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Evidence for male-biased dispersal in bobcats *Lynx rufus* using relatedness analysis

Jan E. Janečka, Terry L. Blankenship, David H. Hirth, C. William Kilpatrick, Michael E. Tewes & Lon I. Grassman, Jr.

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Dispersal is a mechanism hypothesized to have evolved to reduce resource competition, competition for mates and inbreeding. Although bobcats *Lynx rufus* are believed to exhibit high dispersal rates, bobcat dispersal has not been extensively studied due to limitations associated with traditional field research methods. We examined dispersal patterns in a southern Texas bobcat population using eight microsatellites by estimating relatedness within the population and among individuals and observing dispersal events via radio-telemetry. Relatedness among females ($r = 0.050$, $\pm$ 0.042, 95% CI) was significantly higher than among males ($r = -0.075$, $\pm$ 0.031). Pair-wise relatedness distribution for females was significantly different from the expected random distribution and skewed towards 1st and 2nd degree relatives. In contrast, pair-wise relatedness distribution for males was not significantly different from the expected random distribution. Male-biased dispersal and female philopatry were hypothesized to explain the observed patterns in relatedness. Among nine radio-collared females and 12 radio-collared males, two females and six males dispersed away from the study site. This study provides genetic and observational evidence for male-biased dispersal in a solitary felid and is consistent with dispersal trends in mammals.

Key words: Bobcat, dispersal, ecology, Lynx rufus, microsatellite DNA, philopatry, relatedness

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Natal dispersal is defined as the movement of an individual from its site of origin to a new and separate breeding site (Shields 1987, Gompper et al. 1998). Dispersal influences genetic structure, population dynamics and rates of inbreeding and outbreeding (Shields 1987, Blundell et al. 2002). Dispersal affects the impact of local extinction because it influences the probability of recolonization (Chepko-Sade et al. 1987, Blundell et al. 2002). If levels of dispersal are low or highly sex-biased, reintroductions of the non-dispersing sex may be necessary to reestablish a breeding population in areas where it was extirpated (McKelvey et al. 2000, Blundell et al. 2002). The rate and pattern of dispersal also have consequences on social organization and behaviour (Poole 1985). By definition, philopatric individuals in a population live closer to relatives than non-philopatric individuals and may exhibit kin-selected behaviour because the proximity of relatives allows them to impact each other's fitness (Poole 1985, Rubenstein & Wrangham 1987, Shields 1987, Wade & Breden 1987).

In most solitary mammals, females are philopatric, and males disperse from their natal areas (Shields 1987, Blundell et al. 2002). However, there is no consensus on why dispersal is male-biased. In many carnivores, male-biased dispersal may be the ultimate consequence of a mating system where females are solitary, at low densities, and more closely associated with resources due to the energy requirements connected with raising young thereby increasing their tendency for philopatry. In contrast, because males do not assist females in raising young, they may not be as dependent on local resources and are therefore more likely to disperse in search of females (Clutton-Brock 1989). Other hypotheses that explain the evolution of sex-biased dispersal include inbreeding avoidance, resource competition and local mate competition (Greenwood 1980, Dobson 1982, Wolff 1993). Mating systems, resource availability, seasonal cues, hormone levels and adult aggression are proximate factors that influence dispersal patterns in a complex manner, confounding hypotheses on sex-biased dispersal patterns (Mossman & Waser 1999, Dallimer et al. 2002).

It is often difficult and time consuming to obtain data on dispersal using traditional methods, such as radio-telemetry and mark-recapture surveys (Mossman & Waser 1999, Dallimer et al. 2002). The geographical scope of field studies may be insufficient and sample sizes too small for accurate estimates of dispersal rates and distances from observational data (Kamler et al. 2000, Dallimer et al. 2002). In addition, it is often impossible to determine the fate of dispersing individuals and the proportion that become breeders (Vitalis 2002). A consequence of these limitations is that many field studies yield only anecdotal information on dispersal and on the factors that influence it. Bobcats *Lynx rufus* exemplify many of the difficulties noted above in examining dispersal by traditional means. They are solitary, occur at relatively low densities, and subadult bobcats may disperse widely from their natal sites (McCord & Cardoza 1982, Kitchings & Story 1984, Lariviere & Walton 1997).

