. Broadleaf deciduous forest, slope, and Aspect(I) had significant positive parameter estimates; all other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model led to the elimination of Aspect(IV). All forest types (conifer, mixed, and broadleaf deciduous), slope, and Aspect(I) had positive parameter estimates suggesting favorable contribution to bobcat presence. Herbaceous areas, unvegetated areas, Aspect(II), and Aspect(III) had negative parameter estimates (Table 3).

Logistic Regression Model (Conditional Randomization).—Evaluation of univariate logistic regression models resulted in the elimination of 3 variables for males (coniferous forest, transitional areas, and Aspect(III)). Broadleaf deciduous forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates. All other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model led to the elimination of mixed forest. Broadleaf forest, slope, and Aspect(I) retained positive parameter estimates suggesting favorable conditions for bobcat presence.

Unvegetated areas, herbaceous areas, and Aspect(III) had negative parameter estimates with unvegetated areas providing the greatest influence (Table 3).

Evaluation of univariate logistic regression models suggested the elimination of 3 variables for females (transitional areas, slope, and Aspect(IV)). Broadleaf forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates; all other parameter estimates were negative. A multiple logistic regression model was developed from the remaining variables. Evaluation of parameter estimates in the multiple logistic model resulted in the elimination of Aspect(II). All other variables were retained in the final model. All forest types (coniferous, mixed, and broadleaf deciduous) and Aspect(I) had positive parameter estimates suggesting a favorable effect on habitat suitability. All herbaceous areas, unvegetated areas, and Aspect(III) had negative parameter estimates (Table 3).

Logistic regression models developed using conditional randomization identified 46% of the region as suitable for males and 25% as suitable for females. Fifty-one percent of the region was classified as unsuitable for either male or female bobcats. The majority of areas classified as unsuitable consisted of the broadleaf deciduous cover type. All herbaceous and unvegetated areas were classified as unsuitable habitat for both males and females.

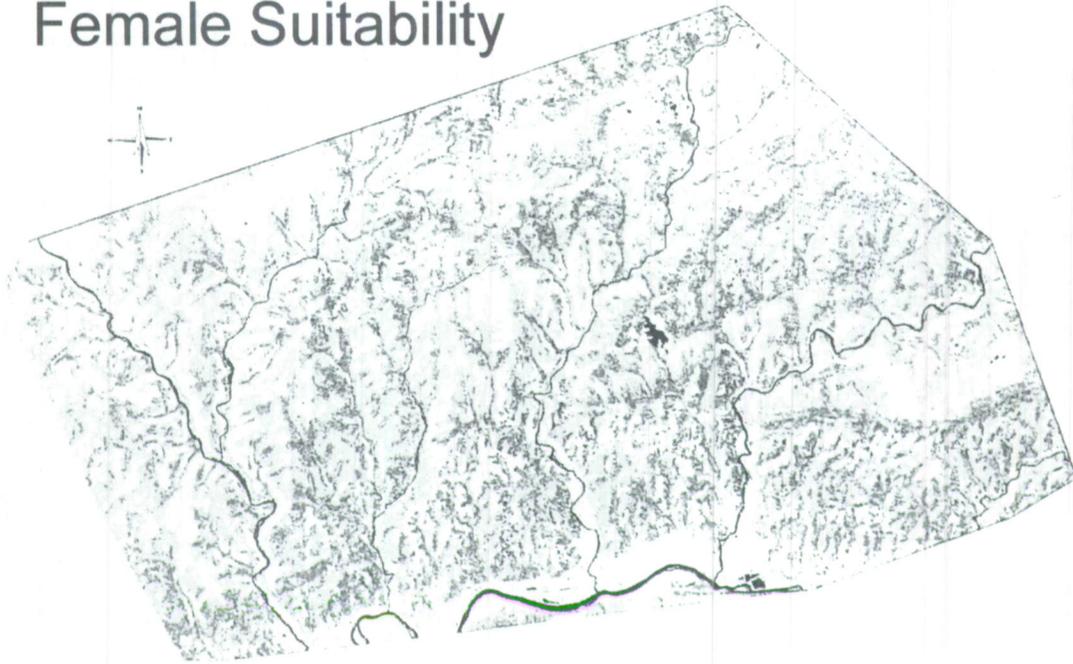
Ninety-seven percent of all areas classified as

Table 3. Parameter estimates and significance tests from multiple logistic regression models of bobcat habitat suitability in northcentral Pennsylvania based on used versus random points. Random points were selected using complete and conditional approaches.^a

Variable	Males				Females				
	Parameter estimate	SE	Wald X^2	P	Variable	Parameter estimate	SE	Wald X^2	P
Complete randomization									
Broadleaf forest	0.3874	0.101	14.629	0.000	Mixed forest	0.2251	0.155	2.1139	0.146
Perennial herb.	-0.9876	0.404	5.983	0.014	Broadleaf forest	0.2149	0.131	2.7083	0.100
Unvegetated	-1.1875	0.524	5.137	0.023	Perennial herb.	-0.1085	0.303	11.0870	0.000
Slope	0.0300	0.005	27.714	0.000	Annual herb.	-0.5842	0.302	3.7414	0.053
Aspect I	0.1309	0.112	1.357	0.244	Unvegetated	-2.0921	0.534	15.3564	0.000
Aspect II	-0.2838	0.118	5.766	0.016	Slope	0.0156	0.005	9.0224	0.003
Aspect III	0.5508	0.135	16.707	0.000	Aspect I	0.8411	0.096	77.0540	0.000
					Aspect II	-0.1813	0.104	3.0131	0.083
					Aspect III	-0.6055	0.120	25.4900	0.000
Conditional randomization									
INTERCEPT	-0.3209	0.226	2.010	0.156	INTERCEPT	-0.4713	0.204	5.3658	0.021
Broadleaf forest	0.5693	0.214	7.063	0.008	Conifer forest	1.4462	0.400	13.0827	0.000
Perennial herb.	-1.8645	0.455	16.803	0.000	Mixed forest	0.8025	0.212	14.3979	0.000
Annual herb.	-1.2450	0.387	10.328	0.001	Broadleaf forest	0.6809	0.183	13.8810	0.000
Unvegetated	-2.4040	0.563	18.251	0.000	Perennial herb.	-1.1137	0.343	10.5328	0.001
Slope	0.0090	0.007	1.703	0.192	Annual herb.	-0.9542	0.340	7.8981	0.005
Aspect I	0.5210	0.143	13.214	0.000	Unvegetated	-2.8180	0.552	26.0841	0.000
Aspect III	-0.7790	0.156	24.800	0.000	Aspect I	1.1860	0.127	86.6519	0.000
Aspect IV	0.2175	0.160	1.850	0.174	Aspect III	-1.1929	0.137	75.8411	0.000

^aRandom points were selected in areas classified as unsuitable based on spectral Mahalanobis distance models.

Female Suitability



Male Suitability

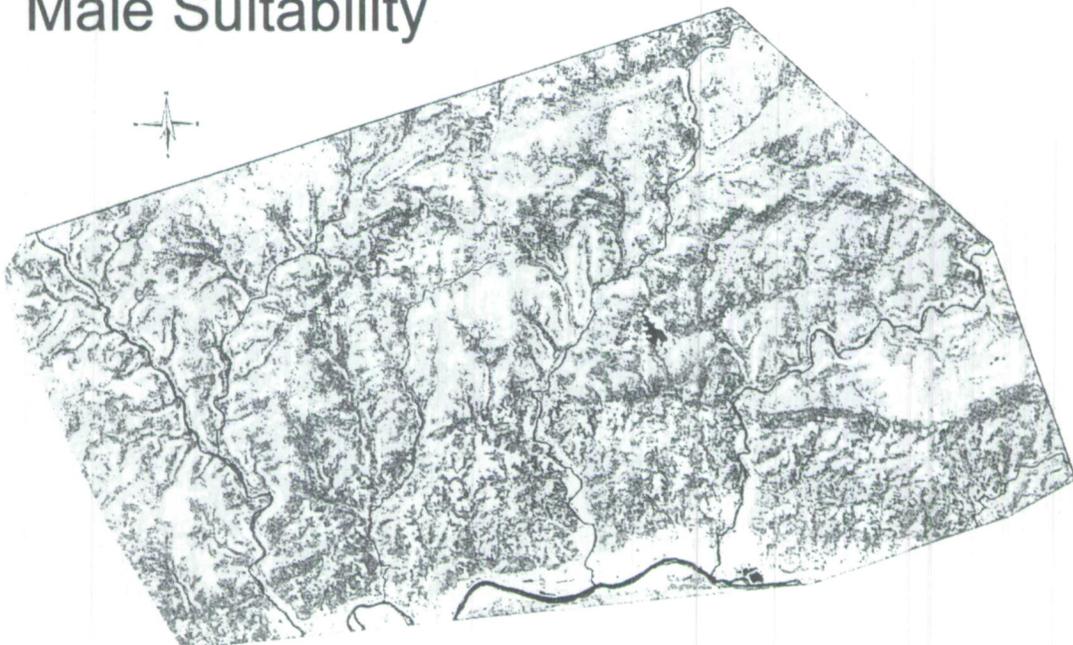


Fig. 2. Bobcat habitat suitability for males and females within Study Area 1 as predicted by Mahalanobis distance-based models using standardized spectral reflectance, aspect, and slope. All areas with $P > 0.10$ (light gray) were considered suitable habitat, whereas areas with $P > 0.50$ (dark) were considered highly suitable.

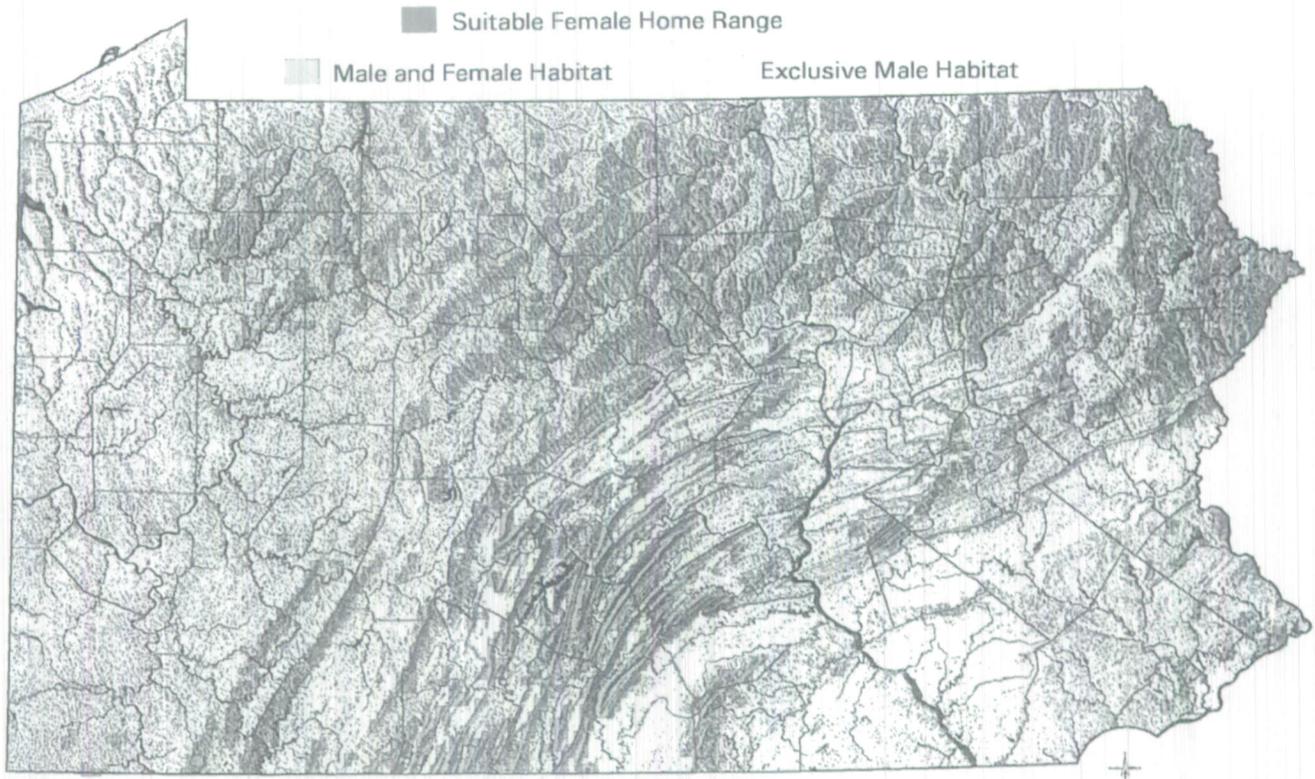


Fig. 3. Statewide distribution of suitable male and female bobcat habitat and potential female home ranges, as predicted from logistic regression models based on cover type, slope, and aspect.

suitable for females were also classified as suitable for males; whereas, 23% of the region was classified as suitable for males but not for females. The majority of areas classified as suitable for males but not for females consisted of broadleaf deciduous habitats. Small amounts (0.6–1.6% of the region) of exclusive female habitats were identified in mixed and coniferous forest and transitional cover types.

Home Range Size Versus Habitat Predictions

We detected significant relationships between bobcat home range size and the amount of suitable habitat within home ranges as predicted by Mahalanobis distance models. Bobcat home range size was negatively correlated ($r = -0.39$, $P = 0.057$) with percent composition of areas classified as suitable. This inverse relationship became increasingly significant as the home range composition of higher suitability levels was examined. For example, the relationship between home range size and percent composition of areas with $P \geq 0.20$ was $r = -0.44$ ($P = 0.031$), and the relationship for $P \geq 0.50$ was $r = -0.48$ ($P = 0.019$).

We observed similar relationships between home range size and the amount of suitable habitat as predicted by logistic regression models using conditional randomization. Home range size was inversely correlated to the amount of habitat classified as $P \geq 0.60$, particularly for females ($r = -0.67$, $P = 0.004$). Suitable habitat of $P > 0.60$ ranged from 17.9–46.4% within female home ranges. Home range size of females with <25% composition of

suitable habitat were large and variable (e.g., 3 F with <25% composition of suitable habitat occupied home ranges >120 km²). As was the case with Mahalanobis distance-based models, inverse relationships between home range size and habitat predictions became increasingly significant as the home range composition of higher suitability levels was examined.

Validating Habitat Models

Cross-validation (Study Area-specific).—Within Study Area 1, jackknife cross-validation techniques reclassified 85.7% of male bobcat locations as occurring in areas classified as suitable habitat by Mahalanobis distance models. Similarly, 86.4% of female locations were located in areas classified as suitable habitat. Disproportionately more locations were in areas of relatively high suitability ($P > 0.50$) than expected based on percent composition of Study Area 1. For example, 82% of male locations were reclassified as occurring in areas with $P \geq 0.50$, whereas only 24.6% of Study Area 1 was classified as $P \geq 0.50$. Similarly, 57% of female locations were classified as occurring in suitable areas whereas these areas only composed 14.9% of Study Area 1.

