

Evidence for female-biased dispersal in North American porcupines (*Erethizon dorsatum*)

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Abstract

Although sex biases in natal dispersal are well known among birds and mammals, female-biased dispersal in polygynous mammals is rare. North American porcupines are polygynous and recent evidence suggests that natal dispersal in this species may be female-biased. We used data on disappearances, immigration, and reproductive behaviours to characterize natal dispersal and examine the extent to which inbreeding avoidance may motivate natal dispersal in porcupines. We predicted that, if female porcupines were the predominant dispersers, rates of disappearance and immigration would be higher for females than for males. Also, if females disperse to avoid mating with fathers, then the mean age of females at first conception should be less than the mean residence time of adult males. Population data suggested that natal dispersal was female-biased because a higher proportion of females (31%) disappeared than males (11%), and 78% of 18 immigrants observed in the population were females. Data on pregnancies indicated that female age at first conception (≈ 25 months) was less than the mean residence time of adult males (≈ 26 months), suggesting that female porcupines may disperse to avoid incestuous matings with fathers. Little is known regarding potential resource competition between mothers and offspring, or on how philopatric males avoid mating with their mothers. Additional data are needed in these areas to interpret dispersal tendencies in porcupines.

Key words: inbreeding avoidance, disappearances, immigration, mate-guarding

INTRODUCTION

The widespread occurrence of natal dispersal in animals is thought to persist because it is an effective strategy to reduce: (1) inter- and/or intrasexual competition; or (2) inbreeding (Pusey, 1987; Clutton-Brock, 1989; Johnson & Gaines, 1990). Natal dispersal, hereafter referred to as 'dispersal' and defined as the movement of an individual from its birthplace to where it first reproduces, is primarily female-biased in birds and male-biased in mammals (Greenwood, 1980). Recent debate has focused on the extent to which competition and inbreeding avoidance explain the pronounced class difference in the sex of dispersing young (Pusey, 1987). Although resource-based competitive interactions may influence dispersal tendencies (Dobson, 1982; Liberg & von Schantz, 1985), evidence is mounting in support of the inbreeding-avoidance hypothesis (Cockburn, Scott & Scotts, 1985; Clutton-Brock, 1989; Wolff, 1992; Bolinger, Harper & Barrett, 1993).

The emigration of either sex can diminish the potential for inbreeding, and Greenwood (1980) argued that differences in the predominant mating system between birds (resource defence and monogamy) and mammals (mate defence and polygyny) accounted for female dispersal in birds and male dispersal in mammals. In monogamous birds, males must acquire and defend territories with sufficient resources to attract females, and because this may be best accomplished near the natal range, males are philopatric and females disperse to avoid inbreeding. In polygynous mammals, however, females are usually philopatric because they invest substantially more in offspring owing to the energetic costs of gestation, lactation, and sole care of offspring. Although this mating systems model was useful for interpreting variation in sex-biased dispersal among birds and mammals, female dispersal among polygynous mammals remained enigmatic.

Dispersal patterns ultimately depend on the relative costs and benefits of dispersal and philopatry to each sex (Pusey, 1987). For example, among polygynous mammals in which female age at first conception exceeded the mean residence time of adult males, males dispersed, whereas when the mean age of first concep-

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tion was the mean residence time of adult males, females dispersed (Clutton-Brock, 1989). These results support the hypothesis that sex-biased dispersal minimizes the probability of females breeding with related males. Subsequently, Wolff (1992, 1993) demonstrated that juvenile dispersal is correlated with the presence of the opposite- but not the same-sex parent in the natal home range, suggesting that inbreeding avoidance rather than intrasexual competition determines which sex disperses.

North American porcupines (*Erethizon dorsatum*) are polygynous mammals for which recent evidence suggests dispersal may be female-biased. Among porcupines in the north-eastern United States, Roze (1989) noted that three juvenile female porcupines dispersed and four juvenile males remained in their natal territories. Although competition for resources and inbreeding avoidance were discussed as factors contributing to female dispersal in this species (Roze, 1989), additional data are needed to verify dispersal tendencies. Also, information on the residence times of adult males may provide insight into whether dispersal is motivated by inbreeding avoidance in porcupines.