Advances in molecular genetics now make it possible to estimate dispersal without extensive field data based on population level estimators (Mossman & Waser 1999, Prugnolle & de Meeus 2002). There are several approaches for analyzing genetic data in dispersal studies (Prugnolle & de Meeus 2002). The first is to infer dispersal rates from estimates of gene flow (i.e. Wright's F_{ST} and Slatkin's R_{ST}) that are primarily used to test population differentiation (Wright 1965, Slatkin 1995, Vitalis 2002). A second approach utilizes likelihood estimation of structure under coalescent approximations (Rousset 2001). A third approach incorporates assignment tests that estimate the likelihood that an individual originated from the population in which it was sampled, compared to the likelihood that it originated in other populations sampled (Cornuet et al. 1999, Mossman & Waser 1999, Waser et al. 2001, Dallimer et al. 2002). These approaches have been used to estimate sex-biased dispersal by comparing dispersal estimates between males and females (Blundell et al. 2002, Dallimer et al. 2002, Vitalis 2002). A fourth approach used to examine sex-biased dispersal is to estimate relatedness between individuals and groups of individuals within populations under the assumption that philopatric individuals will be more closely related (Queller & Goodnight 1989, Girman et al. 1997, Gompper et al. 1998, Blundell et al. 2002, Prugnolle & de Meeus 2002, Radespiel et al. 2003). The first

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three approaches require allelic frequency data from several separate populations. In contrast, differences in relatedness among individuals can be estimated for a single population and is especially relevant for examining differences between sexes. Our study used the relatedness approach because only samples from one population were available.

As part of a long-term ecological and behavioural study of bobcats in coastal southern Texas, we examined relatedness of bobcats using microsatellite DNA data to infer dispersal patterns (Blankenship 2000). We tested two predictions that were consistent with male-biased dispersal: 1) the average relatedness among females was higher than among males in the study area, and 2) the relatedness distribution of females was skewed towards higher relatedness values compared to the relatedness distribution of males. We further monitored radio-collared bobcats to observe dispersal events.

Material and methods

Our study was conducted at the Rob and Bessie Welder Wildlife Refuge (WWR; 28°06'N, 97°24'W), San Patricio County, Texas (Fig. 1). The WWR is 31.6 km^2 and represents a mix of chaparral and grassland communities that extend into neighbouring ranches (Drawe et al. 1978). The WWR is adjacent to large (> 7,000 ha) ranches with suitable habitat and abundant bobcat numbers. The Aransas River forms the northern boundary of the WWR. Bobcats have frequently been observed crossing the river, so the river does not appear to be a barrier to their movements. The region has hot summers and mild winters with mean daily temperatures ranging from 8°C in January to 38°C in July (Norwine 1995). Precipitation peaks during May-June and in September, with a yearly average of 89.9 cm (Blankenship 2000). Bobcats are not harvested in the WWR, but harvesting does occur on adjoining ranches. Bobcat densities were approximately 0.50/km^2 during 2000-2001 when the WWR bobcat population was estimated using camera-trapping surveys to be 15 individuals (Heilbrun et al. 2006).

Trapping effort was distributed over 10 years (1993-2002) with a mean of 807 trap-nights per year (range: 231-1,864) and occurred before, during and after dispersal. Bobcats were captured with modified Tomahawk® live traps (107 × 38 × 51 cm). A 51 × 38 × 51 cm extension was added to the trap and was covered with hardware cloth to hold and protect live chickens used for bait. Live chickens were provided food and water *ad libitum*. Trapped bobcats were immobilized with an intramuscular injection of 10-15 mg/kg body weight of ketamine hydrochloride and 0.05 mg/kg body weight of promazine hydrochloride. Bobcats were measured, sexed and aged. Age classes based on dentition and body development were 1) juvenile, 2) < 2 year old and 3) adult. Individuals were radio-collared and released after full recovery.