Jackknife cross-validation of logistic regression models using the complete randomization scheme indicated a classification success rate of 58% for males and 65% for females. This low classification success was largely due to a large false negative classification error (i.e., classifying bobcat locations as unsuitable). Use of conditional random points in the logistic regression

models improved overall classification rates by 6.3% for males and by 3.1% for females (68.1% correct for F and 64.3% correct for M). Use of conditional randomization reduced false negative classification rates by 33% for males and 27% for females.

Regional Validation.—Eighty-eight percent of female locations were classified as suitable habitat by Mahalanobis distance-based models, whereas only 72% of male locations were classified as suitable. Approximately 10% fewer male and female radiolocations were distributed in broadleaf deciduous forest in Study Area 2 than in Study Area 1. Also, female bobcats were more often located in mixed and coniferous forest and males spent more time in transitional habitats in the validation sites than in the initial study area. Seventy-eight percent of female locations occurred in areas predicted to be suitable habitat by logistic regression models (conditional randomization), whereas, 71% of male locations were classified successfully.

Statewide Model Application

Application of logistic regression models (conditional randomization) on a cell-by-cell basis resulted in classification of 56,875 km² (48.5%) of Pennsylvania as unsuitable habitat for either male or female bobcats. An area of 18,564 km² (15.8%) was classified as suitable for both male and female bobcats, whereas 39,067 km² (33.3%) was suitable for males but not for females. As we observed in Study Area 1, regardless of modeling approach, female habitat was a subset of a broader spectrum of male habitat; only 2,791 km² (2.4%) of exclusive female habitat was identified by logistic regression models. Most suitable habitat was distributed throughout northcentral, northeast, and southcentral Pennsylvania (Fig. 3).

We used percent composition of suitable habitat ($P \geq 0.60$) as a measure to evaluate the potential of simulated ranges to support female bobcats. We selected a critical value of 25% home range composition in suitable habitat as a cut-off value in evaluating home range potential. These criteria were based on relationships between home range size and habitat composition observed on Study Area 1. We estimated the percent composition of suitable habitat within 18,770 simulated female home ranges throughout Pennsylvania. Statewide, 4,222 (22.5%) of simulated home ranges contained >25% suitable habitat.

Statewide Model Validation

We received 128 responses from the WCOs surveyed. Twenty-one (minus non-respondents) reported bobcats were not present in their district. Forty-three percent ($n = 47$) of respondents reported that they occasionally sighted bobcats in their district, but that established populations were not present (Fig. 4). Fifty-six percent ($n = 60$) of respondents reported having established bobcat populations in their districts. Average percent composition of male and female habitat was higher in districts reporting established populations ($\bar{x} = 38.2\%$ and 20.5% for M and F habitat, respectively) than in those reporting occasional

sightings ($\bar{x} = 30.0\%$ and 16.0% for M and F habitat, respectively). Similarly, average percent of simulated home ranges within each district that contained suitable amounts of habitat was greater in districts reporting established populations ($\bar{x} = 31.1$) than in those reporting occasional sightings ($\bar{x} = 14.7$; $t = -4.93$, $P \leq 0.001$).

The percent area of each district believed to support bobcat populations was reported as 1–10% ($n = 7$), 11–25% ($n = 15$), 26–50% ($n = 11$), 50–75% ($n = 19$), and >75% ($n = 8$). Districts described as containing >75% suitable habitat were located in northcentral and northeastern Pennsylvania. We compared the percent composition of male and female habitat within WCO districts to serve as a subjective, statewide validation of the modeling effort. The categorical estimate of percent of each district supporting bobcats was positively correlated to the percent composition of male ($r = 0.68$, $P < 0.001$) and female ($r = 0.52$, $P < 0.001$) habitat as estimated by statewide application of logistic habitat models. Estimates of percent habitat in WCO districts were generally lower than the percent area predicted as suitable by the logistic regression models. Percent of each district supporting bobcats was also positively correlated to the percent of simulated female home ranges which contained >25% suitable habitat ($r = 0.46$, $P < 0.001$).

Six-hundred thirty-nine bobcat mortalities (92% from roadkills) were recorded from 1986–99 in 44 of 67 Pennsylvania counties (Fig. 5). The majority of mortalities were reported in counties throughout the northcentral, northeastern, and southcentral regions, which matched the habitat model well (Fig. 3). Mortalities were also occasionally reported in several southeast and southwest counties.

DISCUSSION

Bobcat Home Range Size and Habitat Selection

Bobcats in northcentral Pennsylvania exhibited strong slope and aspect associations. We suspect these associations related to differences in understory structure and prey availability, as reported by Litvaitis et al. (1986) in Maine. Male and female bobcats in northcentral Pennsylvania selected broadleaf deciduous forest during summer and winter. Females avoided herbaceous and unvegetated areas during summer and winter. However, males avoided herbaceous areas during summer and mixed forest, unvegetated areas, and perennial herbaceous types during winter.

Home range size of male bobcats in Pennsylvania averaged 82 km² (median = 42 km²). This estimate was highly variable, but was comparable to estimates from other northeastern states. Fox (1982) reported average male home ranges of 36–326 km² in New York State, and estimates of male bobcat home range size in Maine ranged from 71–112 km² (Litvaitis et al. 1986). Similarly, estimates of female home range size in Pennsylvania were comparable to estimates of 28–33 km² in Maine (Major 1983).

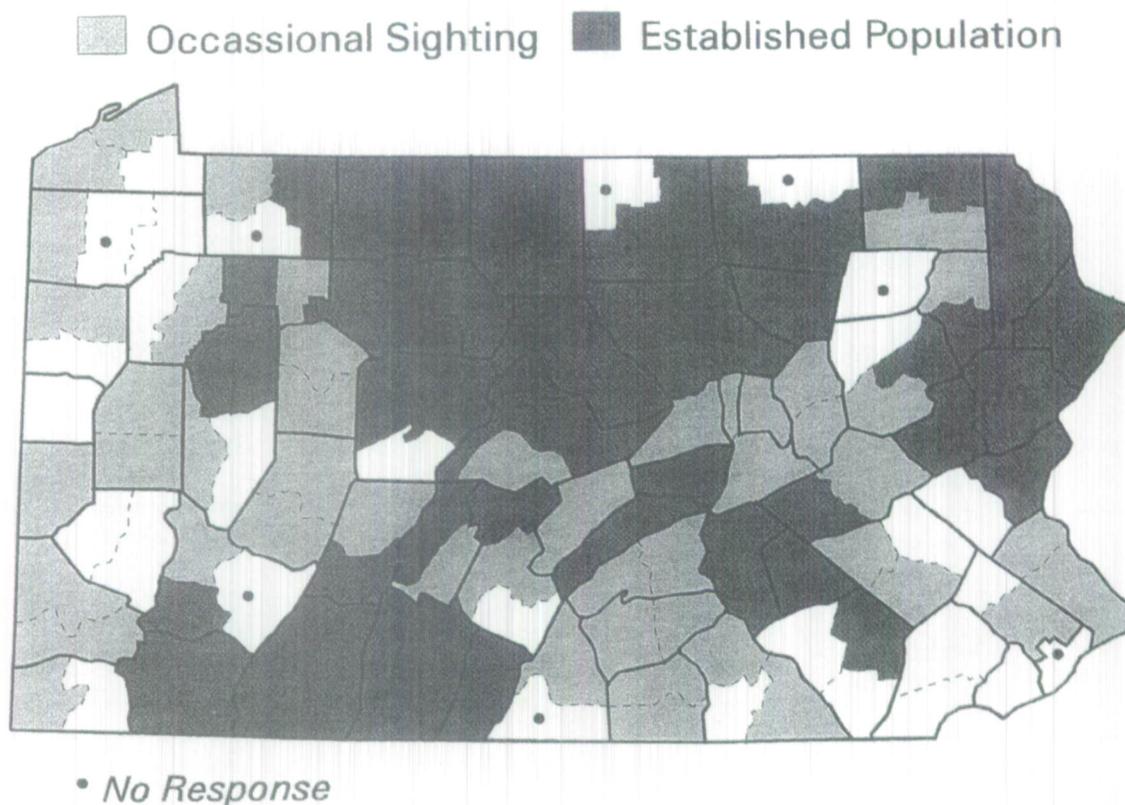


Fig. 4. Distribution of established bobcat populations and of occasional sightings throughout Pennsylvania as reported by Wildlife Conservation Officers during 1994.

Other studies of bobcat behavior have demonstrated intersexual differences in activity, prey use, and habitat selection (Heller and Fendley 1982, Litvaitis et al. 1984, Rolley and Warde 1985, Litvaitis et al. 1986, Lovallo and Anderson 1995). Intersexual differences in habitat selection and home range size that we observed were likely attributed to sex-related size dimorphism exhibited by bobcats throughout the northeast (Gittleman 1989). Although we detected seasonal effects on habitat selection, we chose not to develop season-specific habitat models because we were interested in developing models that predicted habitat suitability on an annual basis and because sample size was limited during summer periods. Significant intersexual differences in cover type use and the association of physiographic characteristics warranted the development and application of sex-specific habitat models.

Mahalanobis Distance Models

Models based on direct spectral band intensity, slope, and aspect produced a map depicting various levels of habitat suitability scaled from 0.0 (unsuitable) to 1.0 (suitable). Although suitability scores were based on *P*-values, these values were only interpreted as a relative scaling, rather than a probability that bobcats would be present, survive, or reproduce in a particular geographic cell (Knick and Dyer 1997). By directly modeling from spectral reflectance, we made no *a priori* assumptions of

habitat or cover type suitability and thereby avoided errors inherent to classification of remotely sensed data. Reflectance data provided spatial information on occurrence and gradients of a variety of vegetative conditions (e.g., stand structure, density of understory vegetation, soil moisture) that may potentially influence habitat selection, but are difficult to represent in a traditional cover-type or habitat mapping approach. Others have detected significant relationships among various forest structure elements and direct spectral band intensity such as the leaf area index, tree density, diameter at breast height, and tree age (Peterson et al. 1986, Running et al. 1986).

Mahalanobis distance-based models successfully predicted the spatial occurrence of bobcats in Study Area 1 and in independent validation sites. Cover type composition and physiographic characteristics associated with areas predicted as suitable habitat by Mahalanobis distance-based models were consistent with patterns of habitat selection estimated from univariate analyses. These results support the use of Mahalanobis distance and direct spectral reflectance as a method to extrapolate multivariate patterns of habitat selection within the geographic extent of model construction.

Logistic Regression Models

Parameter estimates for multiple logistic regression models developed using random points were similar to

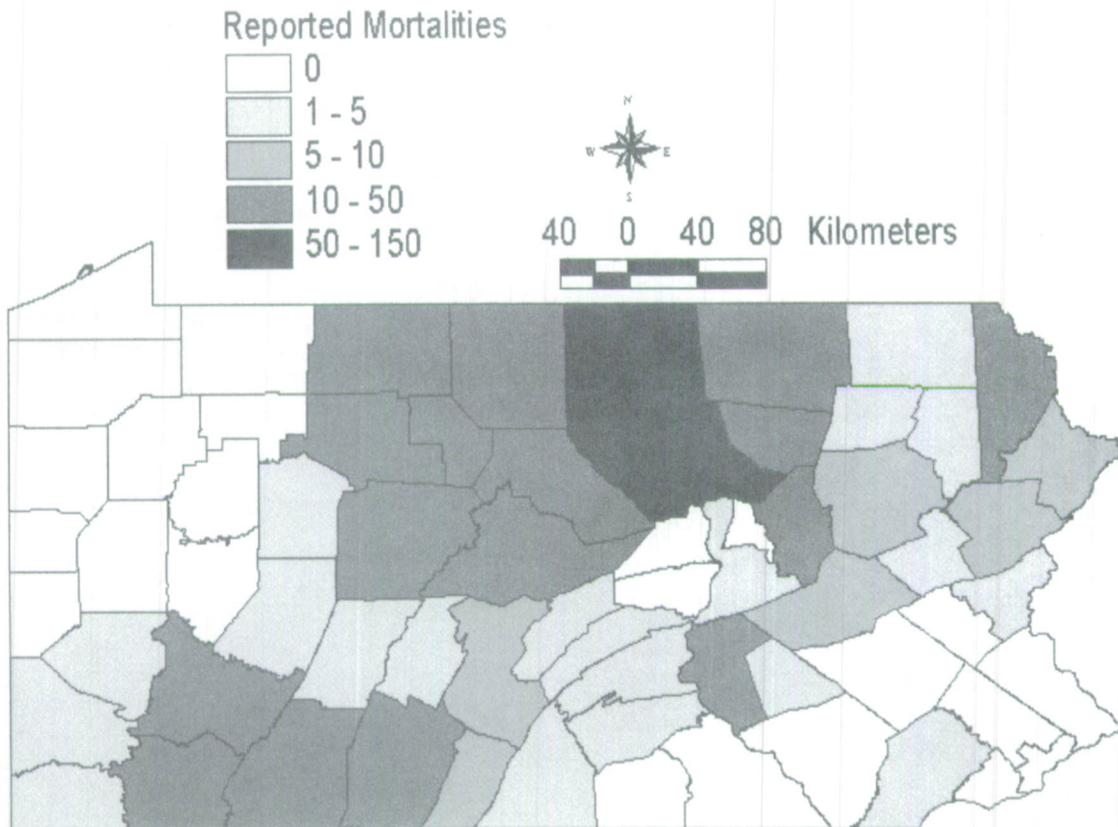


Fig. 5. Spatial distribution of bobcat mortalities ($n = 369$) reported by Pennsylvania counties during 1986–99.

those estimated using the conditional random approach. For example, models from both approaches included negative parameter estimates for herbaceous and unvegetated areas for males and females. Broadleaf deciduous forest had a strong positive influence on male bobcat presence for both approaches as did broadleaf deciduous forest and mixed forest for females. A notable difference was that multiple logistic regression models developed from conditional randomization for females included conifer forest and did not include slope as a significant effect. By using only random points that occurred in areas predicted as unsuitable by the Mahalanobis models, we improved overall classification success of the model by 6% for males and 3% for females.

We observed an inverse correlation between home range size and percent composition of areas classified as suitable habitat; this relationship was particularly strong for females. This relationship became increasingly significant as suitability scores increased suggesting that associated P -values reflected gradients in habitat suitability that were linked to the ability of individuals to acquire resources within home ranges.

Selecting an Approach for Statewide Model Extrapolation

The ability of Mahalanobis distance-based models and logistic regression models to predict the spatial occurrence of female bobcats was greater within the validation site than that estimated by cross-validation

within the geographic extent of model construction. The ability of Mahalanobis distance-based models to predict the spatial occurrence of male bobcats was greater in Study Area 1 and decreased by 13% when applied to Study Area 2. Predictive success of logistic regression models for males was 7% greater in Study Area 2 than that estimated by cross-validation in Study Area 1. It is unknown whether these differences were due to differences in cover type availability between areas, individual variation in habitat selection, or within-scene variance of spectral reflectance in the case of Mahalanobis distance models. No study area boundaries were delineated in the validation site that could be used to determine cover type availability because bobcats were dispersed across an extensive area.