In this paper, we use data on disappearances, immigration, female age at first conception, and residence time of adult males collected during a five-year study in the Great Basin Desert of north-western Nevada to examine dispersal in porcupines. Although the best way to examine dispersal may be through direct observation of emigrating individuals via radiotelemetry (Ferrer, 1992; Schwartz & Franzmann, 1992; Thomson, Rose & Kok, 1992; Van Vuren & Armitage, 1994), an alternative approach is to examine population data on disappearances and immigration (Waser, Creel & Lucas, 1994). We predicted that if females were the predominant dispersers, then both disappearance rates and immigration rates would be higher for females than for males. Second, if subadult females disperse to minimize inbreeding, then the mean age of females at first conception will be less than the mean residence time of adult males.

METHODS

Study area and population data

Porcupines were studied from December 1988 to June 1993 in the Granite Range of north-western Nevada, an insular 2700-m mountain of the Great Basin Desert. The focal site was a 20-km² enclosed basin (Granite Basin; 40°44'N, 119°20'W) between 1520 and 1640 m elevation (Berger, 1986; Sweitzer & Berger, 1992). Individual porcupines were captured by immobilization with a jab stick using a mixture of ketamine hydrochloride (dosage = 10 mg/kg) and xylazine hydrochloride (dosage = 4 mg/kg). Captured or recaptured animals were weighed and measured for mid-sternal chest circumference, mid-dorsal and mid-ventral body length from tip of nose to end of tail, and length of the left foot pad. Body dimensions were not measured

during 1988–89. All animals were ear-tagged with numbered, colour-coded plastic tags (Allflex style C12334–8), and we fitted 44 porcupines with radio-collars for varying periods (AVM Instrument Company, Livermore, California; Custom Electronics transmitters, Urbana, Illinois).

We assessed the size and age structure of the population of porcupines in Granite Basin using data collected during surveys in each of 5 population years from 1988 to 1993. Population years were from 15 April to 14 April, based on parturition from late April through mid-June (Sweitzer & Holcombe, 1993). Most population data were obtained during surveys within the autumn and winter period (September–March) when porcupines occupied winter den sites and congregated to forage in 'groves' of buffalo-berry (*Shepardia argentia*) and willow (*Salix* spp). Porcupines were located using dogs, a spotting telescope, radiotelemetry, night vision equipment, tracking when snow cover was present, and systematic searches of foraging areas and den sites (rock outcroppings, juniper trees, groves) regularly used by porcupines. During the autumn and winter period, surveys were conducted on 37, 65, 36, 50, and 49 days in population years 1988–89, 1989–90, 1990–91, 1991–92, and 1992–93, respectively. On average, we noted 501 locations (range = 336–695) of an average of 63 (S.D. = 15.4) individual porcupines each year from 1988 to 1993.

We assumed that the number of different animals observed approached a total enumeration of porcupines in the study area each year (5 animals located around the periphery of the Granite Basin were not considered part of the population). Thus, the population size was the sum of all individuals observed in the Granite Basin during a given year. Forty-nine dead porcupines located during surveys were categorized as starvation, predation, or unknown, based on examination of carcass remains (Sweitzer, 1996).

Porcupines captured during 1988–89 were aged as juveniles, yearlings and ≥ 2 years old based on body mass (Dodge, 1982), thereafter, newly identified animals observed in the population were aged based on comparisons of body dimensions to those of known-aged individuals or minimum-aged individuals for the oldest cohort. Although we were able to distinguish between 8 age classes by the end of the study, for the analyses in this paper, animals were grouped into 3 age classes; juveniles, yearlings, and ≥ 2 years old.

Immigration and disappearances

Because all resident porcupines were tagged, we were able to identify unknown animals or 'immigrants' in the population from 1989 to 1993. Disappearance rates were calculated by tabulating the number of animals from the population in one year that were unaccounted for in the next year's survey (immigrants and animals known to have died were excluded). We used Rice's conditional binomial exact test (Rice's CBET; Rice,

1988) to compare immigration and disappearance rates between males and females.