A vehicle-mounted, 2-element H-antenna and an ATS R2100 receiver were used to locate bobcats to determine if individuals remained in the WWR or dispersed out of the refuge. Animal locations were estimated using the homing-in technique described by White & Garrott (1990). Driving and walking on roads and fencelines, pipelines and powerlines was used to approach and locate bobcats. Animal

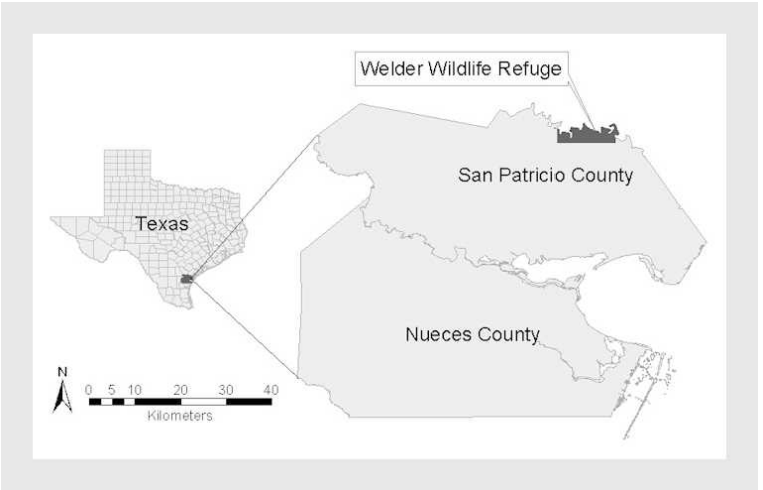


Figure 1. Location of study area in the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas, from which bobcat samples were obtained during 1993-2002.

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locations were plotted on 7.5 USGS topographic maps or aerial photographs. Aerial radio-tracking was conducted periodically to locate bobcats off the WWR. Locations plotted on topographic maps were digitized using PC Arc/Info. Radio-collared bobcats were monitored 3-5 times a month. Bobcats were classified as residents or non-residents. Non-resident bobcats exhibited a nomadic movement pattern with temporary activity areas and eventually moved away from the WWR. Bobcats were residents if they used a defined range for at least six months. Permanent movement out of the WWR was considered a dispersal event.

Blood and hair samples were obtained from 22 bobcats between 1993 and 2001 (Blankenship 2000). Blood samples were maintained in Longmire's lysis buffer (Longmire et al. 1997). Hair samples were placed in paper envelopes and stored in a sealed plastic bag containing silica gel. Genomic DNA was isolated from blood using the conventional proteinase K/phenol/chloroform method (Blin & Stafford 1976, Sibley & Ahlquist 1981). Blood samples that were not successfully extracted were reextracted using a modified Chelex protocol (Walsh et al. 1991). Five hair roots per hair sample were extracted using the method of Higuchi (1989). Hair samples were genotyped twice at homozygous loci to prevent error due to allelic drop out.

We amplified eight microsatellites (FCA 26, FCA 35, FCA 43, FCA 45, FCA 77, FCA 90, FCA 96 and FCA 126; Menotti-Raymond et al. 1999). The polymerase chain reaction (PCR) was conducted in a 15 μl reaction volume containing 0.25 mM of each of dNTP, 1 × PCR buffer (10 mM Tris-HCl [pH 8.3], 50 mM KCl; Perkin Elmer Biosystems Inc.,Wellesley, MA), 2.0 mM $MgCl_2$, 1 unit of AmpliTaq (Perkin Elmer Biosystems Inc.), 2.5 pmoles of forward primer and 2.5 pmoles of reverse primer. The PCR reaction conditions included an initial denaturing step of 94°C for one minute, 10 cycles of 94°C for 15 seconds, 53°C for 15 seconds and 72°C for 45 seconds, followed by 30 or 50 cycles of 89°C for 15 seconds, 53°C for 15 seconds and 72°C for 45 seconds. A final extension step of 72°C for 30 minutes was included for all loci except FCA 26. The denaturing temperature was lowered to 89°C after 10 cycles to decrease the amount of Taq inactivated by the high temperature of each denaturing step (Menotti-Raymond et al. 1999). Blood and soft tissue samples were amplified with 30 cycles and hair samples with 50 cycles.