Within Study Area 1, classification rates for Mahalanobis distance-based models were greater than those of logistic regression models by $\leq 18\%$ for females and 21% for males. Similarly, spectral-based models successfully predicted the spatial occurrence of bobcats in the validation site at a greater rate than did logistic regression models. Although spectral-based models had greater predictive success, anticipated spectral variance among Thematic Mapper scenes and differences in scene dates precluded extrapolation of models based on spectral reflectance to other regions of Pennsylvania. The use of conditional randomization in the logistic regression models provided a method to incorporate the predictive success of Mahalanobis models into a statewide effort to

model the extent and distribution of suitable bobcat habitat.

Model predictions of the statewide distribution of potential female home ranges was geographically consistent with previous reports of established bobcat populations in Pennsylvania (Giles 1986, Merritt 1987). This result suggested that amount and pattern of suitable female habitat, as predicted by multivariate models of habitat selection, may directly relate to potential statewide bobcat distribution. Our method to delineate potential female home ranges was based on percent habitat composition of the home range (e.g., >25%). These results are conservative because female bobcats likely occupy larger home ranges with smaller proportions of suitable habitat beyond the geographic extent identified in these analyses.

Statewide Model Validation

Our results indicated a positive statewide validation of habitat models. Wildlife Conservation Officers consistently overestimated the area capable of supporting bobcats in their districts as predicted by habitat selection models. This result was not surprising because habitat models were developed to identify selected habitat components and these components only comprised a portion (e.g., 18–45%) of a bobcat's home range. It is likely that WCOs considered all areas a bobcat might be encountered (e.g., home range) while subjectively estimating the proportion of their district capable of supporting bobcats. We observed general spatial correspondence between the statewide distribution of suitable female home ranges and WCO reports of established populations, sightings, and incidental captures by trappers. Similarly, statewide data on the location of reported bobcat mortalities provided general correspondence with the WCO survey results and statewide habitat modeling results.

CONCLUSIONS

The statewide application of multivariate habitat selection models for bobcats in Pennsylvania provides an information source for habitat-based management decisions and serves as a basis to develop hypotheses concerning local- and landscape-level habitat associations. Further regional validation should be conducted to better understand geographic variability in bobcat-habitat relationships and to improve predictive success of habitat suitability models.

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IMPACTS OF REESTABLISHED FISHERS ON BOBCAT POPULATIONS IN WISCONSIN

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Abstract: Bobcats (*Lynx rufus*) and fishers (*Martes pennanti*) are allopatric over much of their geographic ranges, but converge in the upper Great Lakes region. We examined evidence for consumptive, territorial, and encounter competition between bobcats and fishers in northern Wisconsin during 1991–95. Such evidence included use of shared resources, spatial interaction, and impacts on 7 bobcat population parameters. Bobcats did not change their diets in the presence of fishers, but fisher diets contained a greater proportion of small mammalian prey and less deer when bobcats were relatively common, suggesting bobcat interference with deer consumption by fishers. Bobcats and fishers did not avoid each other as indicated by overlapping home ranges and by simultaneous paired locations of individual bobcats and fishers when home ranges did overlap. Thus, there was no evidence of territorial competition between these species. Impacts of interference competition were not detected in measured demographic parameters. Encounter competition or predation was inferred from the increase in bobcat kitten mortality and reduction in bobcat population growth. Competition between bobcats and fishers was weak and should result in equilibrium as predicted.

Key words: bobcat, competition, fisher, interspecific interactions, *Lynx rufus*, *Martes pennanti*, sympatric carnivores, Wisconsin.

Bobcats (*Lynx rufus*) and fishers (*Martes pennanti*) are now, and historically have been, allopatric over much of their geographic ranges. Bobcats reach their northern limit in southern Canada (McCord and Cardoza 1982), whereas fishers rarely extend into the U.S. (Strickland et al. 1982). Sympatry occurs in New England, the northern Rockies, and the Great Lakes states. Wisconsin is one of the few areas in North America where bobcats and fishers coexist and offers a unique opportunity to study their interrelationships.

Bobcats were present in Wisconsin prior to European settlement. Habitat changes that took place in the early part of the 20th century benefitted bobcats; older forests were cut and younger forests, with their associated fauna (e.g., snowshoe hares [*Lepus americanus*] and white-tailed deer [*Odocoileus virginianus*]), provided increased food. Bobcats are currently resident in northern Wisconsin and the population supports annual harvests of up to 250 animals (Dhuey 1995).

Fishers were also present in all forested regions of Wisconsin prior to European settlement (Jackson 1961, Pils 1983). Fishers were extirpated in the 1920s due to over-harvest and habitat alteration, which concurrently benefitted bobcats (Powell 1982, Pils 1983). In the 1950s and 1960s fishers were reintroduced to the Nicolet and Chequamegon National Forests (Pils 1983), and protected refuges were established around release sites. Fishers did well following release (Kohn and Creed 1983), and their populations continued to grow and increase in distribution. Wisconsin fisher populations now sustain annual harvests of approximately 1,500 animals (Dhuey 1995).

The evaluation of the fisher restoration effort on Wisconsin's bobcat populations is of interest from a conservation perspective. Success of a restoration effort

can be questioned if the reintroduced species has a negative effect on a resident species, especially if that resident species is already rare or at low densities. Bobcats and fishers occur at relatively low densities (0.1 individuals/km² for bobcats and 0.5 individuals/km² for fishers) and are at the edge of their continental range in Wisconsin. Species at range margins are likely to experience different influences of natural selection than those at the center of their range (Lesica and Allendorf 1995) due to exposure to conditions not experienced by species near range cores. These influences may assist us in understanding the role that competition plays in determining species' range limits. The interaction of fishers and bobcats in northern Wisconsin potentially represented one such case.

There was some indirect evidence that fishers were adversely impacting Wisconsin bobcat populations as early as 1975. The average annual harvest of bobcats from northern Wisconsin declined from 43 bobcats/county in 1963 to 13 bobcats/county in 1976 (Creed and Ashbrenner 1976). Klepinger et al. (1979) attributed these early declines in harvest to a reduction in the bobcat population and not to declines in other factors which may influence harvests (e.g., reduced trapper effort). The average bobcat harvest per county declined further to 10.8 in 1991 (Dhuey 1992). Further, the ratios of kittens to adult females and juveniles to adult females in the bobcat harvest sample were lower in counties with fishers classified as common than in counties with fishers classified as uncommon (W.A. Creed, Wisconsin Department of Natural Resources, personal communication). No differences were detected in average litter sizes between bobcats harvested from these 2 groups of counties, and Creed suggested that the observed differences in ratios

were due to fisher predation on the bobcat kitten and juvenile age classes. Our objectives were to (1) document food habits for bobcats and fishers to determine the extent of shared use of food resources, (2) determine whether sympatric bobcats and fisher home ranges overlap, and (3) examine 7 bobcat demographic parameters in relation to fisher abundance for evidence of competition.

STUDY AREA

The study took place in the northern forest region of Wisconsin (Curtis 1959) (Fig. 1). Animals were captured and radiocollared on 3 primary study areas: the Chequamegon National Forest (CNF), Nicolet National Forest (NNF), and St. Croix National Riverway (SCNR). There is little topographic relief in northern Wisconsin with a maximum elevational change of only 400 m. The region is underlaid with pre-Cambrian bedrock over which glacial drift has been deposited. The soils are largely podzols, but vary from thin rocky soils to deep loams and clays (Curtis 1959). The climate is variable with cold, snowy winters. Mean January temperature is -11°C and mean July temperature is 18°C . Average annual precipitation is 74 cm of water-equivalents. Average snowfall is 125 cm.

Curtis (1959) described the northern forests as containing a wide variety of vegetational types. The forests are typically characterized by the presence of conifers, but a large hardwood component is also present. The lowland forests contain either conifer swamps with

black spruce (*Picea mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) as the most common species; or hardwood swamps dominated by black ash (*Fraxinus nigra*) or yellow birch (*Betula lutea*). The uplands support jack pine (*Pinus banksiana*) or red pine (*P. resinosa*) on the lighter sandy soils, or white pine (*P. strobus*) on the sandy loams. Conifer-hardwood mixed forests with white pine, eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saacharium*), basswood (*Tilia americana*) and yellow birch occupy the richer soils.

METHODS

Connell (1983) described field experiments to measure interspecific competition in which the abundance of one species is changed and the response of the other species is documented. The response measured is usually (1) a change in density, (2) a change in a parameter which could affect density (e.g., fecundity, survival, body fat content), or (3) a change in resource used or in occupied habitat. Under hypotheses of consumptive, encounter (i.e., predation), and territorial competition, we made a number of predictions (Table 1) about the relationship of fisher density to 7 bobcat population parameters. Each hypothesis of competition had an associated series of assumptions and predictions related to the parameters. We evaluated the pattern of responses of bobcat population demography to fisher abundance based on the predictions (Table 1) and used these results to infer competition and to distinguish among the types of competition when possible. For example, consumptive and territorial competition were distinguished by the segregation of home ranges or the avoidance between individuals within home ranges.

We partitioned study areas according to the relative abundance of fishers. Because fisher and bobcat carcasses obtained from hunters and trappers were the source of most population parameters, and the location of kill was recorded only by county, the county was the geographic area for assessing relative fisher abundance. Counties were classified as having either relatively common (C) or relatively scarce (S) fisher populations.

Relative Abundance

We used track counts in snow on 37 16-km transects (Wisconsin Department of Natural Resources, unpublished data) to estimate relative abundance of predator and prey species. Each transect was coded for the presence or absence of bobcats, fishers, and hares, and regression analysis was used to determine the probability of encountering bobcat tracks with fisher and/or hare tracks. Temporal differences in bobcat, fisher, and hare track observation rates during 1991–95 were explored using ANOVA. The relationship among the number of fisher tracks observed per transect, the distance the transect was from the nearest fisher release site, and the year of census was estimated using multiple linear regression.

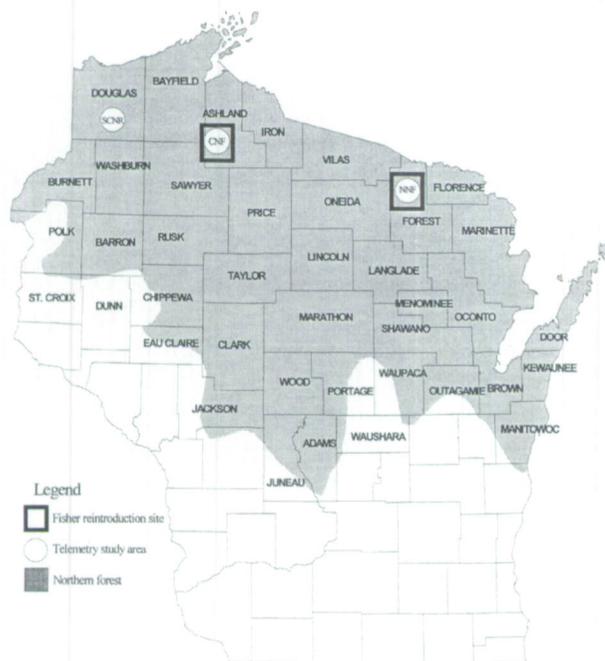


Fig. 1. Location of the northern forest region of Wisconsin (after Curtis 1959). Fisher reintroduction sites and radiotelemetry study areas are delineated (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway).

Table 1. Predictions of 7 population parameters which result from hypotheses of consumptive, territorial, or encounter competition.

Parameter	Consumptive competition	Territorial competition	Encounter competition
Kitten survival	Survival rates of bobcat kittens are lower where fishers are common than where scarce	Survival rates of kittens are lower where fishers are common than where scarce	Survival rates of kittens are lower where fishers are common than where scarce
Adult survival	Survival rates of adult bobcats are lower where fishers are common than where scarce	Survival rates of adults are lower where fishers are common than where scarce	Survival rates of adults are unrelated to fisher density
Fecundity	Bobcat reproductive rates are lower where fishers are common than where scarce	Bobcat reproductive rates are lower where fishers are common than where scarce	Bobcat reproductive rates are unrelated to fisher density
Body condition	Bobcat condition indices are lower where fishers are common than where scarce	Bobcat condition indices are lower where fishers are common than where scarce	Bobcat condition indices are unrelated to fisher density
Population growth	As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density	As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density	As a consequence of reduced kitten survival, bobcat population growth will be inversely related to fisher density
Population density	As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density	As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density	As a consequence of reduced kitten survival, bobcat population growth will be inversely related to fisher density
Home range	Bobcat home ranges will be larger where fishers are common than where scarce	Home ranges of fishers and bobcats will be spatially separate or will avoid each other while within home ranges	Bobcat home ranges will be unrelated to fisher density

Relative abundance maps for bobcats and fishers were generated in ArcInfo (ESRI, Redlands, California, USA) using information from track counts and location-specific harvests. A discrete distribution of the numbers of tracks observed/transect was interpolated to a continuous distribution of tracks across the northern-forest study area using an inverse distance weighting function in ArcView Spatial Analyst (ESRI, Redlands, California, USA). A continuous distribution of harvests was created using a focal-mean smoothing technique on location-specific harvests. The relationship between county-level track counts and harvests was explored by correlation analysis. Track-count and harvest-distribution maps were merged to produce maps of relative abundance for fishers and bobcats. Weighted averages of relative abundance values were calculated for each of the 18 counties, and counties were classified as either above the mean abundance value (common) or below the mean abundance value (scarce).

Relative abundance of snowshoe hares was determined as was done for bobcats and fishers except that only track counts were used. Location-specific information on hare harvest was unavailable. Estimates of deer density were obtained for each deer management unit in

the study area (Vander Zouen and Warnke 1995). Relative abundance maps were created for deer using unit-specific density information.

Relationships among the relative density of fishers, bobcats, hares, and deer were examined. One thousand random points were placed on the maps of relative abundance. Of these, 740 were within the northern-forest study area and intersected the bobcat, fisher, hare, and deer maps. Relative abundance values were appended to each point for each species. Multiple linear regression ($P = 0.1$ to enter forward selection procedures) was then used to examine the relationships among bobcat, fisher, hare, and deer relative densities.

Track counts and trapping were used as indices of abundance on the 3 smaller study areas. Track counts were conducted at least twice monthly following the methodology described above except for snowshoe hares. Hare tracks were noted as present or absent in every 160-m block along each 16-km transect for a total of 100 blocks/transect. Track counts on each study area were summarized as the number of bobcat and fisher tracks observed/transect, and the percentage of 160-m blocks with hare tracks. Live-trapping rates (animals captured/1,000 trap-nights) were used to assign relative abundance

values for bobcats and fishers, and track counts were used to classify hare abundance for each study area.