Although known mortalities were accounted for in analyses, undiscovered deaths might have biased the disappearance data. For example, data on known mortalities indicated that predation rates were very high during the last 2 years of the study compared to the first 3 years; 22 predator-killed porcupines were located in 1991–92 and 1992–93 compared to only 4 in 1988–89, 1989–90, and 1990–91 (Sweitzer, 1996). High disappearance rates during 1991–92 and 1992–93 implied that we did not find all the porcupines that were preyed upon in those years, and because this undiscovered predation could have confounded analyses of presumed dispersal-based disappearances, we limited analyses of disappearances to the first 3 years of the study.

Starvation resulted in 13 mortalities during the study and we used data on body condition to examine how undiscovered starvations might have influenced disappearance rates. It is reasonable to expect that animals that starve overwinter are in poor body condition compared to those that survive. Thus, if the body condition in early winter of porcupines that subsequently disappeared was poor compared to the condition of animals that remained in the population, then disappearance data could have been biased by unidentified starvation mortalities. To evaluate this possibility, we used the residuals from the regression of the natural log of body mass on the natural log of estimated body volume [$\text{LN}(\text{body mass}) = -3.89 + 0.71\text{LN}(\text{body volume})$, $\text{adj } R^2 = 0.90$, $P < 0.0001$, $n = 69$] as a measure of condition as detailed by Sweitzer & Berger (1993); animals with positive and/or larger residuals were considered to be in relatively good condition compared to animals with negative and/or smaller residuals. In earlier work developing this index to body condition based on mass per unit volume, we found that it performed better than body mass alone because it allows for comparisons among individuals varying in absolute body size (Sweitzer & Berger, 1993). We included only one measure per animal collected within the period from September to December in 1989–90 and 1990–91 in the regression model (condition measures for animals from 1988–89 were not calculated because body dimensions were not measured in that year). We used a factorial analysis of variance (ANOVA) with sex, age, and fate as independent variables to examine how body condition may have influenced the probability of an animal's disappearance and to infer whether differences in disappearances were related to biases in undiscovered starvations.

Intrasexual differences in habitat use could also bias disappearance rates if it were more difficult to locate animals in one habitat than another. To evaluate this hypothesis, we examined data on both habitat use and the sexes of porcupines that were not located during one year's survey, but were subsequently relocated in the population in later years. Porcupines used 3 primary habitat types in the Granite Basin: groves, juniper trees, and rock outcroppings. Groves and juniper trees were

used for both foraging and den sites, while rock outcroppings were used for denning only. Grove areas were small compared to rock outcroppings and areas with juniper trees, so porcupines occupying groves were easily located. Numerous rock outcroppings were distributed throughout the study area, but because traditional den sites were known, porcupines were also readily located when in these areas. Juniper trees were widespread and difficult to search effectively, and this type of habitat was the most difficult in which to find animals. Because radio-collared porcupines were located irrespective of the type of habitat they occupied, we analysed data on the locations of radio-collared porcupines to determine whether differences in habitat use by male and female porcupines could have biased disappearance rates. We assumed that observations were independent when separated by one day and used one observation per radio-collared individual per day. Analyses of habitat use were restricted to autumn and winter observations, because most of the individuals included in the population were located during this period. Information on porcupines not observed and then subsequently relocated can also provide insight into whether one sex was more difficult to locate during population surveys.

Female age at first conception and adult male residence times

Inbreeding between fathers and daughters could occur if a male porcupine maintained his breeding status from the time of conception of his female offspring until the time of first conception for that offspring. Observations of mate-guarding associations and evidence from quill impalements and injuries suggest that male porcupines do not enter the breeding population until they are ≥ 29 months old or \geq two years old (Sweitzer & Berger, 1997). We assessed the residence time of adult males by noting the number of breeding seasons (September and October) in which males \geq two years old guarded females (Roze, 1989) and summing the number of months from September of the first active breeding season until October of the last active breeding season. For example, if an adult male guarded females for 3 breeding seasons, his residence time was 26 months. We only included ≥ 2 -year-old males that were observed in the population for a minimum of 3 breeding seasons because animals that disappeared may have guarded females elsewhere. We assessed female age at first conception using information on pregnancy status from serum progesterone levels during the ≈ 210 -day gestation period (Sweitzer & Holcombe, 1993). We defined female age at first conception as the period from birth to first conception + the 7-month gestation period. Including the 7-month gestation period in this definition is consistent with the point that an adult male would need to be in residence from the time of conception of female offspring until she first conceives for close inbreeding to occur.