The PCR product was fractionated on a 1.2% agarose minigel, stained with ethidium bromide (0.5 μg/ml) and observed under ultraviolet light. Samples with visible PCR product were fractionated with an ABI 310 instrument (Applied Biosystems, Foster City, CA, USA) and sized with Genotyper 2.0 software (Applied Biosystems) in the DNA Analysis Facility of the Vermont Cancer Center.

Linkage disequilibrium and Hardy-Weinberg equilibrium (HWE) were tested using the GENEPOP 3.1 software program (Raymond & Rousset 1995). The population was tested for deviations from equilibrium at each locus and for all loci. The population was also tested for heterozygote deficiency and excess at each locus and global equilibrium because both would violate assumptions of the model used to estimate relatedness. A Markov chain algorithm method was used for all exact tests of HWE (Guo & Thompson 1992). Numbers of batches were increased until all standard errors of P values were below 0.01 as recommended by GENEPOP (Raymond & Rousset 1995). Bonferroni corrections for multiple comparisons were applied to test for HWE and linkage disequilibrium (Rice 1989).

Relatedness estimates were used to test sex-biased dispersal hypotheses assuming that differences in dispersal rates of sexes would affect relatedness between and among each sex. The RELATEDNESS 5.0.8 software program was used to estimate the Grafen's relatedness coefficient (r; Queller & Goodnight 1989). This is an estimate of the proportion of alleles that individuals share by common descent, while taking into account the population frequencies of the alleles. Grafen's relatedness coefficients range from -1 to +1, with positive r-values indicating more shared alleles than expected, and negative r-values indicating fewer shared alleles than expected. Two randomly chosen unrelated individuals are expected to have an r-value equal to 0, 2nd degree relatives an r-value of 0.25, and 1st degree relatives (parent-offspring or siblings) to have an r-value equal to 0.5 (Queller & Goodnight 1989, Blouin et al. 1996). Relatedness coefficients were calculated for all dyads (pairs), among and between males and females, between males and all individuals, and between females and all individuals. RELATEDNESS 5.0.8 calculated 95% confidence intervals for all group r-values with the jackknife resampling method across loci (Queller & Goodnight 1989). Statistical differences between group r-values were tested with 95% confidence intervals. The distributions of pair-wise r-values were tested for deviations from the expected random distribution based on mean and standard deviation of r-values with the χ^2 goodness-of-fit test.

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Table 1. Identity, capture date, last location, age at capture, residency status and dispersal events observed for 10 female (F) and 12 male (M) bobcats at the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas, during 1993-2002. In residency status, resident refers to an individual with a distinct home range, and non-resident to an individual with no distinct home range.

Identity	Capture date	Last located	Age at capture	Residency status	Dispersal events
F7	19.11.1993	29.12.1997	Adult	Resident	-
F32	12.06.1995	10.10.2002	Adult	Resident	-
F38	22.04.1996	03.05.1996	Adult	Non-resident	-
F39	24.04.1996	09.12.1999	Adult	Resident	-
F40	30.05.1996	23.12.1999	Adult	Resident	-
F41	16.07.1996	21.07.1996	Adult	Non-resident	Dispersed
F48	20.11.2000	17.06.2001	Juvenile	?[2]	-
mF48[1]	20.11.2000	20.11.2000	Adult	?[2]	-
F52	14.01.2002	16.01.2002	Juvenile	Non-resident	Dispersed
F54	08.03.2002	26.08.2002	Juvenile	Non-resident	-
M12	01.03.1994	23.10.1998	Adult	Resident	-
M42	16.04.1997	23.06.2001	Adult	Resident	-
M43	21.05.1997	03.07.1997	Adult	Non-resident	-
M44	01.03.1998	22.10.1999	Adult	Resident	Dispersed
M46	06.09.2000	14.03.2001	Adult < 2	Non-resident	Dispersed
M47	19.10.2000	14.12.2002	Adult	Resident	-
M49	20.11.2000	13.01.2001	Adult < 2	Non-resident	Dispersed
M50	15.01.2001	31.03.2001	Adult < 2	Non-resident	Dispersed
M51	09.05.2001	14.05.2001	Adult < 2	Non-resident	Dispersed
M53	21.01.2002	06.06.2002	Juvenile	?[2]	-
M55	14.03.2002	03.05.2004	Adult	Resident	-
M56	25.03.2002	29.04.2004	Adult < 2	Resident	Dispersed

[1] The female mF48 was identified as the mother of juvenile F48 based on both behaviour and genetic data.
[2] Died before residency status could be established.