Animal Capture and Radiotelemetry

Bobcats were captured with Number 3 Victor "soft-catch" foot-hold traps (Woodstream Co., Lititz, Pennsylvania, USA) and fishers were captured using Tomahawk box traps (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) with a single door opening 22 cm on a side. Bobcats and fishers were immobilized with ketamine HCl and xylazine (10:1 mixing ratio) at a dose of 10 mg/kg body weight. Animals were aged as kitten, juvenile, or adult based on size, cranial development (Strickland et al. 1982), and tooth eruption (Crowe 1975). All were weighed, measured, inspected for injuries or parasites, and uniquely tattooed inside an ear. Those individuals judged to be adults were radiocollared (Advanced Telemetry Systems, Isanti, Minnesota, USA).

Radiocollared bobcats and fishers were located ≤ 8 times weekly during winter (Nov–Mar), and less frequently during the rest of the year. Locations were estimated from 2–3 bearings using a computer program. Bearing error determined from 10 transmitters placed at known locations averaged 5.5° (SE = 0.1).

Home Range Analysis

Because competition for space and food should be most manifest when resources are in short supply, winter locations were used in home range analyses, and then only when separated by ≥ 6 hr to minimize autocorrelation of locations (Swihart and Slade 1985). Home ranges were delineated using the minimum-area method (MCP) (Hayne 1949) from animals with >30 locations during a single winter. We used *t*-tests ($\alpha = 0.05$) to test for differences in the sizes of home ranges between sexes, species, and study areas.

Area of home-range overlap was calculated for intersecting home-range pairs. For species pairs (bobcat-fisher) with intersecting home ranges, avoidance behavior was inferred from the distribution of distances between telemetry locations taken within 2 hr of each other as compared to distances between random points within the 2 home ranges. We constructed a frequency distribution of separation distances between bobcats and fishers. This observed distribution was compared with the distribution of random distances expected if the animals behaved independently using Chi-square.

Carcass Examination

Hunters and trappers were required to surrender carcasses of harvested fishers and bobcats. The carcasses were collected by WDNR for age determination and for counts of corpora lutea or placental scars. Subsequently, the carcasses were transported to the Great Lakes Indian Fish and Wildlife Commission laboratory to extract fat bodies and examine stomach contents.

Age and Fecundity.—Bobcat ages were determined from cementum annuli (Crowe 1972, Kelly 1977) and used to obtain age-specific fecundity rates, carcass conditions, and food habits. Individuals >1 year were

classified as kits, between 1–2 years as yearlings, and older animals as adults.

Litter size was estimated from counts of placental scars (Wright and Coulter 1967, Crowe 1975). Differences in bobcat pregnancy rates between areas where fishers were common vs. scarce were assessed using *t*-tests. Analysis of variance was used to examine differences in bobcat litter size due to age, year, and relative fisher abundance.

Condition Index.—An index to carcass condition was developed which used a kidney fat index (KFI) (Kirkpatrick 1980) in a non-linear model to predict lipid content of skinned carcasses (J. H. Gilbert, unpublished data). Once parameters were estimated in the model, it was run using the KFI inputs from the sample of bobcat carcasses. Analysis of variance was used on the resulting estimates of the proportion of body mass consisting of lipids to examine differences due to species, age, sex, year, and fisher abundance.

Food Habits.—Stomach contents from harvested bobcats and fishers were separated by food item and weighed. We calculated frequency of occurrence of each food item (i.e., the proportion of all stomachs containing that food item) and proportion biomass (i.e., the proportion of stomach biomass consisting of a particular food item). Chi-square analysis was used to detect differences in the frequency of occurrence of food items in stomach contents by species, sex, and fisher abundance. Multivariate analysis of variance was used with the mean proportion of biomass of 6 food items (deer, hare, medium mammals, small mammals, birds, and vegetation) as response variables to examine effects due to species, age, sex, year, and fisher abundance on biomass measures. Food diversity (Shannon and Weaver 1949) was calculated for each species and sex.

Population Growth

Trends in annual snow-track counts during 1991–95 were used to index population growth of bobcats. The instantaneous rate of population increase was estimated both for the study area as a whole and for C and S counties separately from the slope of the line relating the natural log of the mean number of tracks observed on snow-track transects and the year of observation. An alpha of 0.1 was used for all statistical tests involving track counts.

Survival

Adult survival rates of bobcats were estimated from radiotelemetry and life table analysis. Winter survival estimates were obtained from MICROMORT (Heisey and Fuller 1985). Only winter survival estimates were derived because animals were only monitored intensively in winter and all observed bobcat deaths occurred during this season. Life tables were constructed from the sample of bobcats harvested during 1991–95, and age-specific survival rates for adult bobcats were calculated using the resulting age distributions.

Population Modeling

Kitten and yearling survival rates were derived from population modeling. Two deterministic population models in the form of a Leslie Matrix (Leslie 1945, 1948) were constructed; one each for counties where fishers were common or scarce. Model inputs required were age-specific fecundity and survival rates. Fecundity rates obtained from carcass examination and adult survival from telemetry and life tables were kept constant in each model run. Yearling survival was set halfway between adult survival and kitten survival. Kitten and yearling survival rates were adjusted in successive runs so that the final model output provided a rate of population increase similar to that calculated from location-specific winter track counts. Adult bobcats were modeled to age 15, the age of the oldest individual harvested.

RESULTS

Relative Abundance

Populations of bobcats, fishers, and snowshoe hares, as indexed by track counts and harvests, were not uniformly distributed across northern Wisconsin. Bobcat relative abundance was positively related to hare and deer abundance ($F_{2,35} = 120.90$, $P < 0.001$), but was unrelated to fisher abundance ($F_{1,35} = 0.19$, $P = 0.660$).

Average number of tracks observed were 0.26 (SE = 0.04) and 4.5 (SE = 0.3) for bobcats and fishers, respectively, during 1991–95. An average of 14.7% (SE = 0.48) of transect sub-blocks had hare tracks present. The frequency of fisher tracks observed/transect ranged from 2.6 in 1991 to 6.4 in 1995 and increased over years ($F_{1,4} = 3.82$, $P = 0.040$). Bobcat tracks ranged from 0.17/transect in 1992 to 0.33 in 1994, but did not differ over years ($F_{4,4} = 0.59$, $P = 0.672$). There was significant annual variation in the percent of transect sub-blocks with hare tracks ($F_{1,4} = 2.39$, $P = 0.010$). There was a positive relationship between presence of bobcat tracks vs. fisher ($X^2_2 = 6.20$, $P = 0.020$) and hare ($X^2_2 = 18.80$, $P < 0.001$) tracks.

The number of fisher tracks observed/transect was positively related to year ($F_{1,4} = 6.12$, $P = 0.010$) and distance from nearest reintroduction site ($F_{1,35} = 27.16$, $P < 0.001$). Fisher tracks appeared at later years on transects which were further from reintroduction sites than on transects closer to reintroduction sites.

An average of 146 bobcats and 1,367 fishers were harvested annually in Wisconsin over the study period. Harvested bobcats ranged from 71 in 1991 to 217 in 1992 and harvested fishers ranged from 204 in 1991 to 2,081 in 1994. The index of relative abundance was determined from harvest rates (harvest/100 km²) and track observation rates (tracks/transect). These independent measures of relative abundance were correlated (bobcats: $r = 0.62$; fishers: $r = 0.51$), thus supporting their combined use to index relative abundance. The index of relative abundance of bobcats calculated from tracks and harvests ranged from 0.34 in Bayfield County to 1.56 in Florence County, and averaged 0.77 (Table 2). Eight of the 18

counties had an index >0.77 , and bobcats were thus classified as being common (C). In the remaining 10 counties, bobcats were classified as scarce (S). The index of relative abundance of fishers ranged from 2.83 in Burnett County to 9.87 in Sawyer County (Table 2). Ten counties had an index >7.22 , and fishers were classified as common (C). In the remaining 8 counties, fishers were classified as scarce (S).

We classified CNF and SCNR as having relatively more bobcats than NNF because these study areas had higher bobcat capture rates ($t_3 = 2.62$, $P = 0.040$) than did NNF (Table 3). There were more bobcat track encounters on CNF and SCNR than NNF, which supported this classification, but this difference was not significant ($t_3 = 0.94$, $P = 0.368$). Similarly, we classified the CNF and NNF as having relatively more fishers than SCNR because of higher capture rates ($t_3 = 3.54$, $P = 0.030$) (Table 3). There were more fisher track encounters on CNF and NNF than SCNR supporting the classification, but again this difference was not significant ($t_3 = 1.67$, $P = 0.12$). We classified CNF and SCNR as having relatively more snowshoe hares than NNF because the CNF and SCNR had significantly higher number of tracks present than did NNF ($t_3 = 2.48$, $P = 0.026$) (Table 3).

Home Range Analysis

Sixteen bobcats (10 M, 6 F) and 44 fishers (27 M, 17 F) were caught on the CNF study area during 1992–95. Of the 16 radiocollared bobcats and 20 radiocollared fishers, 9 bobcats (5 M, 4 F) and 13 fishers (7 M and 6 F) lived for ≥ 1 winter and each yielded 30–61 locations. Mean home range size of bobcats was 69 km² for males and 28 km² for females (Table 4). Mean home range size of fishers was 20 km² for males and 7 km² for females (Table 5).

Twenty-two fishers (10 M, 12 F) and 4 bobcats (1 M, 3 F) were captured on the NNF study area during 1992–95 (Wright 1999). Eight fishers (3 M, 5 F) and 3 bobcats (1 M, 2 F) lived for ≥ 1 winter and each provided 31–91 locations. The male bobcats had a home range size of 58 km² and the female bobcats had a mean home range size of 19 km² (Table 4). Mean home range sizes of fishers were 10 km² for males and 6 km² for females (Table 5).

Nineteen bobcats (11 M, 8 F) and 1 fisher (M) were captured on the SCNR study area during 1991–93 (Lovallo 1993). Seven bobcats (4 M, 3 F) and the fisher survived ≥ 1 winter and each yielded 31–110 locations. Mean home range size of male bobcats was 41 km² and that of females was 31 km² (Table 4). The fisher home range was 13 km² in size.

Eight of the possible 16 bobcat home range pairs intersected on CNF. All of the intersecting home-range pairs included ≥ 1 male. The mean area of home range overlap was 14 km² or 29% of mean bobcat home range size (26% for M, 46% for F). Only 4 of the 42 possible fisher home ranges intersected on CNF; the mean area of overlap was 1.1 km² or 8% of the average fisher home range size (6% for M, 17% for F). Twenty-four of the

Table 2. Comparison of bobcat, fisher, and snowshoe hare relative abundance as determined by harvest (harvest/100 km²) and track counts (tracks/transect) in counties of northern Wisconsin during 1991–95. Harvests and track counts were added to derive an abundance index (harvests + tracks). Counties above mean abundance values were rated as having common populations (C). Counties below mean abundance values were rated as having scarce populations (S).

County	Bobcat harvest/100 km ²	Track counts	Harvest & tracks	Bobcat abundance code	Fisher harvest/100 km ²	Track counts	Harvest & tracks	Fisher abundance code	Hare tracks	Hare abundance code
Ashland	0.26	0.15	0.41	S	3.39	3.80	7.19	S	15.09	C
Bayfield	0.18	0.16	0.34	S	3.44	3.72	7.15	S	14.93	C
Burnett	0.71	0.71	1.42	C	1.28	1.55	2.83	S	13.17	S
Douglas	0.44	0.45	0.90	C	2.03	3.59	5.62	S	13.96	S
Florence	0.80	0.77	1.56	C	4.30	3.77	8.07	C	13.76	S
Forest	0.56	0.41	0.97	C	4.47	5.35	9.82	C	14.05	S
Iron	0.26	0.19	0.45	S	3.25	4.09	7.24	C	15.72	C
Langlade	0.24	0.27	0.51	S	4.05	4.55	8.60	C	14.13	S
Lincoln	0.45	0.27	0.71	S	3.59	4.06	7.65	C	15.72	C
Marinette	0.32	0.30	0.62	S	1.92	1.40	3.32	S	13.69	S
Oconto	0.20	0.22	0.42	S	1.46	1.39	2.85	S	12.90	S
Oneida	0.40	0.29	0.69	S	4.27	4.54	8.80	C	13.87	S
Price	0.67	0.28	0.95	C	3.99	4.24	8.22	C	16.84	C
Rusk	0.45	0.32	0.77	C	3.40	6.14	9.53	C	17.31	C
Sawyer	0.39	0.24	0.63	S	3.83	6.04	9.87	C	15.48	C
Taylor	0.51	0.27	0.79	C	1.55	3.67	5.21	S	17.96	C
Vilas	0.22	0.30	0.53	S	3.30	5.15	8.45	C	13.51	S
Washburn	0.61	0.74	1.14	C	2.06	3.93	5.99	S	15.03	C
Means	0.43	0.35	0.77	—	3.09	3.94	7.22	—	14.84	—

Table 3. Relative abundance index measures for bobcats and fishers on 3 study areas (CNF: Chequamegon National Forest, NNF: Nicolet National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during 1991–95. An abundance rating of C indicates common populations and S indicates scarce populations.

Study area	Bobcat			Fisher			Snowshoe hare	
	Captures ^a	Track counts ^b	Rating	Captures ^a	Track counts ^b	Rating	Track counts ^b	Rating
CNF	6.50	0.40	C	34	7.60	C	32	C
NNF	1.50	0.10	S	15	6.00	C	14	S
SCNR	5.80	0.35	C	2	1.40	S	34	C

^aPer 1,000 trap-nights.

^bPer 16-km transect.

Table 4. Sizes (km²) of bobcat home ranges on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during winter.

Study area	Males			Females		
	<i>n</i>	\bar{x} size (range)	\bar{x} locations (range)	<i>n</i>	\bar{x} size (range)	\bar{x} locations (range)
CNF	5	69 (36–86)	45 (30–55)	4	28 (22–30)	41 (30–45)
NNF	1	58	46	2	19 (16–24)	54 (33–75)
SCNR	4	41 (20–98)	51 (31–80)	3	31 (22–38)	77 (37–110)

Table 5. Sizes (km²) of fisher home ranges on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during winter.

Study area	Males			Females		
	<i>n</i>	\bar{x} size (range)	\bar{x} locations (range)	<i>n</i>	\bar{x} size (range)	\bar{x} locations (range)
CNF	7	20 (6–42)	42 (30–61)	6	7 (3–14)	39 (30–59)
NNF	3	10 (9–13)	58 (36–86)	5	6 (3–9)	65 (37–97)
SCNR	1	13	38	---	---	---

possible 63 interspecific pairs of home ranges intersected on CNF, including males and females of both species. The average area of home range overlap between the 2 species was 5.4 km² or 12% of the average bobcat home range size (9% for M, 20% for F) and 39% of the average fisher home range size (28% for M, 77% for F).

The distribution of distances between bobcats and fishers with overlapping home ranges was calculated for 24 bobcat-fisher pairs with 480 locations on CNF. The frequency distribution of separation distances for bobcats and fishers with intersecting home ranges did not differ from random ($X^2_9 = 4.21$, $P = 0.250$).