Table 1. Summary of population data for porcupines from the Granite Range, Nevada. For each age and sex class, N is the number observed in the population, M is known mortalities, D is the number disappearing (i.e. not observed in the subsequent year's population survey), and I is the number of immigrants

Age/sex	Population year																			
	1988–89*				1989–90				1990–91				1991–92				1992–93			
	N	M	D	I	N	M	D	I	N	M	D	I	N	M	D	I	N	M	D	I
Juvenile males	6	0	1		8				15	1	4		13	2	9		5	2	3	
Juvenile females	11	4	2		2				12		11		4	3	1		8	1	7	
Yearling males	2				6		1		8				10	1	4		2			
Yearling females	5	1	1		7	1	2		3	1	2	2	1				1			1
≥ Two-years-old ♂	12	5			10		1		18		4	2	22	4	7		16	4	3	
≥ Two-years-old ♀	20		8		18	1	3		26		4	3	25	4	8	3	14	9	6	
Totals	56	10	12		51	1	2	7	82	2	25	7	75	14	29	3	46	16	19	1

* We could not identify immigrants in 1988–89 because this was the first year of the study

RESULTS

In 1988–89, 1989–90, and 1990–91, proportionally more juvenile and yearling females disappeared (17 of 33) from the population than juvenile and yearling males (5 of 44; Table 1; $P=0.002$, Rice's 1-sided CBET), whereas disappearance rates were similar for ≥ two-year-old females (13 of 64) and ≥ two-year-old males (4 of 35; Table 1, Fig. 1; $P=0.18$, Rice's 1-sided CBET). Also, disappearance rates were higher for juvenile and yearlings than for the older females (Rice's 1-sided CBET = 0.02). Although these results suggest that more juvenile and yearling females dispersed than the males of the same age, disappearance rates could be biased by undiscovered mortalities if there were sex differences among undiscovered deaths.

The two primary sources of mortalities during the study were predation and starvation. Data on known predator kills indicated that the predation rate was low during the first three years when disappearances were female-biased. Only 4 of the 26 predator-killed porcupines found during the study were preyed on in 1988–89, 1989–90, and 1990–91, suggesting that predation contributed little to any potential biases in the disappearance data because of undiscovered mortalities.

Sex biases in starvation are another potential factor influencing disappearance rates. Results from the condition analyses, however, indicated that there were no differences in body condition in early winter of porcupines that disappeared compared to those that did not (factorial ANOVA, $F = 0.84$, $d.f. = 1,60$, $P = 0.36$). Similarly, there were no differences in body condition in early winter between males and females or between juveniles and yearlings and ≥ two-year-olds (factorial ANOVA, $F = 0.49$ for sex, $F = 1.56$ for age, $d.f. = 1,60$, $P > 0.22$ for both comparisons). Also, there were no significant interactions in the model ($P > 0.24$ for all two- and three-way interactions). These results suggest that disappearance rates were not biased because of higher rates of unidentified starvations among disappearing porcupines of different ages or sex. Furthermore, starvations were somewhat male-biased