Results

We captured 56 bobcats between 1993 and 2002. The 30 males and 26 females captured suggested no sex-bias in trapping. A mean of five bobcats were captured per year, yielding a capture rate of one bobcat per 159 trap-nights. Genetic samples were only available for 22 bobcats (10 females and 12 males) captured between 1993 and 2002 (Table 1). Radio-telemetry observations were made on 21 bobcats. Of the 21 bobcats monitored via telemetry, eight (two females and six males) were observed to disperse out of the study area. The remaining 12 stayed in the WWR, although sufficient telemetry data were not available for two cats to classify residency. Of the females, four were classified as resident, four as non-resident and one died before enough data were available to classify residency (see Table 1). There were no telemetry data available for one female. Of the males, six were classified as resident, five as non-resident, and one died before enough data were available to classify residency (see Table 1). Dispersal out of the refuge occurred from the age of 10-20 months. Three females and six males were estimated to be < 2 years of age; of these, one female dispersed, one female remained in the WWR but was classified

Table 2. Number of females (N_f) and males (N_m) examined at eight microsatellite loci, total number of alleles, number of alleles in females (f) and males (m), and observed (H_o) and expected (H_e) heterozygosity for bobcats sampled at the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas, during 1993-2002.

Locus	N_f	N_m	Size	Number of alleles	Number of alleles (f)	Number of alleles (m)	H_o	H_e
FCA 26	10	12	118-134	8	6	7	0.82	0.78
FCA 35	10	12	120-150	10	8	10	0.82	0.85
FCA 43	10	12	112-120	5	5	5	0.76	0.76
FCA 45	8	11	163-171	5	4	5	0.70	0.75
FCA 77	10	12	133-151	7	4	7	0.64	0.69
FCA 90	9	12	111-121	7	6	7	0.86	0.78
FCA 96	10	12	177-203	7	6	6	0.82	0.78
FCA 126	10	10	129-140	6	5	6	0.76	0.80
Mean	9.63	11.63	n/a	6.88	5.5	6.63	0.77	0.77
SE	0.27	0.27	n/a	0.5	0.46	0.56	0.02	0.02

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as a non-resident, and one died (see Table 1). Of the six males that were < 2 years of age, five dispersed and one died in the WWR (see Table 1). Two adult bobcats estimated to be two years of age dispersed; one of these was a male classified as resident and one was a female classified as a non-resident prior to dispersal (see Table 1).

The mean number of alleles per locus was 6.88 (range: 5-10), and the average expected heterozygosity was 0.77 (0.69-0.85; Table 2). All loci were found to be in linkage equilibrium after Bonferroni correction for multiple tests (P = 0.05). The null hypothesis that alleles are in HWE was accepted for all loci after Bonferroni correction (P = 0.05). When all loci were summed using Fischer's method, HWE was accepted (P = 0.391; Raymond & Rousset 1995). Heterozygote deficit and excess was rejected for all loci.

Females as a group and males as a group were related to the whole WWR population with r = -0.045 (± 0.02 and 0.02, 95% CI, respectively; Fig. 2). Relatedness within females was r = 0.050 (± 0.042), within males it was r = -0.075 (± 0.031), and between females and males it was r = 0.020 (± 0.025; see Fig. 2). Relatedness among females was statistically greater than relatedness among males (P < 0.05). Females were statistically more related to each other than to the whole population (P < 0.05). Relatedness among females was greater than the relatedness of females to males, although the difference was not statistically significant. Males were statistically less related to each other than to the whole population (P < 0.05). Relatedness among males was statistically less than the relatedness of males to females (P < 0.05).

The r-value distribution for female dyads (Fig. 3A) was found to be statistically different from the expected random distribution (P < 0.05), but the null hypotheses of random distribution could not be rejected for male and female-male r-value distributions (Figs. 3A and 3C) or for the distribution of r-values for all dyads (Fig. 3D).