Carcass Examination

Age and Fecundity.—We aged 362 bobcats and 801 fishers harvested during 1991–95 (Table 6). Harvested bobcats ranged in age from 0.5–15.5 years. Mean adult bobcat age at harvest was 4.5 years and did not vary significantly between sexes ($t_{360} = 1.12$, $P = 0.210$). The age distribution of bobcats and fishers was skewed toward kits and yearlings.

There were 238 (134 M, 104 F) bobcats harvested in C counties and 124 (75 M, 49 F) harvested in S counties. The mean age of harvested adult bobcats did not differ between C and S counties ($F_{1,8} = 0.89$, $P = 0.370$) (Table 7). Ratios of kittens to adults and yearlings to adults in the harvest were greater for C counties than for S counties.

Forty-six percent of bobcats >0.5 year of age were pregnant (Table 8). Counts of placental scars in pregnant female bobcats >1.5 years averaged 2.4. The number of female young produced/female peaked at 5.5 years. Counts of placental scars did not differ by year ($F_{1,6} = 1.42$, $P = 0.233$).

The proportion of female bobcats ≥ 1.5 years that were pregnant was similar in C vs. S counties ($t_{113} = 0.61$, $P = 0.390$) (Table 9). Mean litter size in S counties (2.7 kits/litter) was greater than for C counties (2.3 kits/litter) ($F_{1,6} = 4.304$, $P = 0.044$), although the size of yearling litters was not significantly different between C and S counties ($F_{1,3} = 0.464$, $P = 0.663$).

Condition Index.—The proportion of bobcat biomass consisting of lipids averaged 0.13. There was no difference in the lipid content of male (0.13) and female (0.14) carcasses ($F_{5,6} = 4.06$, $P = 0.152$). There was no difference detected in bobcat lipid content between C and S counties ($F_{5,6} = 0.155$, $P = 0.694$) (Fig. 2).

Food Habits.—More than 85% of the total food biomass found in bobcat stomachs consisted of either deer or hare, and either one or both of these food items were found in 61% of all bobcat stomachs (Table 10). Other food items such as muskrats (*Odantra zibethica*), squirrels (*Sciurus* spp.), small rodents, and birds were present but in low amounts. Frequencies of occurrence of food items did not differ between male and female bobcats ($X^2_4 = 9.07$, $P = 0.110$), but there were differences in the mean proportional biomass ($F_{1,8} = 6.93$, $P = 0.012$). Males consumed proportionately more deer than did females ($F_{1,10} = 11.51$, $P < 0.001$), whereas females ate proportionately more hares ($F_{1,10} = 3.26$, $P = 0.039$). Female bobcats had a more diverse diet than did males as reflected by a Shannon Diversity Index of 1.05 vs. 0.75 for males (Table 10).

There were differences between male and female fishers in the frequency of occurrence of food items ($X^2_4 = 10.35$, $P = 0.070$) and in the mean proportion of food item biomass ($F_{1,10} = 11.51$, $P < 0.001$). Males consumed more hares than did females ($F_{1,10} = 7.92$, $P = 0.005$) and females ate more small mammals ($F_{1,10} = 7.82$, $P = 0.005$). Fishers had more diverse food habits than did bobcats. The Shannon Diversity Index of food habits was 1.7 and 1.6 for males and females, respectively.

There were differences between bobcat and fisher food habits as measured by frequency of occurrence ($X^2_4 = 168.80$, $P < 0.001$) (Table 10) and by the mean proportion of food biomass of each food item ($F_{1,10} = 48.55$, $P < 0.001$) (Fig. 3). Bobcats tended to consume larger prey whereas fishers ate more small and medium mammals, birds, and vegetation (fruits, nuts, seeds) than did bobcats.

Bobcat diets did not differ between C and S counties, as measured by mean proportion of food item biomass ($F_{1,10} = 0.79$, $P = 0.602$) (Fig. 4) or by frequency of occurrence ($X^2_4 = 3.78$, $P = 0.580$). Bobcats did not alter their diets based on the relative abundance of fishers. Fishers, on the other hand, consumed more smaller food items when in the presence of bobcats. Their diets varied significantly between counties with differing relative abundance of bobcats as measured by frequency of occurrence ($X^2_4 = 24.51$, $P < 0.001$) and mean proportion of food biomass in each food item ($F_{1,10} = 2.27$, $P = 0.045$) (Fig. 5). There were more deer present in fisher stomachs where bobcats were scarce than where bobcats were common ($F_{1,10} = 4.29$, $P = 0.039$), and there were more small mammals in fisher stomachs where bobcats

Table 6. Age-distribution of fishers and bobcats obtained from fur harvesters in Wisconsin during 1991–95.

Age (yr)	Bobcats			Fishers		
	Females	Males	Total	Females	Males	Total
0.5	38	41	79	189	94	283
1.5	35	44	79	205	90	295
2.5	27	36	63	76	32	108
3.5	19	29	48	43	11	54
4.5	9	24	33	34	7	41
5.5	9	15	24	6	1	7
6.5	7	6	13	5	2	7
7.5–15.5	3	3	6	9	14	23
Totals	147	198	345	567	251	822

Table 7. Age-distribution of bobcats harvested from counties where fishers were common or scarce in Wisconsin during 1991–95.

Age (yr)	Common fishers				Scarce fishers			
	Males	%	Females	%	Males	%	Females	%
0.5	28	21	24	23	13	17	14	29
1.5	26	19	27	26	18	24	8	16
2.5	25	19	17	16	11	15	10	20
>2.5	55	41	36	35	33	44	17	35
Totals	134	—	104	—	75	—	49	—

Table 8. Fecundity table for female bobcats harvested in Wisconsin during 1991–95.

Age (yr)	Females	No. pregnant	Prop. pregnant	No. placental scars	No. female young	No. female young/female
1.5	48	12	0.25	2.5	15	0.3
2.5	38	15	0.40	2.5	19	0.5
3.5	28	16	0.57	2.8	23	0.8
4.5	10	7	0.70	2.4	9	0.9
5.5	7	5	0.71	2.6	7	1.0
6.5	10	6	0.60	2.3	7	0.7
7.5–15.5	10	9	0.90	2.1	10	1.0
Total/ \bar{x}	151	70	0.46	2.4	90	0.7

Table 9. Fecundity tables for bobcats harvested from counties where fishers were classified as common or scarce in Wisconsin during 1991–95.

Age (yr)	Females	No. pregnant	Prop. pregnant	No. placental scars	No. female young	No. female young/female
Common fisher counties						
1.5	27	9	0.33	2.5	11	0.21
2.5	17	10	0.59	2.4	12	0.35
>2.5	36	29	0.88	2.2	32	0.45
Total/ \bar{x}	80	48	0.60	2.3	55	0.35
Scarce fisher counties						
1.5	8	3	0.38	2.0	3	0.19
2.5	10	5	0.50	2.6	7	0.33
>2.5	17	14	0.81	2.7	19	0.56
Total/ \bar{x}	35	22	0.63	2.7	30	0.42

Table 10. Mean proportion biomass and frequency of food items found in bobcat and fisher stomachs from northern Wisconsin during 1991–95.

Food item	Bobcats				Fishers			
	Females		Males		Females		Males	
	Frequency	\bar{x} prop. biomass						
White-tailed deer	550	0.46	85	0.64	120	0.16	98	0.19
Snowshoe hare	28	0.22	29	0.15	18	0.02	33	0.07
Medium mammals ^a	20	0.04	21	0.04	81	0.11	55	0.11
Small mammals ^b	17	0.11	16	0.06	147	0.36	107	0.28
Birds	3	<0.01	6	0.03	43	0.05	40	0.07
Vegetation	30	0.17	18	0.08	41	0.30	165	0.28
Total stomachs	136		173		609		487	
Empty stomachs	27		39		108		91	
Food-diversity index	1.05		0.75		1.6		1.7	

^aFor example, beaver, muskrat, and raccoon.

^bFor example, squirrels, voles, and shrews.

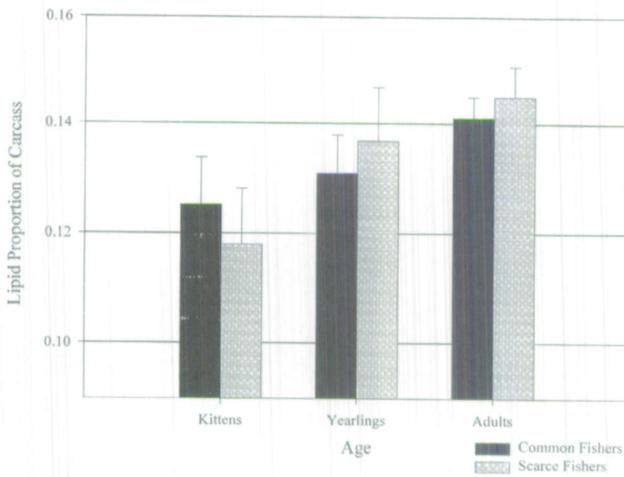


Fig. 2. Proportion of the biomass of skinned carcasses consisting of lipids in bobcats harvested in Wisconsin counties classified as having common or scarce fisher populations during 1991–95.

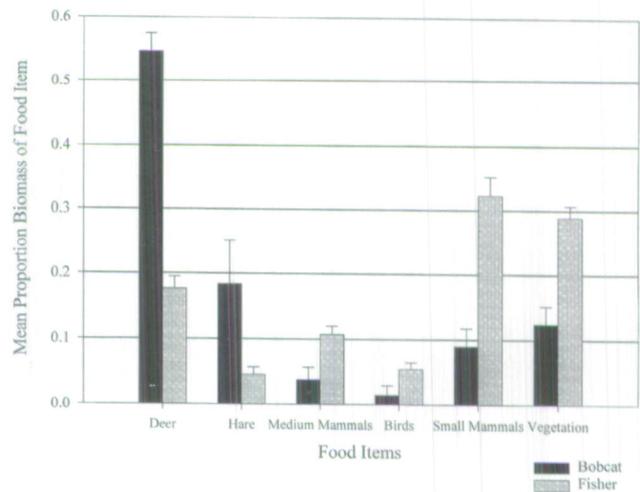


Fig. 3. Bobcat and fisher stomach contents as mean proportion of food biomass found in stomachs from animals harvested in northern Wisconsin during 1991–95.

were common as compared to where bobcats were scarce ($F_{1,10} = 3.76, P = 0.048$).

Population Growth

The mean number of bobcat tracks/transect in C and S counties ranged from 0.18–0.30 and 0.17–0.47, respectively. There was no difference in the number of bobcat tracks observed/transect in C counties ($F_{1,9} = 0.0004, P = 0.952$), whereas number of tracks increased in S counties over years ($F_{1,11} = 3.007, P = 0.087$). The slope of the regression relating the log of number of tracks to year of observation in C counties (slope = -0.01, SE = 0.008) was not significantly different from zero ($t_4 = 0.24, P = 0.826$). However, the slope of the regression line for S counties (slope = 0.11, SE = 0.035) was greater than zero ($t_4 = 4.30, P = 0.020$). This increase of bobcat tracks in S

counties indicated an exponential rate of population increase (r) of 0.11 (SE = 0.035), or a finite rate of growth of 12% annually (Fig. 6).

Survival

The winter survival rate of bobcats on the SCNR study area (scarce fishers) was 0.66, while winter survival on the CNF and NNF study areas (common fishers) was 0.63 and 0.57, respectively (Table 11). Likewise, survival rates of adult bobcats (>1.5) calculated from life tables did not differ between C counties (0.69) and S counties (0.67).

Population Modeling

A post-birth population estimate of 1,000 bobcats was established as the initial input for the model for C counties and 500 was used as the initial population size for S counties, as reflected by relative abundance. Adult survival in the population model was set to 0.62 because this was the midpoint of the range of survival estimates calculated from radiocollared bobcats and the rate reported by Fuller et al. (1995) in their review of bobcat survival studies. Kitten and yearling survival rates were arbitrarily set at 0.55 and 0.6, respectively, for the initial model run.

When the model was run for the C counties using initial inputs, the exponential rate of growth was 0.01, higher than the rate of growth estimated from track counts (-0.01). Therefore, kitten and yearling survival rates were lowered incrementally to 0.52 and 0.58, respectively. The population model with the adjusted kitten and yearling survival rates produced a population estimate which declined slightly.

When the model for S counties was run with initial inputs, the estimated exponential population growth rate was 0.01, lower than the exponential rate of growth indicated by track counts (0.11). Thus, survival rates for kittens and yearlings were incrementally raised to 0.62 for

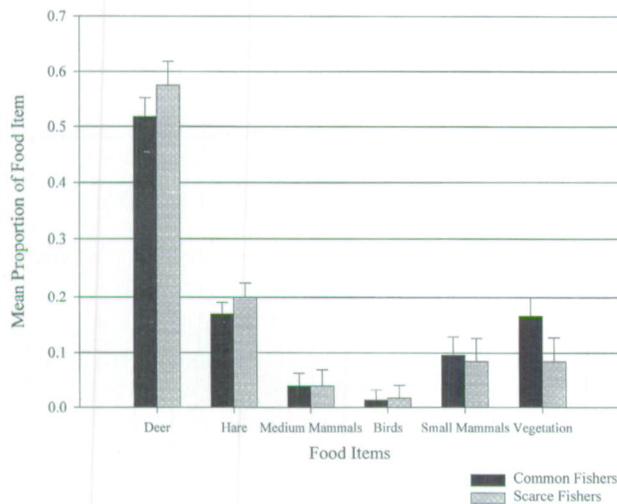


Fig. 4. Bobcat diet as mean proportion of food-item biomass found in stomachs from carcasses harvested in counties with 2 levels of bobcat abundance in northern Wisconsin during 1991–95.

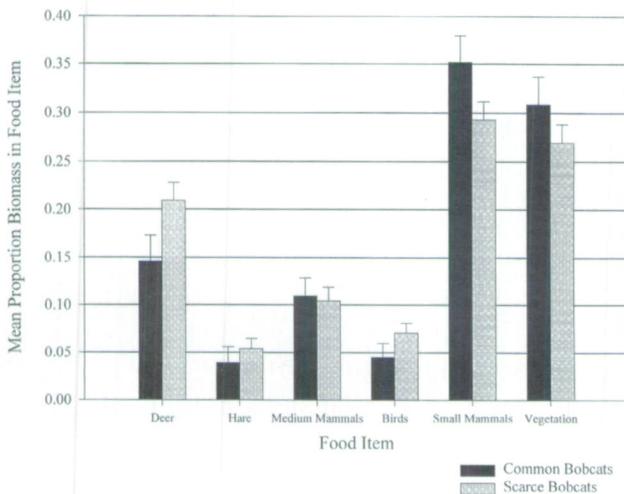


Fig. 5. Fisher diet as mean proportion of food-item biomass found in stomachs from carcasses harvested from counties with 2 levels of bobcat abundance in northern Wisconsin during 1991–95.