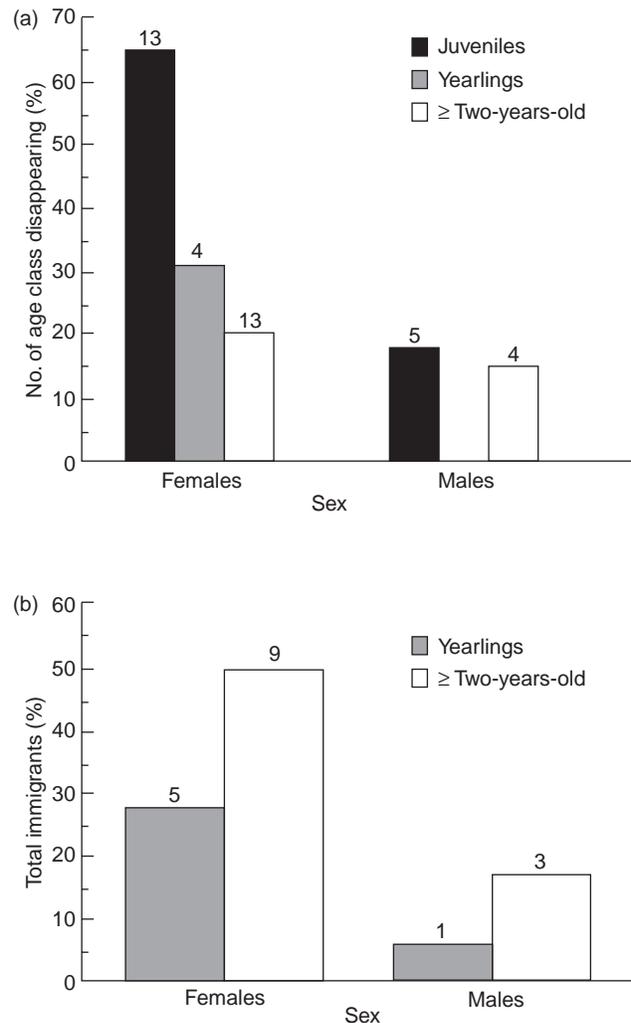


Fig. 1. (a) Proportions of females and males disappearing from the population and (b) male and female immigrants observed in the population. The numbers above the bars are the numbers of disappearances or immigrants noted in each age and sex class.

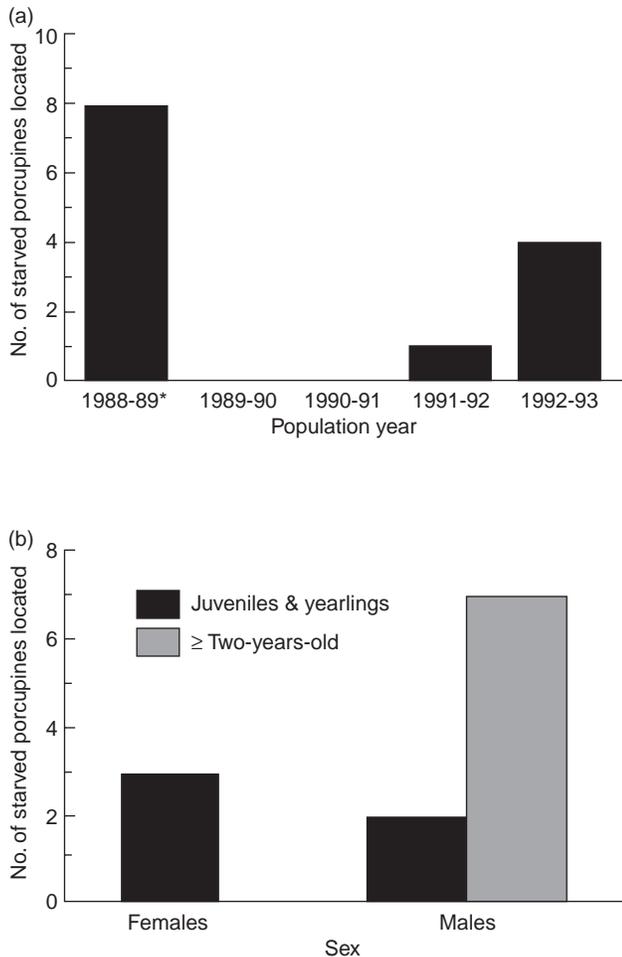


Fig. 2. Distribution of starved porcupines located (a) during five different population years and (b) among male and female porcupines. *In 1988–89 the sex and age of one starved porcupine were not known.