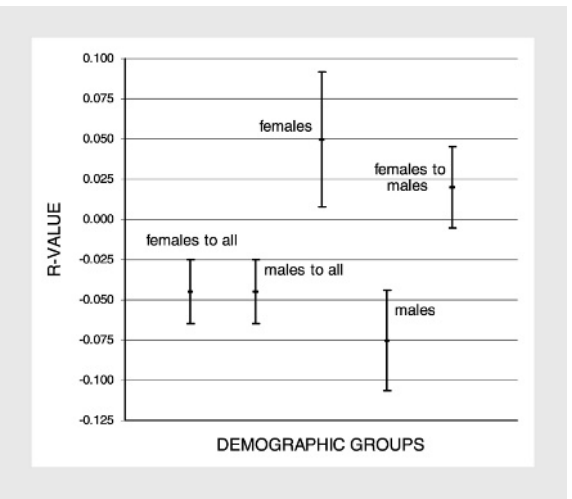


Figure 2. Group r-values and 95% confidence intervals within and between sex-defined demographic groups of bobcats sampled at the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas, during 1993-2002. The y-axis represents Grafen's relatedness coefficient and values were calculated in RELATEDNESS 5.0.8

Discussion

High allelic diversity, relatively high heterozygosity and lack of deviations from the Hardy-Weinberg equilibrium suggest that WWR bobcats are part of a large, admixed population. This is supported by field observations; the WWR is not geographically isolated, and bobcats frequently move to and from the refuge. Eight of 21 bobcats monitored during this study dispersed from the WWR, two of which where adult bobcats > 2 years of age. Bobcats have been observed to move frequently between adjacent areas and to often make long-range dispersal movements (Bailey 1974, McCord & Cardoza 1982, Kitchings & Story 1984, Knick 1990, Lariviere & Walton 1997). Bailey (1974) recaptured five kittens that moved 19-29 km from their natal area. Knick (1990) observed mean dispersal distance in Idaho, USA, to be 22.1 km (range: 0-56) for 10 bobcat females, but did not have data on dispersing males. We did not have data on distance travelled during dispersal events in our study area. In southern Texas, bobcat dispersal has often been observed, even through suboptimal habitat.

The power of relatedness analysis is strongly correlated with number of loci, allele number and heterozygosity (Blouin et al. 1996). Despite only eight loci used in our study, the allele number and heterozygosity were high among the loci sampled, and therefore the loci examined provided sufficient resolution for the relatedness analysis conducted (Blouin et al. 1996). Males and females were statistically less related to the WWR population than would have been expected by chance (r = -0.045 ± 0.02, respectively), which likely reflects bobcat movement between WWR and adjacent areas. Female bobcats were more related to each other than to the population as a whole (see Fig. 2). One explanation for this is that there were proportionately more relatives