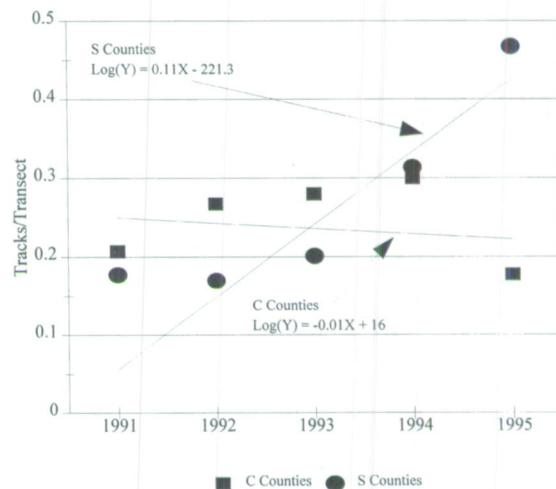


Fig. 6. Results of bobcat snow-track counts in counties with common fishers (C) and scarce fishers (S). Regression line relates \log_{10} of the tracks per transect and year. The slope of this regression line is the estimated instantaneous rate of increase (r) for that bobcat population.

Table 11. Winter survival estimates for bobcats on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during 1991–95.

Study area	Bobcats	Radiodays	Survival	95% CI
CNF	6	2,880	0.63	0.36–0.99
SCNR	12	4,250	0.66	0.35–0.92
NNF	4	1,969	0.57	0.30–1.00

both and the resulting exponential population growth rate was 0.08. This growth rate was less than observed from track counts but no further increase of population growth was possible without kitten and yearling survival exceeding adult survival, which was highly unlikely.

DISCUSSION

Territorial Competition

Territorial and encounter competition both fall within the definition of interference competition (Case and Gilpin 1974). Yet some confusion exists around the everyday usage of the term interference, especially as it relates to competition for space (Schoener 1983). Interference competition has been used to describe processes as diverse as kleptoparasitism (Norris and Johnson 1998, Triplet et al. 1999), territoriality (Carbyn 1982), and predation (Paine 1966, White and Garrott 1997). These processes will have different impacts on species demography and thus must be evaluated separately. Territoriality may occur between members of different species or of the same species (Connell 1983), and it is usually detected by documenting the spatial segregation of the species (Connell 1961, Schoener 1983)

Although territoriality has been observed between sympatric predators, bobcat and fisher home range analysis did not provide any evidence of territorial competition. For example, foxes (*Vulpes fulva*) and coyotes (*Canis latrans*) have been reported to exhibit territorial (interference) competition because of documented spatial segregation (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987). Grey wolves (*Canis lupus*) exclude coyotes from pack territories despite the differences in diets between the species (Carbyn 1982, Thurber et al. 1992). On the other hand, territorial (interference) competition between kit foxes (*Vulpes macrotis*) and coyotes was rejected by White and Garrott (1997) because the species did not segregate spatially. Similarly, Major and Sherburne (1987) concluded that bobcats and coyotes did not interfere with each other because of the lack of spatial segregation of home ranges.

Nearly 40% of bobcat and fisher home ranges overlapped and when this occurred, 40% of fisher home ranges were within bobcat home ranges. Sandell (1989) concluded that individuals whose home ranges overlap by >10% can be said to be non-territorial. Most of the overlap in bobcat and fisher home ranges occurred in the

Spider Lake area of CNF. This lowland conifer swamp supported a high population of overwintering deer (Lewis 1990) and dead deer were common. These deer provided food to resident carnivores, and it is this concentrated food supply which apparently caused the overlap in home ranges.

Analysis of separation distances also failed to detect evidence of territoriality or avoidance within overlapping portions of home ranges. Bobcats and fishers appeared to be using their home ranges independently of each other even while within overlapping home ranges. These results were similar to those obtained by Major and Sherburne (1987) and White et al. (1994) who concluded that the observed random-spacing distances provided little evidence of interference competition.

We detected territoriality within each species, however. Fishers maintained separate home ranges from other fishers (both M and F) on the CNF and NNF. Female bobcats also maintained separate home ranges on the SCNR and CNF. Connell (1983) suggested intraspecific territoriality in home ranges indicated intraspecific competition is a stronger influence than interspecific competition. Our results support this hypothesis.

Consumptive Competition

Consumptive competition occurs when some quantity of resource is consumed by an individual, thereby depriving other individuals of it. For carnivores, the resource most often involved is food, although this need not be the case. Maternal den sites, for example, are resources which are used by both bobcats and fishers (Gilbert et al. 1997) and may be in short supply.

Although direct evidence of territorial or encounter competition can be collected, perhaps all evidence for consumptive competition for food (or other resources) is inferential (Case and Gilpin 1974). One of the primary difficulties in documenting consumptive competition has been demonstrating that the resource sought by both species was in short supply. Thus, in most studies of competition, conclusions have been inferred either from impacts to species demography while in the presence of a competitor or from changes in the utilization distribution of the resource (Ricklefs 1990). If consumptive competition between bobcats and fishers was operating, then all of the demographic parameters investigated in this study should have been lower when bobcats were in the presence of fishers (given the same prey base). However, differences were found in only kitten survival and population growth.

Encounter Competition

Encounter competition is a second form of interference competition (Schoener 1983) and occurs when one species gains access to increased amount of limited resources by interfering with the ability of its competitor to secure the same resources. When this type of interference occurs in feeding ecology, optimal foraging theory predicts that the poorer competitor will constrict its food

habits. If consumptive competition occurs in the absence of interference, then optimal foraging theory predicts that the poorer competitor will broaden its food habits.

Bobcats did not alter food habits while in the presence of fishers. Fishers, on the other hand, consumed a larger biomass of small prey and vegetation where bobcats were abundant. However, in areas where bobcats were scarce, bobcats continued to concentrate on larger prey items, while fishers consumed a broader array of prey, including larger items usually eaten by bobcats. The constriction in fisher diet suggested that bobcats and fishers competed for food, with the bobcat being the dominant competitor (Connell 1983).

Distinguishing Between Consumptive and Encounter Competition

There was evidence that bobcats and fishers competed for food resources. However, only 2 of those predictions associated with consumptive competition were found, whereas, the majority of the predictions associated with encounter competition were supported. Population growth and kitten survival were inversely related to fisher abundance. There was no effect of fisher abundance on bobcat adult survival, body condition, or home range, and little effect on bobcat fecundity. Population density was the only parameter tested which did not conform to the predictions under encounter competition. Thus, it is possible that fishers interfered with (or preyed upon) bobcat kittens as hypothesized.

Population modeling implied bobcat kitten survival was low where fishers were common. Kitten survival, although difficult to document, has been shown to be an important variable in bobcat population dynamics, and has been related to reduced prey availability and to increased predation. Bailey (1974) reported that bobcat kitten survival was nearly zero after a crash in prey populations and Rolley (1985) speculated kitten survival during the first 6 months of life was low due to low prey availability. However, Zezulak and Schwab (1979), found that the scarcity of kittens on their study area was due to predation by male bobcats.

If either consumptive or encounter competition occurred, one would expect bobcat populations to grow at a slower rate when fishers were common. Population modeling by WDNR (R. Rolley, personal communication) indicated the bobcat population increased in the northern forest during the 5 years of this study. We found that this increase in population size was reflected in increased bobcat track observations only in S counties, while track count rates remained stable in C counties. This apparent positive rate of population growth in areas where fishers were scarce was consistent with the occurrence of either encounter or consumptive competition.

If bobcat kitten survival was reduced by fishers and if bobcat population growth was lower in areas where fishers were common, one would expect bobcat density to be inversely related to fisher density (Connell 1983). However, this was not the case. The fisher population in

northern Wisconsin was expanding during this study, as evidenced by the concentric fisher distribution pattern centered on release sites and the significant relationship between distance from release site and occurrence of fisher tracks on snow-track transects. This distribution of fishers reflects population expansion rather than an established pattern based on prey, habitat factors, or competitors. Fishers have not settled into a distinctive pattern of distribution since their reintroduction and thus there was no relationship detected between fisher density and bobcat density. A positive relationship existed, as demonstrated by positive correlation of relative density, between distributions of bobcats, snowshoe hares, and white-tailed deer; species which have had long residency in Wisconsin. Even though an inverse relationship between bobcat and fisher densities was predicted, the lack of a relationship between their densities was not surprising because of the continued expansion of fisher populations during this study.

If consumptive competition for food resources occurred, and fishers thus deprived bobcats of food, the result should have been reduced fecundity of bobcats. However, if only interference competition occurred, one would expect no relationship between fecundity and fisher abundance. Therefore, this parameter is useful in distinguishing between the 2 types of competition.

Previous studies have shown bobcats to have reduced reproductive output during food shortages. The bobcat reproductive parameter most influenced by food shortages is the percentage of yearling females that become pregnant (Rolley 1985, Knick 1990). Bobcat pregnancy rates, the parameter most influenced by food availability, remained constant for both adults and yearlings between areas. However, we found a significant reduction in bobcat litter size in counties with common fishers but no difference in the litter size of yearling bobcats.

In a review of bobcat survival studies, Fuller et al. (1995) concluded that adult bobcat survival ranges from 0.50–0.67 and averages 0.62 for lightly harvested populations. Survival rates showed little variation across the studies these authors examined, except when poaching or harvests were excessive. Thus, little *a priori* evidence existed that adult survival rates would vary over a wide range of environmental conditions including exposure to potential competitors. We found little variation in adult survival rates and thus support this conclusion. In fact, survival rates calculated from radiocollared bobcats and from life table analysis were nearly identical to those cited by Fuller et al. (1995).

If significant competition deprived bobcats of food there should be less lipid content in bobcat carcasses when fishers are common. However, lipid content of bobcat carcasses was not related to fisher abundance. The only consistent finding was that bobcats had more lipids than fishers. Autumn, when carcasses were collected, is a food-rich time of year. It may be that bobcats and fishers

were both well nourished during this time. Evidence of competition may have been apparent if body condition had been evaluated in the late winter or early spring, when food resources for both species may have been reduced.

In summary, bobcats and fishers shared use of space and some food resources, despite overall differences in food habits. Also, we inferred interference competition from the observed constrictions in the diets of fishers while in the presence of bobcats. Finally, we inferred encounter competition, or predation, from the increase in bobcat kitten mortality and reduction in bobcat population growth when fishers were abundant.

Conservation Implications

Erdeman et al. (1998) questioned the success of the fisher restoration, contending that this conservation work had unanticipated consequences. They reported fisher predation caused significant nest failure and increased mortality to adult goshawks (*Accipiter gentilis*) so that the population was no longer sustainable. Similar allegations have been made about fisher predation on bobcats that imply an incompatibility between bobcats and fishers.

We found no evidence that bobcats and fishers are incompatible. Bobcat populations in Wisconsin grew during this study despite suggestions of exploitation or encounter competition. Bobcat populations were stationary even in areas common with fishers. Competition between bobcats and fishers was weak and this weak competition should result in a stable coexistence between the species as predicted by Lotka-Volterra competition models (Gotelli 1998).

The restoration of extirpated species is an important aspect of wildlife conservation. In the past decades there have been several restorations of native Wisconsin fauna including the wild turkey (*Meleagris gallopavo*), American marten (*Martes americana*), trumpeter swan (*Olor buccinator*), and gray wolves. Because these restorations have taken place in an environment greatly altered from conditions which existed prior to species' extirpations, the impacts of these restorations on the remaining flora and fauna may be unpredictable. Wildlife managers and restoration biologists are obliged to evaluate the potential impacts that the species restoration efforts may have on present ecosystems in order to minimize unanticipated consequences.

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SPATIAL AND RESOURCE OVERLAP OF BOBCATS AND GRAY FOXES IN URBAN AND RURAL ZONES OF A NATIONAL PARK

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Abstract: Urbanization reduces and fragments wildlife habitat and threatens the health and natural functioning of populations, communities, and ecosystems. Wide ranging and low density species, such as mammalian carnivores, may be particularly sensitive to the impacts of urbanization. During 1992–95, I studied the ecology of bobcats (*Lynx rufus*) and gray foxes (*Urocyon cinereoargenteus*) in urban and rural zones of Golden Gate National Recreation Area, Marin County, California. Little is known about the interactions between these 2 species or about how these interactions might be affected by humans. In the urban zone, home ranges of bobcats and gray foxes overlapped extensively, although gray foxes used developed areas outside the park and bobcats did not. However, bobcat and fox core areas did not overlap in the urban zone. Gray fox core areas often were adjacent to the park edge or centered around human development within the park. Meadow voles (*Microtus californicus*) dominated the diets of both species in the urban zone. During the wet season when fruits and nuts were not available to foxes, diet overlap was particularly high. A larger predator killed 3 of 8 radiocollared foxes that died in the urban zone. Though bobcats and gray foxes coexist on a broad scale, foxes may avoid bobcat core areas and are at risk to be killed by bobcats. Competition may be intensified in urban landscapes where the amount of suitable habitat is constrained, but foxes may escape competition through the use of developed areas.

Key words: bobcat, competition, core areas, diet overlap, gray fox, home range, *Lynx rufus*, overlap, urban wildlife, *Urocyon cinereoargenteus*.

Interspecific interactions between mammalian carnivores are widespread and can be important on individual, population (Kelly and Durant 2000), and community levels (Crooks and Soule 1999). Competition among carnivores has been studied throughout the world (Schaller 1972, Frame 1986, Johnson et al. 1996). Schoener (1983) specified 6 types of competition in 2 groups: exploitative competition, which included consumptive and preemptive competition, and interference competition, which included territorial, overgrowth, chemical, and encounter competition. While preemptive, overgrowth, and chemical competition generally occur in plants and other sessile organisms, mammalian carnivores compete through consumptive, territorial, and encounter competition. Often intense competition occurs between closely related species because they use similar resources. In carnivores there are many examples of competition between members of the same family, such as Canidae (Johnson et al. 1996), and genus, such as *Canis* (Carbyn 1982, Thurber et al. 1992). However, there are also instances of more distantly related carnivores competing. For example, lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), hyenas (*Crocuta crocuta*), and wild dogs (*Lycaon pictus*) all compete for ungulate prey and for each other's kills in Africa (Schaller 1972, Frame 1986).

In many cases of competition between carnivores, the influence of the superior competitor has been strong enough to affect survival (e.g., kit foxes, *Vulpes macrotis*; Ralls and White 1995), reproduction (e.g., cheetahs, Laurenson and Caro 1994), or spatial distribution (e.g., red foxes, *Vulpes vulpes*; Sargeant et al. 1987) of the

weaker, and generally smaller, species. However, many smaller species that may lose in territorial or encounter competition manage to persist in sympatry. The smaller species may find refugia physically, such as in the dens of kit foxes (Cypher and Spencer 1998) and swift foxes (*Vulpes velox*, Kitchen et al. 1999). Further, the smaller species may be able to use resources that are unavailable to the larger competitor, or it may use the common resource more efficiently (Rosenzweig 1966, Durant 1998). This coexistence depends on a heterogeneous environment, both spatially and temporally, so that there are some conditions that favor each species.