(Fig. 2, $\chi^2 = 3.0$, $d.f. = 1$, $0.05 < P < 0.10$), suggesting that the female-biased disappearance rate was not due to higher risk of starvation among female porcupines.

Habitat use by radio-collared male and female porcupines differed during autumn and winter (Fig. 3; $G = 26.5$, $d.f. = 2$, $P < 0.0001$). Females used rock outcroppings proportionally more than males, whereas males occurred more frequently in the difficult-to-survey juniper forests (Fig. 3), suggesting that any unknown bias in the disappearance data due to differences in habitat use would have caused overestimation of disappearances of male porcupines. Additional data supporting this suggestion is that 11 of the 17 animals that were overlooked during population surveys (five, seven, five, and zero porcupines were not observed but then subsequently relocated in population surveys in 1989–90, 1990–91, 1991–92, and 1992–93, respectively) were males ($\chi^2 = 1.47$, $d.f. = 1$, $P > 0.05$).

More females ($N = 14$) than males ($N = 4$) immigrated into the Granite Basin during the study (Fig. 1, $G = 5.88$, $d.f. = 1$, $P = 0.03$). Disappearance data already presented suggested that primarily subadult (juveniles

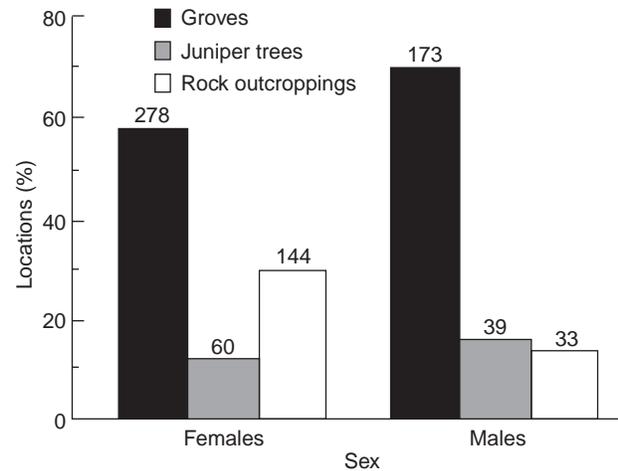


Fig. 3. Proportion of locations of radio-collared male and female porcupines in three different habitat types in the Granite Basin, Nevada. The numbers above the bars are the sample sizes.

and yearlings) females emigrated, leading to the corresponding expectation of high immigration rates for juvenile females. However, because information on mother-offspring associations was limited, it was not possible to discriminate between juveniles that were born in the Granite Basin and those that may have dispersed into the area. Thus, we were unable to assess immigration rates for juvenile porcupines.

Serum progesterone levels indicated that, although a few may conceive when juveniles, all female porcupines conceive their first offspring by the time they are yearlings (age at first conception ≈ 25 months; Fig. 4a). Nine, five, and two out of nine two-year-old male porcupines observed in the population for at least three years were active for two, three, and \geq four breeding seasons, respectively (Fig. 4b). Thus, the estimated mean residence time of adult males was 26 months. Because female age at first conception (≈ 25 months) was less than the mean residence time of adult males (26 months), female porcupines potentially disperse to minimize the chance of mating with their fathers.

DISCUSSION

Both disappearances and immigration supported the hypothesis that natal dispersal is female-biased in porcupines (Fig. 1). Although the unknown circumstances leading to disappearances could have affected the results, we found no evidence from body condition, starvations (Fig. 2), habitat use (Fig. 3), or the sexes of animals that were overlooked during surveys to support the alternative hypotheses that undiscovered mortalities or differences in habitat use resulted in female-biased disappearances. Analyses of these alternatives actually suggested that any unknown biases in disappearances should have favoured males because they were more prone to starvation and more difficult