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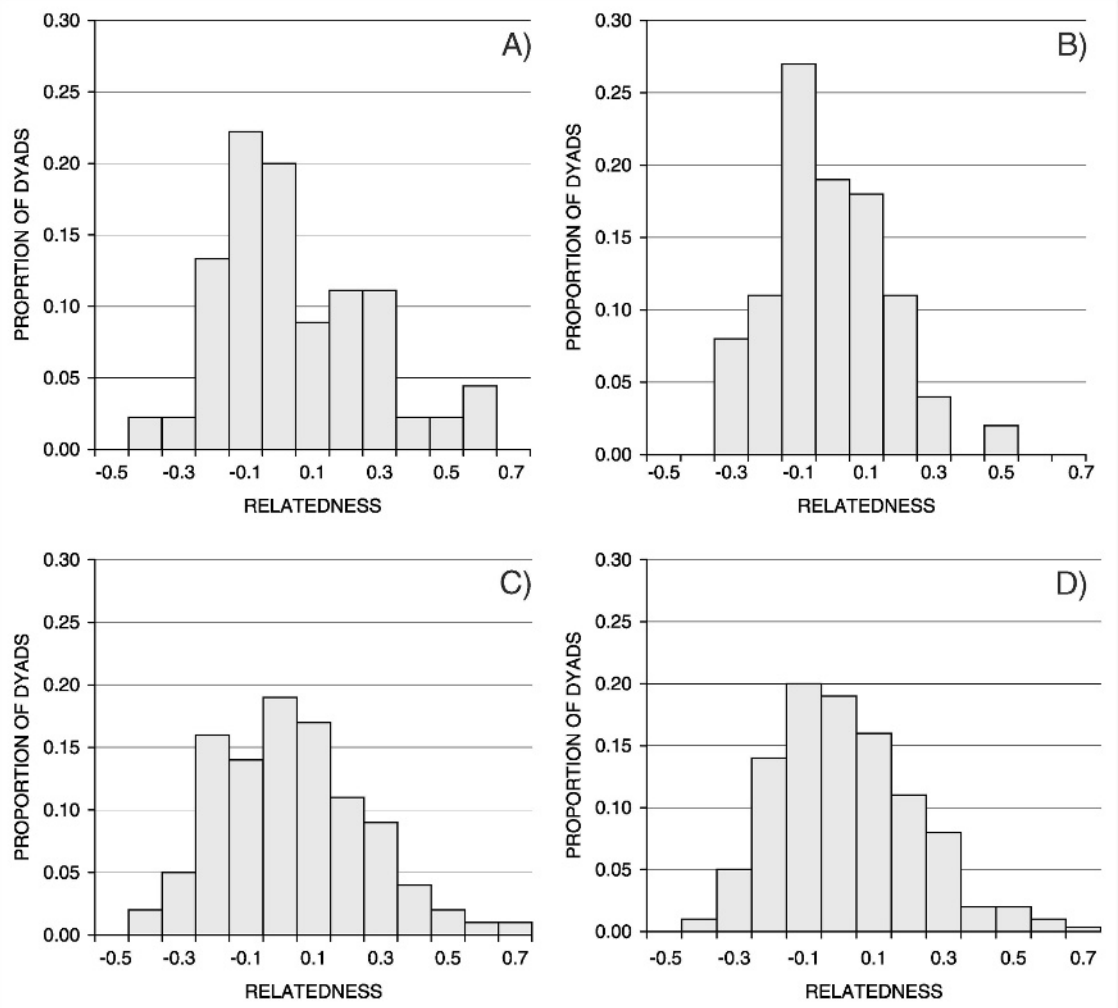


Figure 3. Distributions of pair-wise r-values calculated in RELATEDNESS 5.0.8 for bobcat female dyads (A; N = 45), male dyads (B; N = 91), female-male dyads (C; N = 140) and all dyads (D; N = 276) in the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas sampled during 1993-2002.

among females than among the entire population. This pattern would occur if female offspring were philopatric and tended to stay in their natal area. A second explanation is that females had higher relatedness because they shared alleles through descent due to a population bottleneck (Hartl & Clark 1997). But if the population had undergone a bottleneck, males also would be expected to share alleles through descent and have higher relatedness than expected by chance. However, males were statistically less related to each other than females (see Fig. 2). This pattern is consistent with the hypothesis that females are philopatric and males are the primary dispersers.

The relatedness coefficients (r) for female dyads were found to be statistically different from the expected random distribution. The distribution was skewed towards positive values and showed three asymptotes with peaks around -0.1, 0.2 and 0.6 (see Fig. 3A). The relatedness coefficients suggest that the dyads fell into three categories that corresponded to: 1) unrelated individuals ($-1 < r < 0.125$), 2) 2nd degree relatives ($0.125 < r < 0.375$) and 3) 1st degree relatives ($0.375 < r < 0.625$; Queller & Goodnight 1989, Blouin et al. 1996). This distribution showed that the high group r-value of the females was due to a high proportion of values that are characteristic of 1st and

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2nd degree relatives. In contrast, r-values for male dyads (see Fig. 3B) were not statistically different from a random distribution, which was likely due to higher dispersal rates in males. The distributions of r-values for female-male dyads and all dyads (see Figs. 3C and 3D) were also not statistically different from a random distribution. This suggests that dispersal in bobcats, primarily through males, is adequate to maintain random distributions of pair-wise relatedness values between males and females in an area, and the population as a whole.