One kind of habitat heterogeneity of increasing importance is that produced by humans. Human-altered habitats may have a large impact on carnivore competition and community structure (Buskirk et al. 2000). Species that are better able to coexist with humans may be able to escape pressure from superior competitors through the use of urban, suburban, or agricultural areas or because of human persecution of the larger animal. For example, endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) exist at high densities within the city of Bakersfield where coyotes (*Canis latrans*) are not present (Cypher and Frost 1999). Red foxes may have persisted in central Canada and southeastern Idaho because of coyote harvest and the fox's ability to utilize developed areas (Green and Flinders 1981, Dekker 1983, Voight and Earle 1983). Current research in Illinois shows red foxes persisted given high mortality from coyotes by using urban areas and farmsteads (Gosselink 1999). Cheetahs may also escape lion predation outside national parks in areas where lions are killed and harassed by humans, but cheetahs are tolerated (Kelly and Durant 2000).

Human-altered landscapes could also increase the competitive pressure on some carnivore species. If the superior competitor is actually more adaptable to human

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presence, then human intrusion into wilderness areas may cause increased competition. For example, coyotes may penetrate deeper into prime lynx (*Lynx canadensis*) habitat through the use of trails and roads (Buskirk et al. 2000). When natural habitat is reduced and fragmented, competition may also be more intense in the smaller patches of habitat that remain, potentially causing local extirpation of inferior competitors if they are not able to persist in the developed portions of the landscape.

In this study, I investigated the relationship between bobcats and gray foxes in urban and rural zones of Golden Gate National Recreation Area. I hypothesized consumptive competition would be relatively unimportant between these species because of the broader diet of the more omnivorous fox. I also hypothesized the larger bobcat would be dominant in any encounter or territorial competition, and that if these kinds of interference competition were present they would be more intense in the urban zone of the park where resources and habitat were more limited.

STUDY AREA

The study was conducted in Golden Gate National Recreation Area (GGNRA) in Marin County, California. This area is comprised of 30,000 ha of parkland in the San Francisco Bay Area and is one of the most visited parks in the national park system, receiving approximately 14 million visitors per year. Coastal Marin County is characterized by annual grasslands, a chaparral community dominated by coyote bush (*Baccharus pilularis*), riparian woodlands dominated by willows (*Salix* spp.), and oak-bay woodlands dominated by live oaks (*Quercus* spp.) and California bay trees (*Umbellularia californica*). Evergreen forests in wetter drainages are dominated by coast redwoods (*Sequoia sempervirens*) and Douglas firs (*Pseudotsuga menziesii*).

I studied bobcats and foxes in 2 areas of GGNRA: the southern part of the park, called the Marin Headlands (hereafter, the urban zone), and the northern part of the park, from the town of Stinson Beach, along Bolinas Lagoon to Olema (hereafter, the rural zone; Fig. 1). The urban site is adjacent to Highway 101, a major 6–8 lane freeway, and the urban areas of Sausalito, Marin City, and Mill Valley. The rural study area, which begins 15 km to the northwest, is 7–17 km from any dense human habitation although there are occasional dwellings and small settlements within the park boundary.

METHODS

Live-trapping and Handling

I captured bobcats and gray foxes in homemade box traps (Zezulak 1998) and gray foxes in Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). Both species were chemically immobilized with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride injected intramuscularly. I recorded standard body measurements, eartagged animals in both ears with Monel #4 metal eartags (National Band and Tag Co., Newport, Kentucky, USA), recorded sex, and assessed age as juvenile or adult based on dentition.

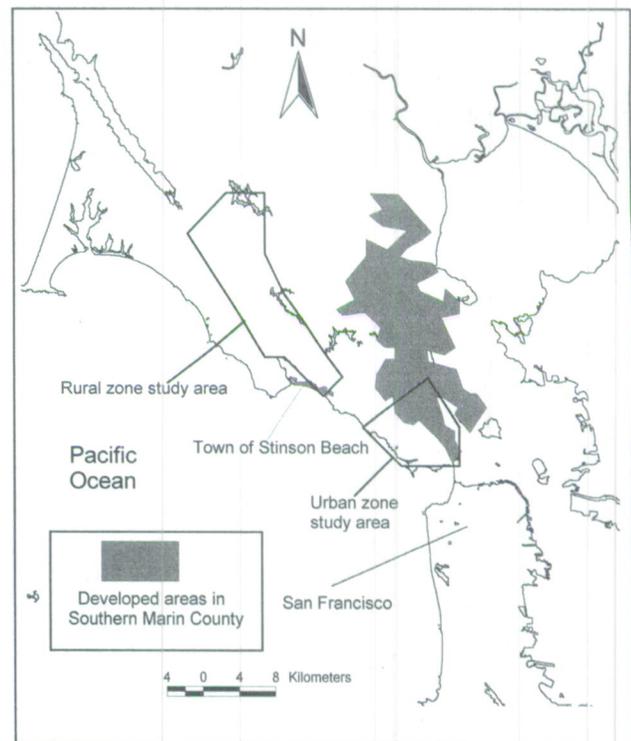


Fig. 1. Study areas in urban and rural zones of Golden Gate National Recreation Area, Marin County, California.

Adults were fitted with Telonics (Telonics, Incorporated, Mesa, Arizona, USA) model 315 (bobcats) and model 225 radiocollars (gray foxes). When animals started to emerge from the effects of the ketamine, an intramuscular injection of yohimbine hydrochloride was given to antagonize the xylazine. When fully recovered, the animal was released at the site of capture. An animal care and use protocol for all capture and handling procedures was approved by the Animal Care and Use Committee at the University of California at Davis (protocol #5328, May 1992).

Radiotelemetry

Animals were intensively radiotracked for ≥ 12 months (Aug 1992–Mar 1994 in the urban zone and Jan 1994–Mar 1995 in the rural zone). Two day locations and 1 night location were obtained/week for each animal for a total of 38 and 26 months of radiotracking in the urban and rural zones, respectively. Locations were determined using 2 (20%) or 3 (80%) compass bearings obtained with a handheld peak antenna system. I was usually able to get to a point of direct line of sight to the animal (i.e., in the same drainage with the animal or on a ridge above the drainage) before taking bearings. The sites from which I took bearings were pinpointed to ≤ 2 –5 m using a Global Positioning System (GPS). I used >360 permanent receiver locations in the urban zone and >460 in the rural zone. Animals, especially bobcats, were also located visually during the day. Visual locations were mapped using compass bearings from 2 known sites or 1 compass bearing and an estimated distance.

Telemetry system accuracy was tested by direct measurement. A field assistant and I placed radiocollars at locations unknown to the other person, but within the home range of a particular animal. The observer then

radiotracked the collar as if it were that animal. The locations of the radiocollars were then located with the GPS and the location coordinates were compared to those of the triangulated location. The mean distance between triangulated locations and the test collars was 76.6 m ($n = 37$, $SE = 53.3$).

Home Range and Core Area Estimation

I computed home ranges and core areas using the minimum convex polygon (MCP) (Hayne 1949) and adaptive kernel methods (Worton 1989). I represented the home range of each animal using a 100% MCP home range and the core area of use (Kaufman 1962) using a 50% adaptive kernel home range.

I computed the percentage of home range overlap for all pairs of bobcats and gray foxes whose home ranges overlapped. For every pair of animals there were 2 data points, one reflecting the percentage overlap of the bobcat on the fox and one of the fox on the bobcat. I also computed the number of different individuals of the other species that overlapped each animal's home range and core area, and the total percentage of each animal's home range and core area that was overlapped by individuals of the other species. I calculated percentage core area overlap for the same animal pairs whose home ranges overlapped. For each species, I tested for differences ($\alpha = 0.05$) between the sites in home range and core area overlap using a Mann-Whitney U test (SYSTAT, Daniel 1990).

Food Habits

I determined bobcat and gray fox food habits with scat analysis. Scats were collected throughout the study period, from fall 1992 through spring 1995 in the urban zone and from fall 1993 through spring 1995 in the rural zone. I determined species by size and shape of scats (Murie 1954) and excluded samples of uncertain origin.

Scats were only collected if they were determined to be recently deposited. Scats were placed in paper bags, air dried, and stored. Before analysis, scats were placed in nylon mesh bags and machine-washed to eliminate the fecal matrix. Scats were allowed to air dry and then hand-separated into hair, bones, and teeth for mammal prey and other diagnostic parts for insect, fruit, bird, reptile, and other food items. I recorded the weight of each group of remains to the nearest 0.1 g. Mammals were identified using a reference collection at the University of California at Davis. Teeth or diagnostic bones were not present in some scats, so remains were classified as small mammal or medium-sized mammal. Insect, fruit, and nut remains were grouped as insects and fruit/nuts for purposes of analysis.

I used 2 methods of food habits analysis: (1) frequency of occurrence, or the number of occurrences of an item divided by the total number of scats and (2) percent fresh weight of prey (%FWP). Frequency of occurrence data were also converted to percentage of occurrence. The weights of hair, bone, and teeth were used in a model based on feeding trials (Kelly 1991, Kelly and Garton 1997) to estimate the fresh weight of each prey item present in each scat. I used program SCAT (Kelly and Garton 1993) to determine %FWP for each item in the diet for which estimators were available.

Diets were determined for both species for each site and for the wet (Nov–Apr) and dry (May–Oct) seasons. I computed diet overlap between species using Pianka's (1973) index of overlap:

$$O_{jk} = \sum p_{ij} p_{jk} / (\sum p_{ij}^2 \sum p_{jk}^2)^{1/2}$$

where p_{ij} is the proportion of item i in the diet of carnivore j . The overlap values are a somewhat conservative estimate of overlap because they are computed on many different diet items, including unidentified small mammals and unidentified medium-sized mammals. Though I pooled insects and lagomorphs, I left small mammal food items at the species level to reflect the importance of particular species.

RESULTS

Spatial Overlap

I radiocollared 20 foxes and 10 bobcats in the urban zone and 15 foxes and 12 bobcats in the rural zone. Home ranges of bobcats and gray foxes overlapped in the urban and rural zones (Figs. 2 and 3). In the urban zone, 13 of 17 fox home ranges were overlapped by 1–5 bobcat home ranges ($\bar{x} = 2.1$, $SD = 1.9$). Home range overlap of foxes by bobcats was 35–100% in the urban zone ($\bar{x} = 63\%$, $SD = 40$). In the rural zone, all 10 foxes were overlapped by 1–4 bobcats ($\bar{x} = 2.9$, $SD = 1.2$). Home range overlap of foxes by bobcats was 5–100% ($\bar{x} = 75\%$, $SD = 36$) and 5 fox home ranges were entirely overlapped by bobcat home ranges. All 8 bobcat home ranges in the urban zone were overlapped by 2–11 fox home ranges ($\bar{x} = 4.5$, $SD = 3.0$) and overlap ranged from 3–81% ($\bar{x} = 40\%$, $SD = 27$). The home ranges of the 4 bobcats in the Bolinas area of the rural zone were overlapped by 5–10 fox home ranges ($\bar{x} = 7.0$, $SD = 2.2$) and overlap ranged from 7–48% ($\bar{x} = 28\%$, $SD = 17$). Home range overlap did not differ between sites for either bobcats ($U_{11} = 13.0$, $P = 0.610$) or foxes ($U_{20} = 108.5$, $P = 0.231$).

Although core areas overlapped extensively in the rural zone (Fig. 5), little core area overlap between bobcats and foxes existed in the urban zone (Fig. 4). In the urban zone only 4 fox core areas were overlapped by bobcat cores ($\bar{x} = 0.29$, $SD = 0.75$) and average overlap was 4% ($SD = 9$). Urban zone bobcat core areas were overlapped by 1–3 fox core areas ($\bar{x} = 0.75$, $SD = 1.04$) and overlap ranged from 0–7% ($\bar{x} = 3\%$, $SD = 5$). In the rural zone, 0–2 bobcat core areas ($\bar{x} = 0.90$, $SD = 0.74$) overlapped fox core areas with overlap ranging from 0–100% ($\bar{x} = 45\%$, $SD = 39$), and 0–3 fox cores ($\bar{x} = 2$, $SD = 2$) overlapped bobcat cores by 0–28% ($\bar{x} = 16\%$, $SD = 13$). Though core area overlap of foxes on bobcats did not differ in the rural zone ($U_{11} = 26.0$, $P = 0.078$), core area overlap of bobcats on foxes was greater in the rural zone ($U_{26} = 138.0$, $P = 0.002$).

Diet Overlap

I analyzed 325 bobcat scats ($n = 188$ in the urban zone and $n = 137$ in the rural zone, Table 1) and 247 gray fox scats ($n = 132$ in the urban zone and $n = 115$ in the rural zone, Table 2). Meadow voles were the most important items in both species' diets. Urban zone overlap between bobcat and gray fox diets was 0.61 for percent occurrence ($n = 14$ items) and 0.92 for %FWP (n

Table 1. Diets (% fresh weight of prey and % occurrence) of bobcats in urban and rural zones of Golden Gate National Recreation Area, Marin County, California, 1992–95.

	Urban zone		Rural zone		Urban zone, wet season	
	% FWP	% Occurrence	% FWP	% Occurrence	% FWP	% Occurrence
Meadow vole (<i>Microtus californicus</i>)	67.5	50.1	53.3	42.4	65.6	51.7
Lagomorphs (<i>Sylvilagus</i> and <i>Lepus</i>)	13.3	7.8	7.9	7.0	10.7	7.0
Pocket gopher (<i>Thomomys bottae</i>)	8.7	13.8	17.9	21.8	10.9	16.3
Mule deer (<i>Odocoileus hemionus</i>)	4.8	2.2	15.1	7.4	8.1	4.1
White-footed mouse (<i>Peromyscus maniculatus</i>)	1.7	8.3	1.5	4.8	1.5	7.6
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	1.7	1.8	1.8	2.6	1.4	1.7
Unknown med. mamm.	1.2	2.5	1.1	2.2	1.5	2.9
Birds	0.7	3.4	0.6	2.6	0.1	2.3
Insects	0.1	3.1	0.1	2.2	0.1	2.9
Harvest mouse (<i>Reithrodontomys megalotis</i>)	0.1	0.6	0.1	0.4	0.2	0.6
Unknown small mamm.	0.0	0.0	0.4	2.6	0.0	0.0
Reptiles		3.1		3.5		2.3

Table 2. Diets (% fresh weight of prey and % occurrence) of gray foxes in urban and rural zones of Golden Gate National Recreation Area, Marin County, California, 1992–95.