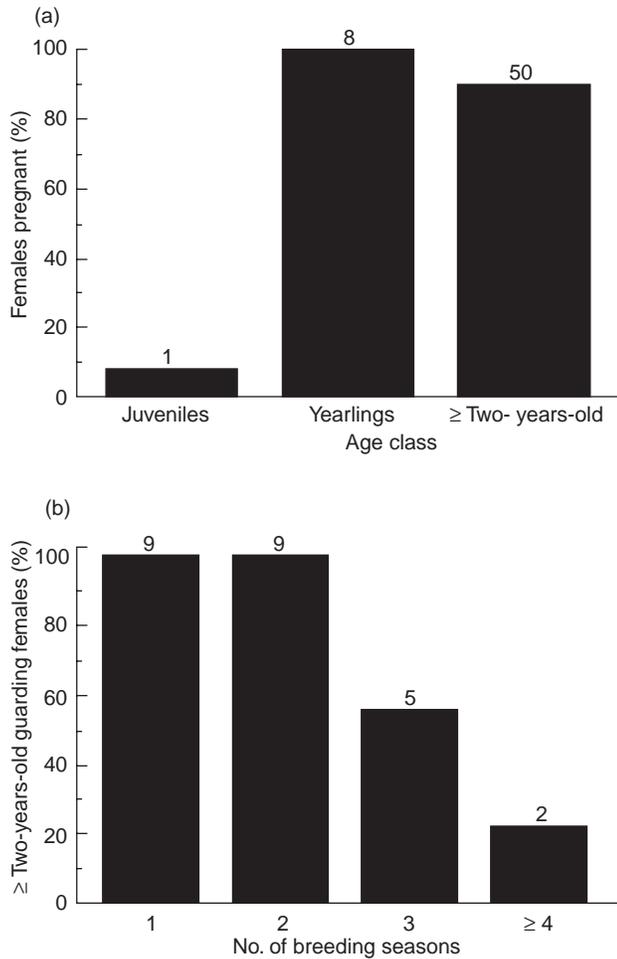


Fig. 4. (a) Proportion of female porcupines that were pregnant among three different age groups in 1990–91, 1991–92, and 1992–93; pregnancy status was based on serum progesterone levels 4 ng/ml during the gestation period (Sweitzer & Holcombe, 1993). (b) Proportion of male porcupines observed guarding females from one to four breeding seasons. The numbers above the bars are sample sizes. We do not know if the two male porcupines that were in residence for four years were reproductively active after the end of the study in 1993.

to locate (Figs 2, 3). Furthermore, the adult sex ratio (yearlings) during the study was 120 female:106 males ($\chi^2 = 0.87$, *d.f.* = 1, $P > 0.1$), implying that there were no differences in mortality rates between the sexes that would have explained higher disappearances in females. Because none of the plausible alternative hypotheses accounted for sex-biased disappearances and immigration, we suggest that more females dispersed than males. Information on the movements of individual porcupines from elsewhere also suggests that dispersal is female-biased in porcupines. Three juvenile females dispersed an average of 3.7 km from their natal territories, whereas four juvenile males remained within their natal ranges among porcupines in the north-eastern United States (Roze, 1989).

Natal dispersal by female porcupines is interesting because this pattern is atypical among polygynous

mammals (Clutton-Brock, 1989). In general, females are predicted to be philopatric in polygynous species because: (1) they invest more time and energy in offspring than males; and (2) they may be better able to acquire sufficient resources to reproduce in familiar natal areas (Greenwood, 1980; Waser & Jones, 1983). Female porcupines gestate and lactate for a combined 11 months of the year, whereas males are reproductively active for only about two months each year (Shadle, 1948; Roze, 1989; Sweitzer & Holcombe, 1993). Thus, female porcupines should remain philopatric to natal ranges because they invest considerably more in reproduction than males. Nevertheless, Roze (1989) suggested that it was adaptive for female porcupines to disperse because dominant males maintained their breeding positions over long periods and philopatric daughters would run a high risk of mating with their fathers.