The genetic evidence for the male-biased dispersal hypothesis is consistent with our radio-telemetry data on bobcats in the WWR. Radio-telemetry data were available for 21 individuals analyzed in this study. Of the nine female bobcats captured, seven remained in the WWR. Four of these had established home ranges and one died before establishing a home range. In contrast, of the 12 males captured and radio-collared, six remained in the refuge and all six established a home range. Two females and six males were observed to disperse from the WWR. Five of six captured male bobcats < 2 years of age dispersed from the WWR in contrast to the one of three females < 2 years that dispersed. Radio-telemetry data on bobcat residency and dispersal supported the male-biased dispersal hypothesis used to explain higher relatedness among females.

The dispersal patterns observed in bobcats in the WWR are consistent with other studies that have found dispersal in mammal species to be primarily male-biased (Greenwood 1980, Dobson 1982, Cockburn et al. 1985, Gompper et al. 1998, Kerth et al. 2002, Radespiel et al. 2003, Möller & Beheregray 2004). Higher relatedness among females than among males has been observed in African lion *Panthera leo* prides, and has been explained by kin selection in females and inbreeding avoidance in males (Packer et al. 1991, Spong et al. 2002). In solitary felids such as European lynx *L. lynx*, cougars *Puma concolor* and tigers *Panthera tigris* there are field data that suggest that female juveniles may establish home ranges in their natal areas (Eisenberg 1986). This is consistent with the higher relatedness among females in our study.

Sex-biased dispersal is hypothesized to have evolved in response to inbreeding depression, resource competition and local mate competition (Greenwood 1980, Dobson 1982, Shields 1987, Wolff 1993). The mating system in bobcats may be the most important factor in sex-biased dispersal (Dobson 1982, Shields 1987). Females are a limiting resource for males during the mating season (Shields 1987). Males compete directly for females, and their fitness is directly related to the number of females with which they breed (Shields 1987). Yearling male bobcats are likely subordinate to territorial males and appear to be pushed out of their natal area, unless there is a vacant territory (McCord & Cardoza 1982). This is consistent with observations indicating that offspring most often disperse at the beginning of their first active breeding season (McCord & Cardoza 1982, Kitchings & Story 1984, Lariviere & Walton 1997).

In contrast to males, female fitness is limited by intrinsic reproductive constraints and not by the number of males with which they breed, and therefore males are not a limiting resource (Krebs & Davies 1993). It is believed that female bobcats do not compete with other females during the mating season (Shields 1987). Pressure from adults will thus not be as great for yearling females as for males. Pressure on daughters should be even lower from their mothers than from unrelated females. If a daughter can mate and have offspring, and there are enough resources in the natal area to support both, the fitness of the mother also increases (Shields 1987, Krebs & Davies 1993). Therefore, mothers should be tolerant toward daughters sharing their home range. Kitchings & Story (1984) documented two adult female bobcats with young simultaneously using the same territory. Chamberlain et al. (2003) also reported instances where home ranges and core areas of two females nearly completely overlapped. Overlapping home-range patterns, that depart from the typical bobcat social structure, may eventually be explained by mother-daughter relationships between individuals.

Sex-biased dispersal is further adaptive because male dispersal minimizes inbreeding costs (Greenwood 1980, Wolff 1993). It is believed that in mammals, females benefit more from familiarity with food resources than males because of the higher energy requirement for females when providing parental care (i.e. nursing, feeding and protection), and therefore they should have greater tendency for philopatry (Greenwood 1980, Shields 1987). Variability observed in dispersal patterns is likely due to changing environmental conditions that alter the costs and benefits of dispersal and philopatry for each sex.

In this study, we used microsatellite data to provide evidence for male-biased dispersal of bobcats. Two genetic analyses and telemetry observations of dispersal events supported the hypothesis that bobcat dispersal is male-biased. These patterns are consistent

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with studies of other carnivores that have found male dispersal to be the primary mechanism for minimizing inbreeding and resource competition (Greenwood 1980, Dobson 1982, Cockburn et al. 1985, Moehlman 1987, Shields 1987, Gompper et al. 1998). Our study demonstrates the utility and sensitivity of relatedness analyses for examining dispersal with molecular data from a single population.

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