	Urban zone		Rural zone		Urban zone, wet season	
	% FWP	% Occurrence	% FWP	% Occurrence	% FWP	% Occurrence
Meadow vole (<i>Microtus californicus</i>)	46.1	21.4	35.8	22.7	47	29.3
Fruit/nuts	14.3	19.0	9.4	21.0	4.1	10.6
Unknown small mamm.	7.9	6.8	5.9	9.7	9.8	8.9
Insects	5.9	23.1	4.6	23.5	3.2	23.6
Unknown med. mamm.	5.7	2.0	3.3	3.4	10	4.1
Lagomorphs (<i>Sylvilagus</i> and <i>Lepus</i>)	4.7	2.0	11.1	4.2	6.7	3.3
Mule deer (<i>Odocoileus hemionus</i>)	4.6	0.7	15.9	1.3	8.2	1.6
Birds	3.7	5.4	2.9	2.9	3.7	6.5
White-footed mouse (<i>Peromyscus maniculatus</i>)	2.3	2.4	6.0	3.8	3.4	4.9
Pocket gopher (<i>Thomomys bottae</i>)	2.3	2.0	1.0	0.4	3.0	3.3
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	2.3	1.0	3.0	1.3	0.7	0.8
Harvest mouse (<i>Reithrodontomys megalotis</i>)	0.1	0.7	1.2	0.8	0.2	1.6
Reptiles		1.0		1.7		0.8
Human food (Trash, etc.)		2.0		1.3		0.8

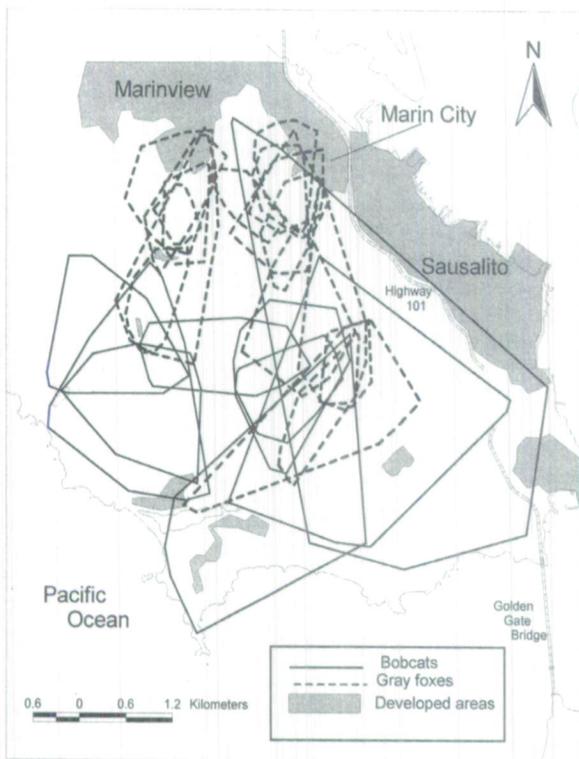


Fig. 2. Minimum convex polygon home ranges (100%) of bobcats and gray foxes in the urban zone of Golden Gate National Recreation Area, Marin County, California.

= 12 items, omitting reptiles and human items such as trash). Rural zone dietary overlap was 0.56 for percent occurrence ($n = 16$ items) and 0.90 ($n = 13$ items, omitting snakes, dog food, and human items) for %FWP. In the urban zone, wet season overlap was 0.75 for percent occurrence ($n = 15$ items) and 0.95 for %FWP ($n = 12$ items, omitting reptiles, trash, and bats). In the rural zone, wet season overlap was 0.55 for percent occurrence ($n = 16$ items) and 0.90 for %FWP ($n = 13$ items, omitting reptiles, dog food, and trash).

Potential Intraguild Predation

Eight of 20 radiocollared foxes died in the urban zone and 3 of these were killed by a larger carnivore, although none of them was eaten. Necropsy and field evidence could not identify the carnivore responsible. No foxes were killed by other predators in the rural zone. In June 1992, just before the study began, I observed a bobcat chasing a gray fox across a rock outcropping above a fire road. The bobcat stopped to look at a vehicle and the fox continued to sprint away out of sight. The area was later frequented by 2 radiocollared male bobcats.

DISCUSSION

Bobcats and gray foxes were abundant in both the urban and rural zones of Golden Gate National Recreation Area, and on a landscape scale these carnivores clearly coexisted. The high degree of interspecific home range overlap at both study sites also indicates that these species regularly utilize the same space. In addition to the high degree of overlap on a broad scale, closer examination

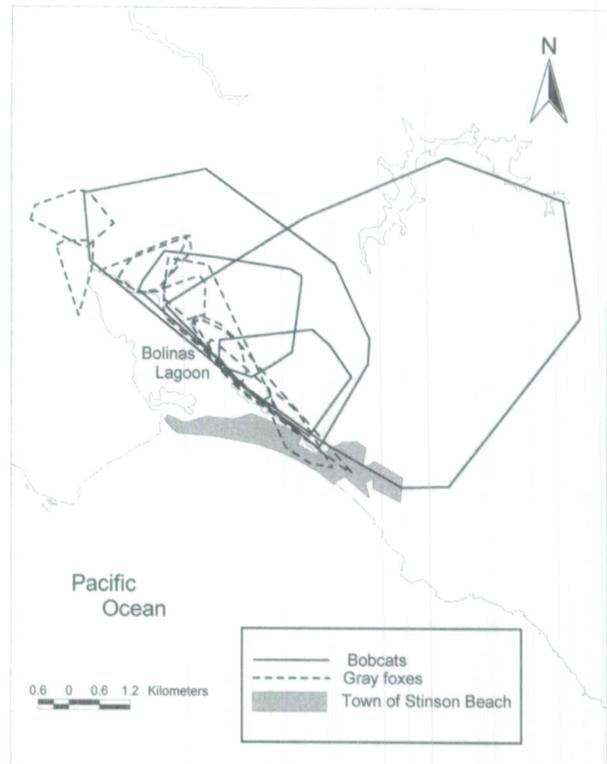


Fig. 3. Minimum convex polygon home ranges (100%) of bobcats and gray foxes in the rural zone of Golden Gate National Recreation Area, Marin County, California.

revealed that individual bobcats and gray foxes interact and may directly compete for resources.

In the urban zone, bobcat core areas did not overlap those of foxes. Past studies showing interspecific territoriality between carnivores have found little spatial overlap at all between competing species, and the authors have inferred that the smaller species is avoiding the larger one (Sargent et al. 1987, Harrison et al. 1989). In this case, it may be that gray foxes tolerate spatial overlap on the periphery of their home range but not in their areas of most concentrated activity. A similar relationship of home range overlap but little core area overlap was found between coyotes and wolves in Montana (Arjo and Pletscher 1999). Young foxes would likely be especially vulnerable to attack from bobcats, and so gray fox pairs would likely choose denning areas that were less frequented by potential competitors. One of the few published accounts of a bobcat-gray fox interaction details a fox pair harassing and chasing a bobcat that was near their den (Dudley 1976).

Dietary overlap between bobcats and gray foxes as measured by percent occurrence was low in both zones because of omnivorous fox diets. However, fox diets varied considerably seasonally, with fruit occurring predominantly during the dry season. Bobcat diet was focused very heavily on a single prey item, the meadow vole (*Microtus californicus*). Voles were also the most important mammalian prey for foxes by both measures. Therefore, during the wet season dietary overlap was higher between the species because of the increased reliance on voles by foxes. Overlap values for the %FWP

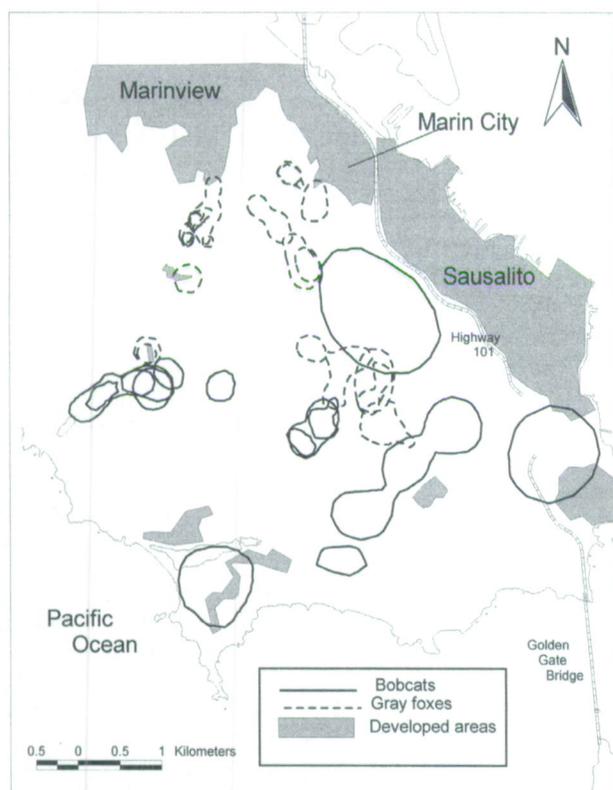


Fig. 4. Adaptive kernel core areas (50%) of bobcats and gray foxes in the urban zone of Golden Gate National Recreation Area, Marin County, California.

diets were higher than those for the percent occurrence diets because of low values for fruit and insects and the large percentage of fresh weight represented by voles in both species' diets.

It may be that, in spite of high dietary overlap during the winter, consumptive competition did not occur between bobcats and foxes. Competition over a resource requires that the resource is scarce or at least limiting, and voles appeared to be abundant. There are other examples of very high resource overlap in sympatric carnivores that did not appear to be competing. For example, Witmer and DeCalesta (1986) studied coyote and bobcat populations in Oregon that were both relying almost entirely on mountain beaver (*Aplodontia rufa*) with diet overlap values >0.97 . However, many small mammal populations frequently cycle with great amplitude (Krebs and Myers 1974, Lidicker 1988), and competition could occur during the trough of a cycle. Studies of lynx in Canada have found that interspecific competition in the form of killing and eating other carnivores (i.e., intraguild predation; Polis et al. 1989) such as red foxes increases markedly during the low period of the snowshoe hare cycle (Stephenson et al. 1991, O'Donoghue et al. 1995), although other studies have reported that many red fox kills by lynx are uneaten (Sunde et al. 1999). However, central coastal California is very different from high latitude Canada and microtine cycles tend to be more common and more dramatic at high latitudes (Hanski et al. 1991), so perhaps bobcats and foxes can coexist over the long term on high-density vole populations.

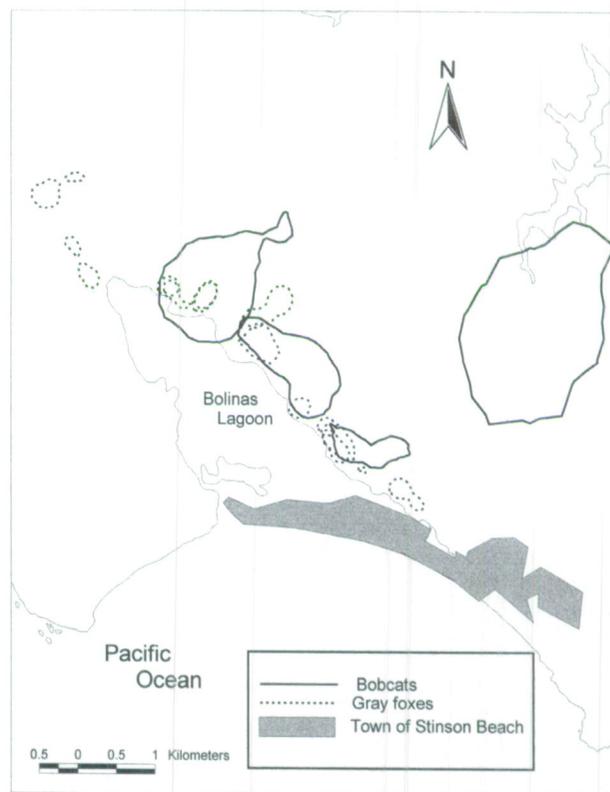


Fig. 5. Adaptive kernel core areas (50%) of bobcats and gray foxes in the rural zone of Golden Gate National Recreation Area, Marin County, California.

Regarding encounter competition, gray foxes in this study, particularly in the urban zone, are at risk of being attacked and killed by other carnivores. Three of the 8 dead foxes in the urban zone were killed, though not eaten, by another predator. While it is difficult to unequivocally suspect bobcats in these cases, bobcats were definitely the most abundant larger carnivore in the urban zone and I observed a bobcat chasing a fox on one occasion. Other instances of bobcats attacking or harassing gray foxes have been reported (Trapp and Hallberg 1975, Dudley 1976), and 2 of 11 gray foxes killed by predators in southern California were killed by bobcats (Fedriani et al. 2000). Bobcats also attacked and killed endangered San Joaquin kit foxes and were the leading cause of mortality in one study (Disney and Spiegel 1992). The closely related lynx has also been known to attack and kill red foxes (Stephenson et al. 1991, Sunde et al. 1999). Though coyotes are a significant mortality factor for gray foxes in southern California (Fedriani et al. 2000) and for other small foxes such as kit foxes (Ralls and White 1995) and swift foxes (Sovoda et al. 1998, Kitchen et al. 1999), coyotes had been previously extirpated from the urban zone and were just beginning to reenter the area during the study (S. Riley, personal observation). Presently, coyotes appear to be much more abundant in southern Marin County (S. Riley, personal observation), but their potential effects on the gray fox population are unknown.

Interactions between bobcats and gray foxes seemed to be more intense in the urban zone than in the rural

zone. Home ranges and core areas overlapped extensively in the rural zone, whereas in the urban zone there was essentially no interspecific overlap of core areas. Certainly not every animal was radiocollared at either site, but uncollared foxes that were seen or trapped in the urban zone were in areas not within bobcat core areas. Further, although predators caused mortalities of urban zone foxes, no such mortalities were reported in the rural zone. Finally, dietary overlap was higher in the urban zone than in the rural zone, especially during the wet season.

The increase in competitive pressure in the urban zone may be related to its smaller area and the hard constraints of development on the east side and the ocean on the west side. In the rural zone, bobcat home ranges are much larger (Riley 1999), which would likely lead to less intense use of the home range and fewer interspecific encounters. The rural zone also included more forested habitat and less grassland, which may have allowed the smaller fox more cover and probably contributed to a decreased reliance on voles by both species. Voles were more important in the diet of urban zone bobcats by both percent occurrence and %FWP. In the urban zone, voles were present in 90% of scats while in the rural zone voles were present in 70% of scats.

The difference in bobcat and fox spatial use in the urban zone was certainly associated with the use of different habitats. In the urban zone, adult female bobcats placed core areas in grasslands near stream courses. Alternately, fox core areas existed in areas of oak woodland and thick coastal chaparral. Foxes also used developed areas in a way that bobcats did not. No bobcats left the natural habitats of the park to enter developed areas outside the park and adult female bobcats did not even utilize areas adjacent to the urban edge (Riley 1999). Conversely, 10 of 20 radiocollared foxes were located in developed areas outside the park and another 4 foxes regularly utilized developed areas within the park such as barns and residences. Three of the other 6 foxes had home ranges adjacent to the urban edge (Riley 1999).

Gray foxes probably do not utilize developed areas solely in order to escape from competitors, but also to take advantage of resources such as ornamental fruits, trash, pet food, and residents who regularly feed wildlife. However, the use of developed areas may also allow foxes to escape competition with larger carnivore species, such as bobcats, that are less able to adapt to humans. Peterson (1988) suggested that humans may sometimes act as a keystone species in carnivore communities by eliminating certain species and thereby allowing inferior competitors to persist. While competition between bobcats and gray foxes may not be so intense as to drive foxes to local extirpation, use of developed areas may allow foxes to maintain higher densities when sympatric with bobcats.

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