Clutton-Brock (1989) predicted that females in polygynous mammal species should disperse to avoid inbreeding when their mean age at first conception was less than the mean residence time of adult males. For a male porcupine to encounter and mate with a daughter, he would have to be reproductively active from the year in which he bred with her mother until at least the first breeding season that a daughter is reproductively active (25 months), or a minimum of three breeding seasons. The observation that the residence times of adult males commonly exceeds three breeding seasons (Fig. 4) is consistent with the idea that females disperse to avoid mating with fathers. This argument for inbreeding avoidance, however, should work best in species with relatively closed social groups (Clutton-Brock, 1989). Porcupines exhibit few social tendencies except during winter when up to eight animals may share dens (Wolfe, 1990; Sweitzer & Berger, 1997), and when they congregate in loose groups of up to 20 individuals in winter foraging areas (Sweitzer & Berger, 1992). However, Clutton-Brock's (1989) inbreeding avoidance hypothesis may also work in less social animals when females do not recognize their fathers. In porcupines for example, males do not contribute to parental care, nor do they closely associate with female-offspring pairs during the lactation period (Roze, 1989, pers. obs.). Thus, there should be little opportunity for females to learn to recognize their fathers, or for males to learn to recognize their daughters. This is important because in the breeding season it is common for several males to converge on the location of a pre-oestrous female whereupon they vigorously vie for position and the dominant male guards the female for one to three days prior to copulation (Roze, 1989; Sweitzer & Berger, 1997). Although a female porcupine must arch her heavily-quilled tail over the back for the male to mount and copulate (Shadle, 1951) and could thereby be selective, limited ability of females to discriminate among related or unrelated males could result in father-daughter matings. Over the long term, selection would favour those females that dispersed prior to conception, thereby producing relatively healthy, viable offspring (Ralls, Ballou, & Templeton, 1988).

Resource competition models suggest that parents should encourage those offspring that are most costly in terms of shared resources to disperse (Liberg & von Schantz, 1985). Female porcupines defend relatively small exclusive territories, whereas males occupy large, undefended home ranges (Roze, 1989). Because of the larger ranging patterns of males, females would face less competition and share fewer resources with male offspring than with female offspring. Thus, female porcupines should compel their female offspring to disperse. Alternatively, Wolff (1992, 1993) suggested that competition for resources was less important than inbreeding in determining the sex of dispersing offspring because juvenile dispersal was correlated with the presence of the opposite- but not same-sex parent in the natal home range. Additional data on social interactions among porcupines are needed to discriminate between these two hypotheses.

Although our data are consistent with the hypothesis that females disperse to avoid mating with fathers, we know little about how philopatric males avoid mating with their mothers. Elsewhere, we present data on body size and quill impalements which suggest that most males do not reach effective reproductive maturity until they are at least three-years-old (Sweitzer & Berger, 1997). Thus, the probability of a philopatric male encountering his surviving mother during his first mating season may be relatively low, and the close association between mothers and their offspring during the four-month lactation period (Sweitzer & Holcombe, 1993) should facilitate recognition. For example, Roze (1989) noted one instance in which a reproductively mature male distanced himself from his mother during the breeding season. Irrespective of these considerations, however, costs of inbreeding to males will be low relative to females because of the low reproductive investment by males.

Two potential benefits of philopatry are avoiding predation during dispersal, and familiarity with resources in natal ranges. Although dispersal can be costly in terms of increased predation (Isbell, Cheney & Seyfarth, 1993; Van Vuren & Armitage, 1994), heavily-quilled porcupines may suffer low predation compared to other mammals. Also, because porcupines are broad generalists which consume a wide variety of herbaceous vegetation, woody shrubs, and tree bark (Dodge, 1982), familiarity with resources in natal ranges may be relatively unimportant compared to the high fitness costs to females of inbreeding (Ralls, Ballou & Templeton, 1988).

In summary, data on disappearances and immigration from this study, as well as information on individual dispersal movements from elsewhere, suggest that dispersal is female-biased in North American porcupines. Data on the reproductive activities of porcupines support the hypothesis that female porcupines disperse to avoid inbreeding. However, little is known about how factors such as intrasexual resource competition may compel females to disperse, or on why males remain philopatric. Additional data on social interac-

tions among porcupines are needed to elucidate the proximal mechanisms for female-biased dispersal in this species.

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